DISSERTATION

GENETICS, GENOMICS, GROUSE, AND CONSERVATION: USE OF GENETIC AND GENOMIC DATA TO EVALUATE CONSERVATION ACTIONS AND CHARACTERIZE POPULATIONS OF GUNNISON SAGE-GROUSE

Submitted by

Shawna Jean Zimmerman

Department of Ecosystem Science and Sustainability

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 2019

Doctoral Committee:

Advisor: Cameron L. Aldridge
Co-Advisor: Sara J. Oyler-McCance

W. Chris Funk
Mevin B. Hooten

ABSTRACT

GENETICS, GENOMICS, GROUSE, AND CONSERVATION: USE OF GENETIC AND GENOMIC DATA TO EVALUATE CONSERVATION ACTIONS AND CHARACTERIZE POPULATIONS OF GUNNISON SAGE-GROUSE

Alteration of sagebrush-steppe plant communities has been a lasting mark on the western portion of the United States. This alteration has led to dramatic declines in sagebrush cover on the landscape, and a subsequent decline of many of the species that rely on this community for habitat. The Gunnison sage-grouse (*Centrocercus minimus*) is a sagebrush obligate avian species whose range has been reduced to seven discrete populations in southwestern Colorado and southeastern Utah. Range-wide estimates of the species indicate fewer than 5,000 individuals remain. The vast majority of the species (~85-90%) persists in a single population within the Gunnison Basin, while the smaller satellite populations support the remaining individuals. Dispersal and gene flow between populations is infrequent resulting in high genetic differentiation and relatively high rates of genetic diversity loss to genetic drift. In addition to being geographically discrete, the populations are also located within a matrix of landscape components known to impede dispersal of grouse species. Variable environmental conditions and habitat compositions exist within each population as well. Habitat within the largest population is interrupted by the city of Gunnison at its center, multiple roadways, and agriculture. Population declines and genetic diversity loss has resulted in concerns about the long-term persistence of the species, and ultimately a federal listing of threatened under the Endangered Species Act in 2014.

Conservation actions by Colorado Parks and Wildlife have been ongoing, even prior to the designation of federal protection. Actions have included habitat restoration, population monitoring, and translocation of individuals from the largest population to augment the smaller satellite populations. When the decision was made to augment satellite populations, there was real concern for their extirpation and individuals were captured opportunistically within the Gunnison Basin for relocation. While short term monitoring of the fate of some translocated individuals gave managers an indication of survival for the first year, an overall impact on the recipient population and long-term fate of translocated individuals was unknown. Genetic data offers a unique opportunity to provide some insights into questions of conservation concern. The lek mating system of sage-grouse lends itself to non-invasive collection of samples from breeding grounds, and therefore a larger proportion of the population can be sampled than with more invasive methods. Samples collected on leks can provide indications of gene flow among leks, or leks can be grouped within populations to evaluate gene flow among populations. Technological and methodological advancements in processing genomic sequence data has led to an explosion of studies asking questions beyond neutral genetic processes, such as gene flow and drift, for wildlife species. These advancements have begun to provide insights into non-neutral evolutionary processes like local adaptation, which could be a critical consideration when restoring habitat for species with specialized habitat requirements such as sage-grouse.

In my second chapter, I evaluated the genetic impact of translocation efforts on satellite populations. I found that all satellite populations that received translocated individuals showed some indication of genetic change, though the magnitude of genetic change varied. Between 2000 and 2014, 306 birds from the largest and most genetically diverse population (Gunnison Basin) were translocated to five much smaller satellite populations to augment local population

size and increase genetic diversity. The observed variability in the amount of genetic change that was detected, indicates multiple local factors likely impacted the success of translocation efforts, such as local population characteristics (habitat quality, environmental conditions, population size), characteristics of the individuals translocated (sex, age, number of individuals), and season of action. I also demonstrated that there was a population estimate increase for the two populations which also showed the strongest genetic change, corresponding to the translocation period, which could be an indicator of genetic rescue. These results suggest that translocation efforts impacted satellite populations, with current data providing a new baseline for genetic diversity among populations of this imperiled species.

In my third chapter I used a landscape genetics approach to identify the ecological processes underlying gene flow at two scales: among populations range-wide and among leks within the largest population, the Gunnison Basin. I found that, while presence of habitat is important at both scales, gene flow within populations was more a function of habitat structure and quality than presence of sagebrush habitat. My findings also support the previous assumptions that the formation of isolated populations of Gunnison sage-grouse is largely a result of conversion of habitat for anthropogenic use. In addition to providing insight into how the landscape impacts effective dispersal, estimation of the impact different landscape components have on gene flow can be used in conservation planning by identifying specific impediments or facilitators of movement and locating them on the landscape to identify areas for potential conservation, or restoration as a potential dispersal route, or when making land-use change decisions.

In my fourth chapter, I used 15,033 single nucleotide polymorphism (SNP) loci in genomic outlier analyses, genotype-environment association analyses, and gene ontology (GO)

enrichment tests to examine patterns of putatively adaptive genetic differentiation within populations. I found 191 genes associated with biological functions or pathways that were overrepresented in the assemblage of outlier SNPs. Four of these genes (TBXAS1, CYP2R1, CYP2C23B, CYP4B1) belong to the cytochrome P450 gene family and could impact metabolism of plant secondary metabolites, a critical challenge for sagebrush obligates. Additionally, SNPs in four genes (CYB5R4, DDX60, INPP5E, SETX) had non-synonymous variants predicted to moderately impact gene function. These results suggest adaptive divergence in multiple genes and in multiple metabolic and biochemical pathways may be occurring. This information can be useful in managing a species of conservation concern, e.g., to identify unique populations for conservation, to avoid translocation or release of individuals that may swamp locally adapted genetic diversity or guide habitat restoration efforts.

In my fifth chapter, I used microsatellite and SNP data sets generated from a Gunnison sage-grouse sample set to evaluate concordance of the results obtained from SNPs and microsatellites for common metrics of genetic diversity (H_O, H_E, A_R, F_{IS}) and differentiation (F_{ST}, G_{ST}, D_{Jost}). Additionally, I evaluated clustering of individuals using putatively neutral, putatively adaptive, and a combined data set of putatively neutral and adaptive loci. I found high concordance between microsatellites and SNPs for most diversity and all differentiation estimates in ability to rank populations, though the magnitude of the values was quite different. In almost all cases, the increased precision from SNP data allowed significant differences among the populations to be detected that were not detected using microsatellite data. Additionally, the clustering analyses showed similar patterns among all data sets though microsatellites had lower power to distinguish populations and the putatively adaptive loci appear to show a stronger pattern of divergence in some populations than with other data sets. This chapter demonstrates

that different marker types may provide different interpretations for conservation actions if limitations of each metric or marker type are not considered in the biological context of the focal species.

Overall, the body of work I describe in the following chapters is intended to utilize genetic and genomic data to contribute to the conservation of an imperiled species, with specialized habitat requirements, on a small geographic scale. Each chapter addresses a different aspect of conservation of Gunnison sage-grouse. I provided a retrospective evaluation of the impact of past translocation actions which could serve as a baseline for further efforts should they continue. I identified the main facilitators and inhibitors of gene flow within and among populations. I characterized populations for divergent selection and provide a tentative link to genes of know function, some of which could impact the ability of the species to digest plant secondary metabolites found in sagebrush leaves, a critical dietary component for sage-grouse. I compared common metrics used to evaluate species of conservation concern and demonstrate that there are subtle signatures of evolutionary independence in two or three of the populations, which may indicate these populations are of particular conservation concern.

ACKNOWLEDGEMENTS

I owe many thanks to my advisors, Cameron Aldridge and Sara Oyler-McCance, who provided great support and encouragement during the entirety of my program. I am grateful for the hours they both spent reviewing manuscripts, providing feedback, and helping me perfect talks. They were the right combination of encouragement and structure to help me develop into a real scientist (hopefully). I am also grateful to my committee member W. Chris Funk for providing helpful comments at every step. My other committee member, Mevin B. Hooten, also provided guidance along the way, but was instrumental in helping me develop more statistical prowess. Jennifer Fike is genius in the lab and helped me, not only improve my laboratory skills, but made sure supplies were available when I needed them, and that the lab environment was colorful and festive. Without the guidance and work of Kevin P. Oh, my chapter on local adaptation would have much less substance. And without R. Scott Cornman I would have had to add at least another year to also learn how to properly utilize bioinformatics tools all on my own. There are many other people whom I have asked for help in one way or another in the past few years. I owe thanks to each of them, in no particular order: Kim Melville-Smith, Jennifer Neuwald, Jonathan Straub, Nancy Gus, Mike O'Donnell, Joanne Saher, Julie Heinrichs, Dave Edmunds, Adrian Monroe. Similarly, acces to the the yeti server at the USGS made fitting complex connectivity models possible. I owe Jeff Falgout my appreciation for granting access to this resource, and also probably apologies to those who were also using the server, for fitting a LOT of models.

Though I thoroughly enjoyed the days I got to spend visiting lek sites to collect samples, my data would have been severely lacking without the help of individuals at Colorado Parks and

Wildlife, National Park Service, United States Geological Survey, and Western State Colorado University. I cannot express enough gratitude. Additionally, I am grateful to Tony Apa for agreeing to be a co-author for someone he had yet to meet, and for sharing additional information about the historical samples he collected which added great value to the work I present here.

My time spent at Colorado State University would have been much less fun without my cohort: Jennifer Timmer, Shelley Spear, Kristin Davis, Greg Wann, Danny Martin, and Nick Van Lanen. Whether we were running, camping, hiking, birding, talking statistics, or just hanging out at happy hour these people made the grad school life infinitely more enjoyable, and to that I am forever grateful.

I must acknowledge my other half, who graciously became my husband during this journey, and has helped me to keep the appropriate perspective on all unforeseen hurdles and small victories. I am grateful he at least pretended to listen as I droned on and on about modeling, genetic data, genomic data, sage-grouse, sage-grouse, sage-grouse. Without him, there may have been many more curse words uttered in the last few years. I must also thank Duke and Jasper, our dogs, for reminding me that taking long walks and respecting dinner time are essential to sanity. Lastly, my family has always been supportive of my educational pursuits. Though I think they are still wondering if I will ever really be done and have a ‘real’ job. Without their influence I wouldn’t be who I am today, and for that I owe them my gratitude.

DEDICATION

To my boys: Keith, Duke, and Jasper.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I. INTRODUCTION

Conservation and management of wildlife species are increasingly common objectives for scientific studies, with multiple scientific journals focusing soley on this topic (e.g., Journal of Wildlife Management, Conservation Biology, Biological Conservation). Historically, conservation focused studies have utilized data based on movement measured with techniques like telemetry to evaluate things like resource utilization (e.g., Aldridge and Brigham 2002, Hooten et al. 2017) and population size and demographic rate estimates (e.g., Wann et al. 2014, Stanley et al. 2015, Ketz et al. 2018). Recent decades have seen a shift in technological capabilities and methodological approaches that now allow the use of molecular approaches to investigate issues of conservation importance to a broader group of organisms. The use of genetic data, and more recently genomic data, has seen marked increase in application in recent years (Desalle and Amato 2004, Allendorf et al. 2010). While the distinction between genetic and genomic may seem like an exercise in semantics at first glance, there are notable differences. Though both types of data are based on DNA, the regions of the genome and the number of locations sampled with each type of data are markedly different. Genetic data are typically composed of 10s of loci sampled in highly repetitive regions thought to be subject only to neutral genetic processes (i.e., gene flow, drift). Genomic data are composed of upwards of 1,000s of loci sampled throughout the genome, including coding regions, and therefore are subject to neutral and non-neutral genetic processes (i.e., gene flow, drift, selection, inbreeding). These differences are important to note because they indicate different types of questions we can ask about conservation using genetic or genomic data; genetic data mainly being used for questions of gene flow and drift and genomic data being used to investigate questions involving both neutral and functional processes (e.g., selection and gene function).

At present the use of genetic and genomic data to directly inform conservation or management actions have been rare (Shafer et al. 2015). There are several reasons why there is a lack of translation from science to implementation including the cost to develop genetic resources, the difficulty involved in identifying ecologically important genetic regions, and the cost to implement genetic monitoring. There are, however, notable examples where genetic data has been utilized in conservation for monitoring (e.g., Hansen et al. 2000, Wasko et al. 2004, Bateson et al. 2014). The ability to generate large multilocus genomic data sets representing neutral and non-neutral genetic processes for species of conservation concern has greatly improved in recent years, increasing the number of loci sampled with less effort and lower cost in comparison to microsatellite development and genotyping as well as allowing new questions to be asked (Schlötterer 2004). Use of genetic and genomic tools in wildlife conservation and management is just beginning to be fruitful and has a promising future.

Genetic and genomic data have been particularly useful in addressing questions of conservation concern for sage-grouse (*Centrocercus* sp.), such as population structure (Benedict et al. 2003, Oyler-McCance et al. 2005*a*, *b*, 2014, 2015, Bush et al. 2011, Jahner et al. 2016), optimal monitoring (Hanks et al. 2016), taxonomic subdivisions (Kahn et al. 1999, Oyler-McCance et al. 1999, 2010, Benedict et al. 2003), dispersal and gene flow (Row et al. 2015, 2018, Cross et al. 2017), lek fidelity (Bush et al. 2010), signatures of local adaptation (Oh et al. in review), and evaluation of polygamy (Stiver et al. 2008, Bird 2013, Bird et al. 2013). Perhaps one of the most important contributions of genetic data to sage-grouse is the identification of distinct species within the genus. Though there are two recognized species of sage-grouse at present, greater sage-grouse (*C. urophasianus)* and Gunnison sage-grouse (*C. minimus)* were assumed to belong to the same species until morphological (Beck and Braun 1978, Hupp and

Braun 1991, Young et al. 2000) and behavioral differences (Young 1994, Young et al. 2000) were observed (see Figure 1.1 for distributions of both species). Successive genetic investigations confirmed birds in the southeastern most portion of the sage-grouse range were indeed a distinct species (Kahn et al. 1999, Oyler-McCance et al. 1999). Both members of the genus *Centrocercus* are similar in appearance with dark brown wings and bodies, black underparts, and modified feathers arising from the back or side of the neck (filoplumes), long, brown tail feathers (retrices) with coarse black bars, gray brown feathered tarsi and rounded, greenish-yellow cervical air sacs (apteria) within the scale-like feather covered white upper breast (Young et al. 2000). Male Gunnison sage-grouse differ morphologically from greater sage-grouse having more pronounced white bars on their retrices, filoplumes that are greater in number and length and arise from the back of the neck as opposed to the sides. While females of both species have a smaller body size relative to males and lack the specialized feathers, Gunnison sage-grouse males and females are smaller than their greater sage-grouse counterparts (Young et al. 2000).

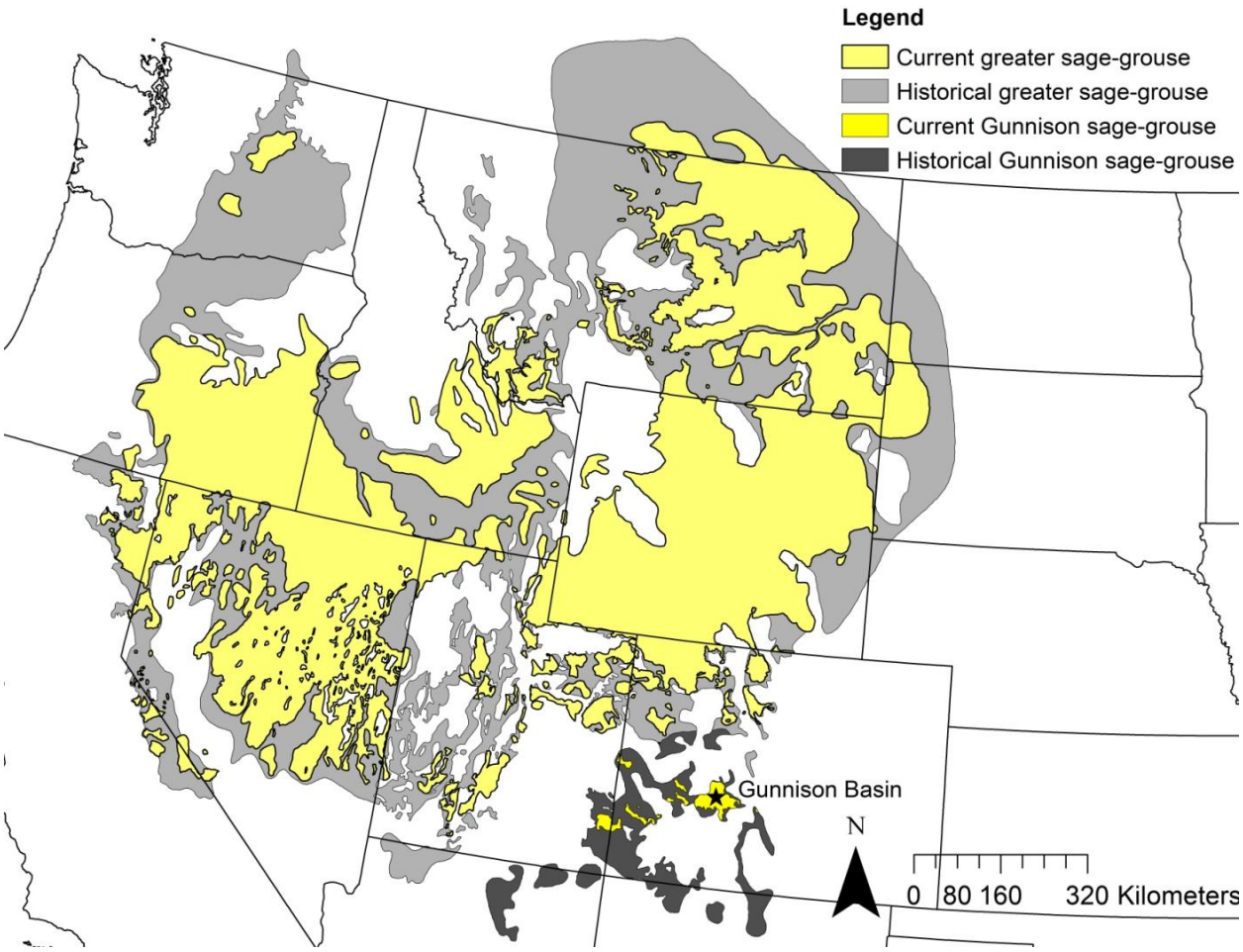

Figure1. 1- The historical (shades of gray) and current (shades of yellow) distributions for the greater and Gunnison sage-grouse. For reference, the largest population of Gunnison sage-grouse is marked (★) and labeled.

Sage-grouse are sagebrush obligates, which rely on live, robust, tall sagebrush (*Artemisia* spp.) shrubs for food and shelter throughout their life cycle (Patterson 1952). Because the Gunnison sage-grouse has only officially been recognized since 2000, most information on habitat preferences for sage-grouse is specific to the greater sage-grouse. The dietary needs of both species of sage-grouse change with the seasons, as do the habitat requirements. In the spring, a mixed cover of tall sagebrush (40-80 cm) with 15-25% canopy cover and tall (>18cm)

grass and forbs with at least 12-15% cover is required (Schoenberg 1982, Braun et al. 2005). Sage-grouse have a lek mating system, where males congregate on a relatively shrub free area with short vegetation to perform a display for females in attempt to win reproductive rights. Leks are typically found on relatively bare, open areas surrounded by sagebrush for cover when quick escape from predators is necessary (Braun et al. 1977, 2005). Males strut on leks in Colorado from mid-March to late May (Gunnison sage-grouse Rangewide Steering Committee 2005). Sagebrush cover, typically within 3-5 km of a lek is needed for nest concealment, where nests closer to a lek tend to have higher success rates when nest density is low (Holloran and Anderson 2005).

In addition to the need for tall (over 50 cm), dense (15-30% cover) live sagebrush, abundant forbs (cover of 10-12%), and tall grass within 15 m of the nest are also preferred (Aldridge and Brigham 2002). Adequate winter and spring precipitation for grass and forb growth is also necessary (Braun et al. 1977, Young 1994, Braun et al. 2005, Holloran et al. 2005). Forbs are an important dietary component for healthy hens and chicks (Barnett and Crawford 1994). Predation is the most common reason for nest failure (Webb et al. 2012) making lateral nest cover (mostly from forbs and sagebrush) important for successful nests as well (Watters et al. 2002). Brood rearing occurs within 200-1,000 m of the nest site for the first few days (Braun et al. 2005) and occurs within a moderate sagebrush canopy cover (Braun et al. 1977), high forb cover for food (Sveum et al. 1998), and tall grass for concealment, all of which contribute to abundant insect populations is needed as a food source (Braun et al. 1977, 2005). Sage-grouse travel greater distances as the brood matures and summer approaches. Summer habitat is driven by the need for forage and cover, requiring approximately 25% sagebrush canopy (Braun et al. 1977), and abundant, succulent forbs, and insects (Young 1994, Braun et al.

2005). Movements to seek out these resources vary, depending mostly on moisture availability and thus, distribution of mesic sites (Braun et al. 2005). In areas with high agricultural use, the edges of hay, bean, and potato fields may be used for habitat (Young 1994, Braun et al. 2005). As summer progresses to fall, sage-grouse move higher up to benches and ridges seeking out any remaining succulent vegetation (Braun et al. 2005) and begin shifting their diet to sagebrush leaves, reaching nearly 99% by peak winter (Braun et al. 1977, Young 1994, Braun et al. 2005). Winter habitat includes windswept ridges, south facing slopes, draws with tall sagebrush reaching at least 25-35 cm above the snow, and with 10-30% canopy cover (Braun et al. 2005). Gunnison sage-grouse in the Gunnison Basin rely on taller shrubs present in drainages and on slopes with south or west aspects, especially in winters with persistent snow (Hupp and Braun 1989; Figure 1.1). All areas of the species range do not experience the same level of snow accumulation as the Gunnison Basin. At the end of winter (February to March), movement back toward the breeding grounds begins (Braun et al., 1977, 2005). Location of breeding grounds can be adjacent to wintering grounds or relatively distant, the extent of seasonal movement varies with the severity of winter weather, topography, and vegetation cover (Beck 1977). As snow melts, diet shifts from solely sagebrush in winter until it is forb and insect dominated once again (Braun et al. 1977, Young 1994). Recent statistical developments suggest, however, that many studies on resource use may provide overly confident inference if uncertainty in location of the individual animal is not considered (Gerber et al. 2018), and therefore we may find these habitat relationships are less precise in future analyses.

The Homestead Act of 1862 encouraged the expansion of settlements throughout the western United States, especially into sagebrush-steppe plant communities. This resulted in the claiming of arable land for private ownership and development for agricultural use, and the

subsequent fragmentation, degradation, and alteration of the landscape (Bock and Webb 1984, Braun 1998, Beck and Mitchell 2000, Knick et al. 2003, Holloran 2005). Declines in sagebrush habitat as a result of settlement, associated activities, and population growth have been extensive (Connelly et al. 2004, Schroeder et al. 2004), leaving sagebrush-steppe communities endangered (Anderson and Inouye 2001). Human activities have created extensive habitat edge (Braun et al. 2005), primarily through residential and exurban sprawl (Theobald et al. 1996). Though the original distribution of sagebrush habitat was naturally fragmented by forests, deserts, river valleys, and mountain ranges (Patterson 1952), undisturbed habitats dominated by sagebrush no longer remain (Braun 1998). Of the remaining sagebrush habitat in the United States, 65% is in public ownership, yet only 2% is permanently protected in a federal reserve or national park despite the dramatic conversion that has taken place (Wright et al. 2001). This makes habitat loss and fragmentation the greatest threat to species' persistence (Wilcove et al. 1998), particularly species within the sagebrush ecosystem.

Colorado has been no exception to the loss, fragmentation, and degradation of sagebrush habitat with an average yearly loss of sagebrush in southwestern Colorado of 0.64% (5,033 ha), and a cumulative loss of 20% (15,567 ha) between 1958 and 1993 (Oyler-McCance et al. 2001). In addition, the rapid development of land for human use in southwestern Colorado, especially sprawling residential ranchettes, resulted in fragmentation causing direct and functional habitat loss (see Aldridge and Boyce 2007), reduction of potential habitat, and modification of the physical environment (Primack 1993, Theobald et al. 1996). The human population within the Gunnison Basin has continually increased since 1980, and estimates project population growth in the Gunnison River Basin to more than double (2.3 times) by 2050 (Colorado Water Conservation Board 2009). The rate of land development and conversion is expected to keep

pace with human population growth (Theobald et al. 1996, United States Fish and Wildlife Service 2014). Climate change is also affecting loss and degradation of sagebrush habitats. The southwestern U.S. is warming more rapidly than the rest of the country, changing seasonal precipitation patterns and temperature (Karl et al. 2009), which ultimately affects sagebrush persistence via environmental tolerances (Miller et al. 2011) and decreases in fire return intervals (United States Fish and Wildlife Service 2014).

Historically, Gunnison sage-grouse was patchily distributed within intermountain basins, found along linear habitat strips and riparian areas, with population centers thought to be connected by dispersal along habitat corridors (Braun et al. 2014).The species historical range included northwestern New Mexico, northeastern Arizona, southeastern Utah, and southwestern Colorado covering an estimated 46,521 km^2 (21,376 mi^2; Schroeder et al. 2004). Currently, the entire species occupies 3,798 km^2 (1,822 mi^2), ~8% of the historical range, in Colorado and Utah (Schroeder et al. 2004, Braun et al. 2014). The population centers connected by dispersal have been reduced to seven isolated populations with very low levels of natural dispersal (Oyler-McCance et al. 2005*a*). Sagebrush dominated habitat patches still exist between each population though they are now fragmented and evidently no longer function as dispersal corridors (Braun et al. 2014). The core population of Gunnison sage-grouse is located near the town of Gunnison, within the Gunnison Basin, and five much smaller populations are scattered to the west, extending just over the border into Utah; a single very small population exists to the east of the Gunnison Basin (Connelly et al. 2004; Figure 1.1). The Gunnison Basin population is the stronghold supporting approximately 84% (~3,978 birds) of the estimated spring breeding population (United States Fish and Wildlife Service 2014). This population is the most genetically diverse, and occupies the largest land area (Oyler-McCance et al. 2005*a*). Located

eight miles southwest of the town of Crawford, the population of the same name had approximately 30 strutting males as of 2014 (United States Fish and Wildlife Service 2014). South of Crawford, the Cerro Summit/Cimarron-Sims Mesa (Cimarron hereafter) population had approximately 10 strutting males in 2014 (United States Fish and Wildlife Service 2014), and may act as an intermediary for gene flow between San Miguel and Gunnison Basin (Oyler-McCance et al. 2005*a*). The San Miguel population had the second largest estimated size in 2014, and was considered stable or slightly declining with an estimated 50 strutting males (United States Fish and Wildlife Service 2014). This was the most genetically diverse satellite population and is composed of 6 fragmented subpopulations. San Miguel may facilitate gene flow out of the Gunnison Basin to other populations (Oyler-McCance et al. 2005*a*). The Dove Creek/ Monticello (Dove Creek hereafter) population is composed of two disjunct subpopulations; the larger one is near the town of Monticello in Utah and the Dove Creek subpopulation is in western Dolores County, Colorado. Overall, the population was decreasing as of 2014, with only an estimated 35 strutting males (United States Fish and Wildlife Service 2014), and genetic evidence indicated significant isolation of Dove Creek from other populations of Gunnison sage-grouse as of 2005 (Oyler-McCance et al. 2005*a*). The Piñon Mesa population, located in the northwestern end of the Uncompahgre Plateau in Mesa County (22 miles southwest of Grand Junction) supported approximately 30 strutting males in 2014 (United States Fish and Wildlife Service 2014), had the lowest genetic diversity as of 2005, and also displayed evidence of significant isolation from other Gunnison sage-grouse populations (Oyler-McCance et al. 2005*a*). The population at Poncha Pass is located in Saguache County to the east of the Gunnison Basin population across Monarch Pass. Though fossil evidence supports the existence of sage-grouse in the area, by the early 1960s discussion of transplanting birds from the

Gunnison Basin into Poncha Pass indicates birds were thought to be locally extirpated (Braun et al. 2014). Currently, the population is known to contain only birds transplanted from the Gunnison Basin population starting in the 1970s (Oyler-McCance et al. 2005*a*, Braun et al. 2014).

As previously discussed, the fragmentation and degradation of sagebrush habitat is one of the main known threats to the persistence of the species that rely on that habitat. For Gunnison sage-grouse, alteration of sagebrush communities appears to have resulted in the isolated, small, and declining population structure that exists today. The realization that the satellite populations had low levels of genetic diversity (Oyler-McCance et al. 2005*a*) and the observed population declines (Gunnison sage-grouse Rangewide Steering Committee 2005) sparked concern over the long-term persistence of the species, and particularly the satellite populations. Beginning in 2005, Colorado Parks and Wildlife (CPW) began translocating birds from the Gunnison Basin to satellite populations. Initially, radio transmitters were used to track many of the translocated birds for the first year (United States Fish and Wildlife Service 2014), though long-term fate of translocated birds and potential genetic impact was unknown. Movement of birds from the Gunnison Basin continued until 2014 when translocation efforts were halted by the state in response to the threatened status granted under the Endangered Species Act.

The need for translocation could be eliminated if natural dispersal could be facilitated through habitat restoration or targeted conservation of important areas of gene flow. Currently, the lack of gene flow between populations is thought to be a function of geographic distance and intervening unsuitable habitat. While these factors likely play a role, especially range-wide, a more formal evaluation of the way gene flow of Gunnison sage-grouse is impacted by the landscape could provide unique insights into restoring gene flow between populations or

preventing further fragmentation within existing populations. Little is currently know about how the landscape impacts gene flow for Gunnison sage-grouse, though information is available on how Gunnison sage-grouse select habitat patches and respond to different landscape components (Commons 1997, Lupis 2005, Lupis et al. 2006, Aldridge et al. 2012, Rice et al. 2017, Doherty et al. 2018). We know even more about how greater sage-grouse select and utilize habitat (Aldridge and Boyce 2008, Aldridge et al. 2008, Hagen et al. 2011, Blickley et al. 2012, Blomberg et al. 2012, Baruch-Mordo et al. 2013, Harju et al. 2013, Knick et al. 2013, Green et al. 2017, Severson et al. 2017). Though studies on physical movement and resource selection can theoretically provide some insight into the potential impact on gene flow, there is still much to understand about how gene flow is specifically impacted by landscape change for both species of sage-grouse.

The level of genetic differentiation and isolation of populations currently observed across the species range, in addition to the variety of environmental characteristics present, could conceivably lead to locally adapted genotypes. Previous genomic work across both species of sage-grouse found signals of adaptive differentiation in isolated populations related to immune function (Oyler-McCance et al. in review) and within the cytochrome P450 gene family (Oh et al. in review), which has particularly interesting ecological implications for sage-grouse. The cytochrome P450 family has been previously implicated in the ability of sage-grouse and the closely related chicken (*Gallus gallus*), to digest plant secondary metabolites (Miyazawa et al. 2001, Skopec et al. 2013) such as those found in sagebrush (Kelsey et al. 1982). Identifying whether populations of Gunnison sage-grouse are locally adapted could have implications for translocation efforts, habitat restoration, and any potential captive rearing which may be considered in the future. If populations are locally adapted, diluting the genetic make up of local

populations could be contradictory to the long-term conservation of individual populations and the species.

The identification of management and conservation units is an increasingly popular objective being addressed with genetic and genomic data (Pante et al. 2014, Funk et al. 2016, Prince et al. 2017, Langin et al. 2018). While the explosion of technological advancements has dramatically expanded availability of genomic information, there is some uncertainty about how to use genetic and/or genomic data to appropriately characterize populations and identify groups for conservation and management purposes. While the Gunnison sage-grouse is fragmented into discrete and demographically independent groups, insight into the level of evolutionary independence could further aid in prioritizing conservation resources and informing decisions on translocation, habitat restoration, and potential captive breeding. It follows that populations that are not evolutionarily independent could be treated similarly in conservation efforts.

The overall goal of my dissertation was to use genetic and genomic data to further our understanding of questions of conservation and management for Gunnison sage-grouse. I had four main objectives within this goal. My first objective was to evaluate the genetic effects of translocation efforts on satellite populations which might be useful as an indicator of translocation success. I used genetic samples collected before and after individuals were translocated between populations to evaluate genetic changes, tying those to translocation efforts (Chapter 2). Criteria used to evaluate change as a result of translocated individuals included increased genetic diversity, decreased genetic differentiation between source and recipient populations, and evidence of increased genetic ancestry from the source population within individuals in the recipient population that would indicate reproduction of translocated individuals. This chapter has been accepted for publication in The Condor: Ornithological

Applications. My second objective was to characterize how gene flow is impacted by landscape features among populations as well as among leks within the largest population, the Gunnison Basin (Chapter 3). I used a landscape genetics approach to identify the ecological processes underlying gene flow at two scales: among populations and within the largest population. I found that, while presence of sagebrush cover is important at both scales, gene flow within populations is more a function of sagebrush habitat structure and quality than presence of sagebrush habitat. My findings also support the previous assumptions that the formation of isolated populations of Gunnison sage-grouse is largely a result of conversion of habitat for anthropogenic use. This chapter is intended for publication in a peer-reviewed journal. My third objective was to evaluate the populations of Gunnison sage-grouse for evidence of adaptive divergence (Chapter 4). I used a reduced representation sequencing approach to sample the genome, followed by a search for loci displaying signatures of selection (outlier locus analysis and genotype-environment associations), and identification of the putative function of gene regions holding strong signals of selection (gene ontology (GO) term enrichment analyses). This chapter is currently under review for publication in Evolutionary Applications. My last objective was to provide an empirical comparison of genetic and genomic data to characterize populations and identify conservation units (Chapter 5). I compared the results of common genetic diversity, genetic differentiation, and clustering analyses using both genetic and genomic data for consistency and unique insights provided by specific data sets. This chapter is also intended for publication in a peer-reviewed journal.

LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: Habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–26.

Aldridge, C. L., and M. S. Boyce. 2008. Accounting for fitness: Combining survival and selection when assessing wildlife-habitat relationships. Israel Journal of Ecology & Evolution 54:389–419.

Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. Journal of Wildlife Management 66:433–444.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983–994.

Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for gunnison sage-grouse: A spatially explicit hierarchical approach. Journal of Wildlife Management 76:391–406.

Allendorf, F. W., P. A. Hohenlohe, and G. Luikart. 2010. Genomics and the future of conservation genetics. Nature Reviews 11:697–709.

Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecological Monographs 71:531–556.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage-grouse hens in Oregon. Journal of Range Management 47:114–118.

Baruch-Mordo, S., J. S. Evans, J. P. Severson, D. E. Naugle, J. D. Maestas, J. M. Kiesecker, M.

J. Falkowski, C. A. Hagen, and K. P. Reese. 2013. Saving sage-grouse from the trees: A proactive solution to reducing a key threat to a candidate species. Biological Conservation 167:233–241.

Bateson, Z. W., P. O. Dunn, S. D. Hull, A. E. Henschen, J. A. Johnson, and L. A. Whittingham. 2014. Genetic restoration of a threatened population of greater prairie-chickens. Biological Conservation 174:12–19.

Beck, J. L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage-grouse habitat. Wildlife Society Bulletin 28:993–1002.

Beck, T. D.I. . 1977. Sage-grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management 41:18–26.

Beck, T. D. I., and C. E. Braun. 1978. Weights of Colorado sage-grouse. The Condor 80:241–243.

Benedict, N. G., S. E. Oyler-McCance, C. E. Braun, and T. W. Quinn. 2003. Evaluation of the Eastern (*Centrocercus urophasianus urophasianus*) and Western (*Centrocercus urophasianus phaios*) subspecies of sage-grouse using mitochondrial control-region sequence data. Conservation Genetics 4:301–310.

Bird, K. . 2013. Observation of polyandry in endangered greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Northwestern Naturalist 94:247–252.

Bird, K. L., C. L. Aldridge, J. E. Carpenter, C. A. Paszkowski, M. S. Boyce, and D. W. Coltman. 2013. The secret sex lives of sage-grouse: Multiple paternity and intraspecific nest parasitism revealed through genetic analysis. Behavioral Ecology 24:29–38.

Blickley, J. L., D. Blackwood, and G. L. Patricelli. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conservation Biology 26:461–71.

Blomberg, E. J., J. S. Sedinger, M. T. Atamian, and D. V. Nonne. 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. Ecosphere 3:1–20.

Bock, C. E., and B. Webb. 1984. Birds as grazing indicator species in southeastern Arizona. Journal of Wildlife Management 48:1045–1049.

Braun, C. E. 1998. Sage-grouse declines in western North America: What are the problems? Pages 139–156 *in*. Proceedings, Western Association of Fish and Wildlife Agencies.

Braun, C. E., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage-grouse habitats. Wildlife Society Bulletin 5:99–106.

Braun, C. E., J. W. Connelly, and M. A. Schroeder. 2005. Seasonal habitat requirements for sage-grouse : Spring , summer, fall, and winter. USDA Forest Service Proceedings RMRS-P-9-38 38–42.

Braun, C. E., S. J. Oyler-McCance, J. A. Nehring, M. L. Commons, J. R. Young, and K. M. Potter. 2014. The historical distribution of Gunnison sage-grouse in Colorado. The Wilson Journal of Ornithology 126:207–217.

Bush, K. L., C. L. Aldridge, J. E. Carpenter, C. A. Paszkowski, M. S. Boyce, and D. W. Coltman. 2010. Birds of a feather do not always lek together : Genetic diversity and kinship structure of greater sage-grouse (*Centrocercus urophasianus*) in Alberta. The Auk 127:343–

353.

Bush, K. L., C. K. Dyte, B. J. Moynahan, C. L. Aldridge, H. S. Sauls, A. M. Battazzo, B. L. Walker, K. E. Doherty, J. Tack, J. Carlson, D. Eslinger, J. Nicholson, M. S. Boyce, D. E. Naugle, C. A. Paszkowski, and D. W. Coltman. 2011. Population structure and genetic diversity of greater sage-grouse (*Centrocercus urophasianus*) in fragmented landscapes at the northern edge of their range. Conservation Genetics 12:527–542.

Colorado Water Conservation Board. 2009. 2050 population projections for the state of Colorado municipal and industrial water use projections. Final report prepared for Colorado Water Conservation Board, Appendix B in Colorado's water supply future: State of Colorado 2050 municipal and industrial.

Commons, M. L. 1997. Movement and habitat use by Gunnison sage-grouse (*Centrocercus minimus*) in southwestern Colorado. Master's Thesis. Univeristy of Manitoba.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencis. Unpublished Report. Cheyenne, Wyoming. Unpublished Report, Cheyenne, Wyoming.

Cross, T. B., D. E. Naugle, J. C. Carlson, and M. K. Schwartz. 2017. Genetic recapture identifies long-distance breeding dispersal in greater sage-grouse (*Centrocercus urophasianus*). The Condor 119:155–166.

Desalle, R., and G. Amato. 2004. The expansion of conservation genetics. Nature Reviews 5:702–712.

Doherty, K. E., J. D. Hennig, J. B. Dinkins, K. A. Griffin, A. A. Cook, J. D. Maestas, D. E. Naugle, and J. L. Beck. 2018. Understanding biological effectiveness before scaling up range-wide restoration investments for Gunnison sage-grouse. Ecosphere 9:e02144.

Funk, W. C., R. E. Lovich, P. A. Hohenlohe, C. A. Hofman, S. A. Morrison, T. S. Sillett, C. K. Ghalambor, J. E. Maldonado, T. C. Rick, M. D. Day, N. R. Polato, S. W. Fitzpatrick, T. J. Coonan, K. R. Crooks, A. Dillon, D. K. Garcelon, J. L. King, C. L. Boser, N. Gould, and W. F. Andelt. 2016. Adaptive divergence despite strong genetic drift: Genomic analysis of the evoutionary mechanisms causing genetic differentiation in the island fox (*Uryocyon littoralis*). Molecular Ecology 25:2176–2194.

Gerber, B. D., M. B. Hooten, C. P. Peck, M. B. Rice, J. H. Gammonley, A. D. Apa, and A. J. Davis. 2018. Accounting for location uncertainty in azimuthal telemetry data improves ecological inference. Movement Ecology 6(14):1-14.

Green, A. W., C. L. Aldridge, and M. S. O'Donnell. 2017. Investigating impacts of oil and gas development on greater sage-grouse. Journal of Wildlife Management 81:46–57.

Gunnison sage-grouse Rangewide Steering Committee. 2005. Gunnison sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado USA.

Hagen, C. A., M. J. Willis, E. M. Glenn, and R. G. Anthony. 2011. Habitat selection by greater sage-grouse during winter in southeastern Oregon. Western North American Naturalist 71:529–538.

Hanks, E. M., and M. B. Hooten. 2013. Circuit theory and model-based inference for landscape connectivity. Journal of the American Statistical Association 108:22–33.

Hanks, E.M., M.B. Hooten, S.T. Knick, S.J. Oyler-McCance, J.A. Fike, T.B. Cross, and M.K. Schwartz. 2016. Latent spatial models and sampling design for landscape genetics. The Annals of Applied Statistics 10(2): 1041-1062.

Hansen, M. M., E. E. Nielsen, D. E. Ruzzante, C. Bouza, and K.-L. D. Mensberg. 2000. Genetic monitoring of supportive breeding in brown trout (*Salmo trutta* L.), using microsatellite DNA markers. Canadian Journal of Fisheries and Aquatic Sciences 57:2130–2139.

Harju, S. M., C. V Olson, M. R. Dzialak, J. P. Mudd, and J. B. Winstead. 2013. A flexible approach for assessing functional landscape connectivity, with application to greater sage-grouse (*Centrocercus urophasianus*). PloS one 8:e82271.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Phd Dissertation. University of Wyoming.

Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous sagebrush habitats. The Condor 107:742–752.

Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. Journal of Wildlife Management 69:638–649.

Hooten, M.B., D.S. Johnson, B.T. McClintock, and J.M. Morales. 2017. Animal movement: statistical models for telemetry data. Taylor and Francis Group, Boca Raton, USA.

Hupp, J. W., and C. E. Braun. 1989. Topographic Distribution of Sage Grouse Foraging in Winter. The Journal of Wildlife Management 53:823–829.

Hupp, J. W., and C. E. Braun. 1991. Geographic variation among sage-grouse in Colorado. The Wilson Bulletin 103:255–261.

Jahner, J. P., D. Gibson, C. L. Weitzman, E. J. Blomberg, J. S. Sedinger, and T. L. Parchman. 2016. Fine-scale genetic structure among greater sage-grouse leks in central Nevada. BMC Evolutionary Biology 16:127.

Kahn, N. W., C. E. Braun, J. R. Young, S. Wood, D. R. Mata, and T. W. Quinn. 1999. Molecular analysis of genetic variation among large- and small-bodied sage grouse using mitochondrial control-region sequences. The Auk 116:819–824.

Karl, T. R., J. M. Melillo, and T. C. Peterson. 2009. Global climate change impacts in the United States. Cambridge University Press, New York, New York.

Kelsey, R. G., J. R. Stephens, and F. Shafizadeh. 1982. The chemical constituents of sagebrush foliage and their isolation. Journal of Range Management 35:617–622.

Ketz, A. C., T. L. Johnson, R. J. Monello, J. A. Mack, J. L. George, B. R. Kraft, M. A. Wild, M. B. Hooten, and N. T. Hobbs. 2018. Estimating abundance of an open population with an N-mixture model using auxiliary data on animal movements. Ecological Applications 28:816–825.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegan, and C. I. van Riper. 2003. Teetering on the edge of too late? Conservation and research issues for avifauna of sagebrush habitats. The Condor 105:611–634.

Knick, S. T., S. E. Hanser, and K. L. Preston. 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: Implications for population connectivity across

their western range, U.S.A. Ecology and Evolution 3:1539–51.

Langin, K.M., C.L. Aldridge, J.A. Fike, R.S. Cornman, K. Martin, G.T. Wann, A.E. Seglund, M.A. Schroeder, C.E. Braun, D.P. Benson, B.C. Fedy, J.R. Young, S. Wilson, D.H. Wolfe, and S.J. Oyler-McCance. 2018. Characterizing range-wide divergence in an alpine-endemic bird: A comparison of genetic and genomic approaches. Conservation Genetics: In press.

Lupis, S. G. 2005. Summer ecology of Gunnison sage-grouse (*Centrocercus minimus*) in San Juan County, Utah, Master's Thesis. Utah State University.

Lupis, S. G., T. A. Messmer, and T. Black. 2006. Gunnison sage-grouse use of conservation reserve program fields in Utah and response to emergency grazing: A preliminary evaluation. Wildlife Society Bulletin 34:957–962.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. . Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–184 *in*. Greater sage-grouse: Ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38). University of California Press, Berkeley, CA.

Miyazawa, M., M. Shindo, and T. Shimada. 2001. Oxidation of 1, 8-cineole, the monoterpene cyclic ether originated from *Eucalyptus polybractea*, by cytochrome P450 3A enzymes in rat and human liver microsomes. Drug Metabolism and Disposition 29:200–205.

Oh, K. P., C. L. Aldridge, J. S. Forbey, C. Y. Dadabay, and S. J. Oyler-McCance. In Review. Conservation genomics in the sagebrush sea: Population divergence and adaptive metabolic variation in sage-grouse.

Oyler-McCance, S. J., N. W. Kahn, K. P. Burnham, C. E. Braun, and T. W. Quinn. 1999. A

population genetic comparison of large- and small-bodied sage grouse in colorado using microsatellite and mitochondrial DNA markers. Molecular Ecology 8:1457–65.

Oyler-McCance, S. J., K. P. Burnham, and C. E. Braun. 2001. Influence of changes in sagebrush on Gunnison sage-grouse in southwestern Colorado. The Southwestern Naturalist 46:323–331.

Oyler-McCance, S. J., J. St John, S. E. Taylor, A. D. Apa, and T. W. Quinn. 2005*a*. Population genetics of Gunnison sage-grouse: Implications for management. Journal of Wildlife Management 69:630–637.

Oyler-McCance, S. J., S. E. Taylor, and T. W. Quinn. 2005*b*. A multilocus population genetic survey of the greater sage-grouse across their range. Molecular Ecology 14:1293–310.

Oyler-McCance, S. J., J. St. John, and T. W. Quinn. 2010. Rapid evolution in lekking grouse: Implications for taxonomic definitions. Ornithological Monographs 114–122.

Oyler-McCance, S. J., M. L. Casazza, J. A. Fike, and P. S. Coates. 2014. Hierarchical spatial genetic structure in a distinct population segment of greater sage-grouse. Conservation Genetics 15:1299–1311.

Oyler-McCance, S. J., R. S. Cornman, K. L. Jones, and J. A. Fike. 2015. Genomic single-nucleotide polymorphisms confirm that Gunnison and greater sage-grouse are genetically well differentiated and that the Bi-State population is distinct. The Condor 117:217–227.

Oyler-McCance, S. J., K. P. Oh, S. J. Zimmerman, and C. L. Aldridge. In Review. The transformative impact of genomics on sage-grouse conservation and management. Page in review *in*. Population Genomics: Wildlife. Springer.

Pante, E., J. Abdelkrim, A. Viricel, D. Gey, S. C. France, M. C. Boisselier, and S. Samadi. 2014. Use of RAD sequencing for delimiting species. Heredity 114:450–459.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Wyoming Game and Fish Commission Sage Books, Inc., Denver, CO.

Primack, R. B. 1993. Essentials of Conservation Biology. Sinauer Associates Inc, Sunderland, MA.

Prince, D. J., S. M. O'Rourke, T. Q. Thompson, O. A. Ali, H. S. Lyman, I. K. Saglam, T. J. Hotaling, A. P. Spidle, and M. R. Miller. 2017. The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. Science Advances 3:e1603198.

Rice, M. B., A. D. Apa, and L. A. Wiechman. 2017. The importance of seasonal resource selection when managing a threatened species: Targeting conservation actions within critical habitat designations for the Gunnison sage-grouse. Wildlife Research 44:407–417.

Row, J. R., S. J. Oyler-McCance, J. A. Fike, M. S. O'Donnell, K. E. Doherty, C. L. Aldridge, Z. H. Bowen, and B. C. Fedy. 2015. Landscape characteristics influencing the genetic structure of greater sage-grouse within the stronghold of their range: A holistic modeling approach. Ecology and Evolution 5:1955–1969.

Row, J. R., K. E. Doherty, T. B. Cross, M. K. Schwartz, S. J. Oyler-McCance, D. E. Naugle, S. T. Knick, and B. C. Fedy. 2018. Quantifying functional connectivity: The role of breeding habitat, abundance, and landscape features on range-wide gene flow in sage-grouse. Evolutionary Applications 11:1305–1321.

Schlötterer, C. 2004. Opinion: The evolution of molecular markers — just a matter of fashion? Nature Reviews Genetics 5:63–69.

Schoenberg, T. J. 1982. Sage-grouse movements and habitat selection in North Park, Colorado. Colorado State University.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. The Condor 106:363–376.

Severson, J. P., C. A. Hagen, J. D. Tack, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017. Better living through conifer removal : A demographic analysis of sage-grouse vital rates. PloS one 12:e0174347.

Shafer, A. B. A., J. B. W. Wolf, P. C. Alves, L. Bergström, M. W. Bruford, I. Brännström, G. Colling, L. Dalèn, L. De Meester, R. Ekblom, K. D. Fawcett, S. Fior, M. Hajibabaei, J. A. Hill, A. R. Hoezel, J. Höglund, E. L. Jensen, J. Krause, T. N. Kristensen, M. Krützen, J. K. McKay, A. J. Norman, R. Ogden, E. M. Österling, N. J. Ouborg, J. Piccolo, D. Popović, C. R. Primmer, F. A. Reed, M. Roumet, J. Salmona, T. Schenekar, M. K. Schwartz, G. Segelbacher, H. Senn, J. Thaulow, M. Valtonen, A. Veale, P. Vergeer, N. Vijay, C. Vilá, M. Weissensteiner, L. Wennerström, C. W. Wheat, and P. Zielinski. 2015. Genomics and the challenging translation into conservation practice. Trends in Ecology and Evolution 30:78–87.

Skopec, M. M., J. R. Malenke, J. R. Halpert, and M. Denise Dearing. 2013. An in vivo assay for elucidating the importance of cytochromes P450 for the ability of a wild mammalian

herbivore (*Neotoma lepida*) to consume toxic plants. Physiological and Biochemical Zoology 86:593–601.

Stanley, T. R., C. L. Aldridge, D. J. Saher, and T. M. Childers. 2015. Gunnison sage-grouse nest survival: Assessing local- and landscape-scale drivers. The Wilson Journal of Ornithology 127:59–71.

Stiver, J. R., A. D. Apa, T. E. Remington, and R. M. Gibson. 2008. Polygyny and female breeding failure reduce effective population size in the lekking Gunnison sage-grouse. Biological Conservation 141:742–781.

Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998. Nesting habitat selection by sage-grouse in south-central Washington. Journal of Range Management 51:265–269.

Theobald, D. M., H. Gosnell, and W. E. Riebsame. 1996. Land use and landscape change in the Colorado mountains II: A case study of the East River Valley. Mountain Research and Development 16:407–418.

United States Fish and Wildlife Service. 2014. Endangered and Threatened Wildlife and Plants;Threatened Status for Gunnison sage-grouse, 79 Fed. Reg. ss 224 (final rule Nov. 20, 2014) (to be codified at 50 C.F.R. part 17).

Wann, G. T., C. L. Aldridge, and C. E. Braun. 2014. Estimates of annual survival, growth, and recruitment of a white-tailed ptarmigan population in Colorado over 43 years. Population Ecology 56:555–567.

Wasko, A. P., C. Martins, C. Oliveira, J. A. Senhorini, and F. Foresti. 2004. Genetic monitoring of the Amazonian fish matrinchã (*Brycon cephalus*) using RAPD markers: Insights into

supportive breeding and conservation programmes. Journal of Applied Ichthyology 20:48–52.

Watters, M. E., T. L. M. C. Lash, C. L. Aldridge, and R. M. Brigham. 2002. The effect of vegetation structure on predation of artificial greater sage-grouse nests. Ecoscience 9:314–319.

Webb, S. L., C. V Olson, M. R. Dzialak, S. M. Harju, J. B. Winstead, and D. Lockman. 2012. Landscape features and weather influence nest survival of a ground-nesting bird of conservation concern, the greater sage-grouse, in human-altered environments. Ecological Processes 1:4.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Threats to imperiled quantifying species in the United States. BioScience 48:607–615.

Wright, R. G., J. M. Scott, S. Mann, and M. Murray. 2001. Identifying unprotected and potentially at risk plant communities in the western USA. Biological Conservation 98:97–106.

Young, J. R. 1994. The influence of sexual selection on phenotypic and genetic divergence among sage grouse populations. PhD Dissertation. Purdue University.

Young, J. R., C. E. Braun, S. J. Oyler-McCance, J. W. Hupp, and T. W. Quinn. 2000. A new species of sage-grouse (Phasianidae: *Centrocercus*) from Southwestern Colorado. The Wilson Bulletin 112:445–453.

CHAPTER II. EVALUATION OF GENETIC CHANGE FROM TRANSLOCATION AMONG GUNNISON SAGE-GROUSE (*CENTROCERCUS MINIMUS*) POPULATIONS

Summary

Maintenance of genetic diversity is important for conserving species, especially those with fragmented habitats or ranges. In the absence of natural dispersal, translocation can be used to achieve this goal, although the impact of translocation can be difficult to measure. I evaluated genetic change following translocation in Gunnison sage-grouse (*Centrocercus minimus*), a species reduced to seven discrete populations with low levels of gene flow and high levels of genetic differentiation. Between 2000 and 2014, 306 birds from the largest and most genetically diverse population (Gunnison Basin) were translocated to five much smaller satellite populations to augment local population size and increase genetic diversity. Although the magnitude of the effect varied by population, I found evidence of increased genetic variation, decreased genetic differentiation from Gunnison Basin, and reproduction between translocated individuals and resident birds. These results suggest that translocations are impacting satellite populations, with current data providing a new baseline for genetic diversity and differentiation among populations of this imperiled species.

Introduction

Habitat alteration is a major contributor to declines in global biodiversity (Sala et al. 2000, Fahrig 2003). Continued fragmentation and loss of habitat can create distinct and increasingly geographically distant populations with decreased dispersal, reduced gene flow, and increased genetic drift (Reed 2004, Frankham 2005, Ezard and Travis 2006, Fischer and Lindenmayer 2007). This, in turn, reduces adaptive potential and makes a species more susceptible to genetic and demographic stochasticity and inbreeding depression (Caughley 1994, Allendorf et al. 2013). Translocation (or reinforcement), the deliberate movement of organisms from one site to another for measurable conservation benefit, has been used for decades as a management technique to augment isolated and declining populations for genetic and demographic benefits (Fischer and Lindenmayer 2000, Ewen et al. 2012, IUCN/SSC 2013). Beyond increasing genetic diversity, translocations have the potential to alleviate fitness declines when new genetic variation masks deleterious alleles in a genetically depauperate population, increasing population growth (Blomqvist et al. 2010, Whiteley et al. 2015). The potential for genetic rescue persists even if both source and recipient are inbred (Fredrickson et al. 2007, Heber et al. 2013)

The Gunnison sage-grouse (*C. minimus*) is a sagebrush (*Artemisia* spp.) obligate species thought to have historically inhabited ~ 46,500 km^2 of sagebrush habitat in Colorado, Utah, New Mexico, and Arizona (Schroeder et al. 2004). Land-use changes in sagebrush habitat have limited the species to southwestern Colorado and southeastern Utah, just 8% of its historical range (Schroeder et al. 2004, Braun et al. 2014). The species persists as a single, relatively large and stable population in the Gunnison Basin with ~85-90% of the remaining birds, surrounded by six much smaller satellite populations: Poncha Pass, Cerro Summit-Cimarron-Sims Mesa

(Cimarron hereafter), Crawford, Dove Creek-Monticello (Dove Creek hereafter), Piñon Mesa, and San Miguel Basin (United States Fish and Wildlife Service 2014; Figure 2.1). Although the species has low genetic diversity range-wide (Oyler-McCance et al. 2005, 2015), the Gunnison Basin population has the highest genetic diversity and the most individuals (Oyler-McCance et al. 2005). Genetic data indicate natural dispersal between populations is low, resulting in significant genetic differentiation (Oyler-McCance et al. 2005). Gunnison sage-grouse is currently listed as threatened under the federal Endangered Species Act (United States Fish and Wildlife Service 2014), but has been of conservation concern to local stakeholder working groups and state management agencies even prior to designation as a distinct species in 2000 (Young et al. 2000, Gunnison sage-grouse Rangewide Steering Committee 2005).

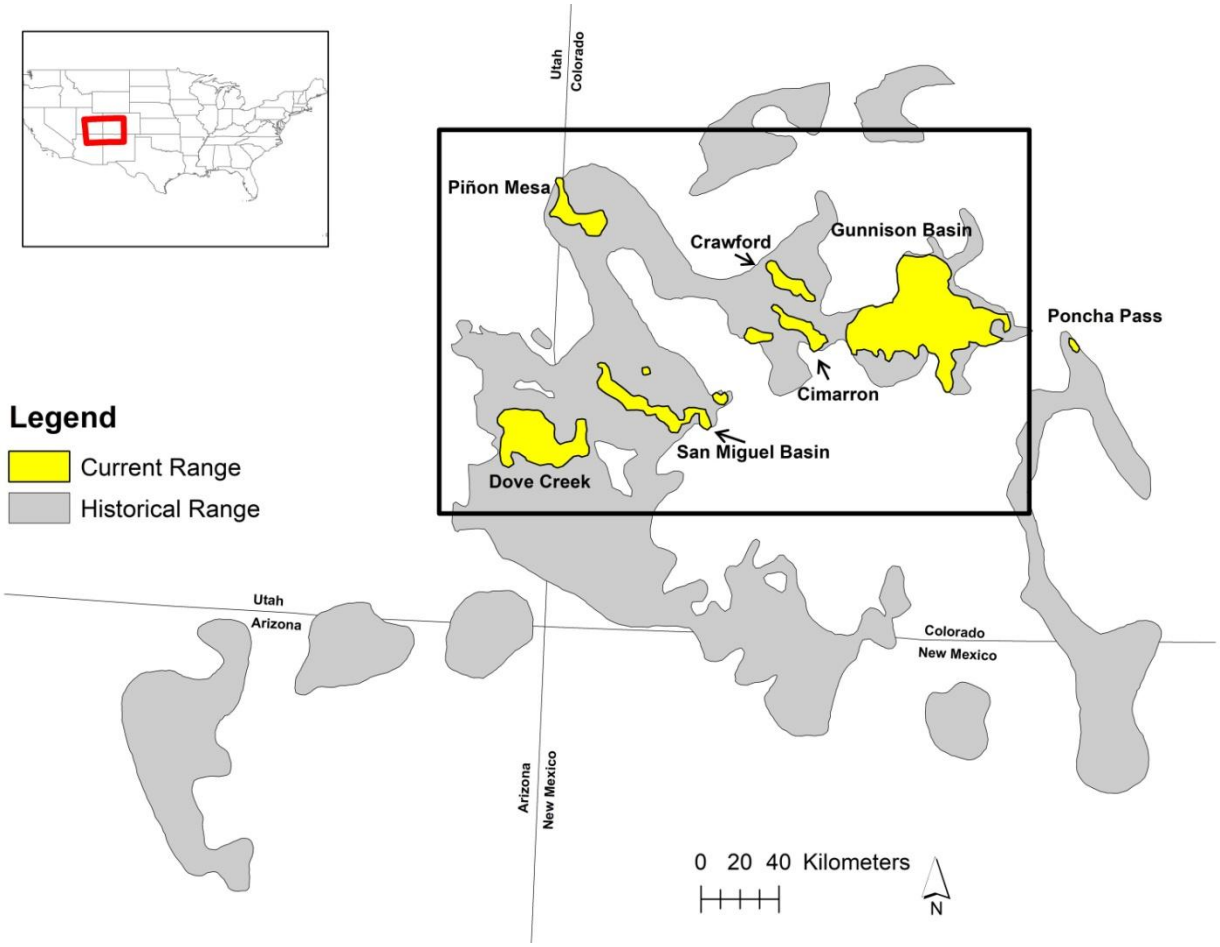

Figure 2. 1- Gunnison sage-grouse current (yellow) and historical (gray; Braun et al. 2014) range. The study area is delineated with a heavy black rectangle. The two portions of the current range north and northeast of San Miguel correspond to recent extirpations. The two northern most portions of the historical range correspond to an unknown species of sage-grouse and are not verified by Colorado Parks and Wildlife (Gunnison sage-grouse Range-wide Steering Committee 2005).

In response to declining population size and low genetic diversity in satellite populations, Colorado Parks and Wildlife (CPW) began translocating individuals from Gunnison Basin to the satellite populations in 2000 (Table 2.1). Although contemporary translocation began for Poncha Pass in 2000, the population was thought to have been extirpated in the 1950s and re-established with Gunnison Basin birds in the 1970s (Nehring and Braun 2000), making this population most likely a genetic subsample of Gunnison Basin. Six individuals translocated to Cimarron in 2000

were released in the southwestern most portion of the population, ~30 km southwest of the currently occupied Cimarron lek, but were never relocated despite being radio-tagged (A. Apa, unpublished data). Lekking activity has not been observed in the release area since 2003 (United States Fish and Wildlife Service 2014). In 2005, translocation began to the remaining western satellite populations. Between 2000 and 2014, CPW translocated a total of 306 birds from the Gunnison Basin into all satellite populations (Table 2.1). Translocation efforts were halted by the state of Colorado following the Endangered Species Act listing decision by the United States Fish and Wildlife Service in 2014.

Table 2. 1- Distribution of samples and translocation efforts across populations of Gunnison sage-grouse. The proportion of the population sampled are based on 2005 (pre, not shown) and 2014 (post) population estimates. The percentage of missing genotypes for each data set is displayed along the bottom. Survival rates (12 month survival of 176 birds translocated in 2013), population estimates, translocation timing and numbers of individuals were obtained from the Federal Register (United States Fish and Wildlife Service 2014).

	Pre		Post			Translocation		
Population	# Samples	% Population	# Samples	% Population	2014 Est.	#	Years	Survival
Gunnison Basin	116	2.4	624	15.7	3978	source population		
Cimarron	4	16.0	8	10.8	74	6	2000	0.00
Crawford	21	11.0	31	19.8	157	72	2011-2013	0.60
Dove Creek	43	21.9	8	8.2	98	42	2005-2013	0.60
Piñon Mesa	19	11.4	74	40.7	182	93	2010-2013	0.40
San Miguel[a]	51	15.3	40	19.4	206	74	2005-2013	0.35
Poncha Pass[b]	-	-	-	-	10	108	1971-2014	0.20
Total	254		785					
% Missing Data	3.6		9.8					

[a]Some of the translocated individuals (23) in San Miguel were released fall 2013; and would not have contributed offspring, though could have contributed to genetic diversity and differentiation metrics.
[b] Not included in this study.

Genetic sampling can be used to evaluate translocation impact based on changes in genetic structure in the recipient population (Carden 2009, Johnson et al. 2010, Miller et al. 2012). One study of two populations with no current gene flow was able to identify offspring of pairing between resident and introduced individuals (Bateson et al. 2014). As relatively large, lek-breeding birds, sage-grouse are ideal for non-invasive genetic monitoring because dropped feathers can be collected from leks (e.g., Bush et al. 2005, 2010; Row et al. 2015; Cross et al. 2016, 2017).

I used genetic sampling methods to evaluate the impact of translocation on genetic composition and to identify individuals that were products of reproduction between translocated and resident individuals in Gunnison sage-grouse. My specific objectives were to determine: 1) if there was a detectable increase in genetic diversity in satellite populations nine years after translocation began; 2) if genetic differentiation between satellite populations and the Gunnison Basin source population decreased; and 3) if translocated Gunnison Basin birds successfully bred. I expected that, if translocated individuals persisted and integrated into satellite populations, I would see increased genetic diversity, decreased genetic differentiation between the Gunnison Basin and satellite populations, and individuals with mixed ancestry. Further, I expected to see no change in genetic diversity for the two populations that effectively did not receive translocated individuals (Cimarron and Gunnison Basin).

Methods

Study Area

My study included Gunnison Basin and the western satellite populations (Figure 2.1). The Poncha Pass population was excluded due to the longer history of translocation from

Gunnison Basin and the assumption this population is a reintroduction. Cimarron was included under the assumption that the translocation efforts in the southwestern portion of the population in 2000 did not survive or no longer remain in Cimarron, and pre-translocation data represent true Cimarron individuals.

Each population is centered in a relatively isolated area of the species' range. These areas vary in topography, habitat composition, precipitation, and temperature (see Gunnison sage-grouse Range-wide Steering Committee 2005 for further details). Estimated population size in 2014 also ranged widely, from 74 to 3,978 (United States Fish and Wildlife Service 2014; Table 2.1). Three populations include geographically separated subpopulations: Cimarron with three subpopulations (only one currently occupied), Dove Creek with two subpopulations, and San Miguel Basin with six subpopulations (Gunnison sage-grouse Range-wide Steering Committee 2005).

Data

The pre-translocation data set was composed of blood samples from 254 birds (Table 2.1) captured using spotlight trapping methods (Giesen et al. 1992, Wakkinen et al. 1992) between 1996 and 2004 as part of a previous study (Oyler-McCance et al. 2005). DNA was extracted using either a phenol-chloroform method (Kahn et al. 1999) or the Genomic Prep Blood DNA Isolation Kit (Amersham Biosciences, Buckinghamshire, UK).

The post-translocation data set was composed of 785 feathers (Table 2.1) non-invasively collected range-wide in the spring after peak lekking season between 2006 and 2014 from 73 of the 106 active leks. I also used samples from mortalities, individuals from mark-recapture studies, and many of the individuals trapped in the Gunnison Basin for subsequent translocation.

Samples from individuals trapped for translocation were considered part of the Gunnison Basin population. Some leks yielded no feathers, and other leks were on inaccessible private or reservation land. Sample collection was accomplished in cooperation with state and federal agencies (CPW, Western State College, Bureau of Land Management, U.S. Fish and Wildlife Service, National Park Service, Forest Service, U.S. Geological Survey, Colorado State University, Utah Division of Wildlife Resources). The majority (96%) of the samples were collected between 2012 and 2014.

Molecular Characterization

I amplified 22 grouse-specific microsatellite loci using the Polymerase Chain Reaction (PCR) with components and concentrations as described in Oyler-McCance and Fike (2011) and thermal profiles as originally published. Microsatellite primers used included: MSP11, MSP18, reSGCA5, reSGCA11, SG21, SG23, SG24, SG28, SG29, SG30, SG31, SG33, SG36, SG38, SG39, SGCTAT1, SGMS06.4, SGMS06.8, TTT3, TUT3, TUT4, and WYBG6 (Segelbacher et al. 2000, Piertney and Hoglund 2001, Taylor et al. 2003, Caizergues et al. 2003, Oyler-McCance and St. John 2010, Fike et al. 2015). A sexing locus was also characterized (Kahn et al. 1998). All PCR products were multi-loaded based on product size and primer label, combined with GeneScan LIZ 600 internal lane size standard (Applied Biosystems, Foster City, California, USA), and electrophoresed through a capillary gel matrix using an AB3500 Genetic Analyzer (Applied Biosystems, Foster City, California, USA). Allele sizes were determined for each locus using GeneMapper v4.1 software (Applied Biosystems, Foster City, California, USA). All feather samples were amplified until two independent and matching genotypes were obtained to minimize impact of allelic dropout and PCR-generated false positives (Taberlet et al. 1999). Loci

that failed to produce two matching genotypes or did not amplify, were coded as missing data. All loci in both data sets were tested for violations of Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium within populations using Genalex (Peakall and Smouse 2006, 2012) and Genepop (Raymond and Rousset 1995, Rousset 2008), respectively. Significance was evaluated based on a Benjamini-Yekutieli multiple comparison adjustment (Benjamini and Yekutieli 2001; Narum 2006).

For the post-translocation data set I used a combination of the R (R Core Team 2017) package 'allelematch' (Galpern et al. 2015) and the stand-alone program Dropout (McKelvey and Schwartz 2005) to remove duplicates from non-invasive samples. I used the *amUniqueProfile* function in 'allelematch' to determine the optimal threshold for declaring samples unique or duplicate and a molecular tag length of 19 for Dropout (e.g., 19 loci needed to be considered to distinguish between duplicates and siblings). I relied predominantly on 'allelematch' to account for missing data.

Genetic Diversity

For each population, I estimated observed heterozygosity (*H*) and identified private alleles using Genalex. Because sample sizes among populations varied, I estimated rarefied allelic richness (*A*) by population using 'Gstudio' (Dyer 2014) in R. Each pre- and post-translocation population comparison was rarefied to 10, unless one of the populations had fewer than 10 samples. For the populations with fewer than 10 samples, estimates of allelic richness were rarefied to the smallest sample size in the comparison. Crawford, Gunnison Basin, Piñon Mesa, and San Miguel were rarefied to a sample size of 10, while Cimarron and Dove Creek were rarefied to four and eight, respectively.

To account for random genetic diversity loss from drift in diversity estimates (Allendorf et al. 2013), I used pre-translocation data to simulate expected diversity loss with BottleSim (Kuo and Janzen 2003). I assumed completely overlapping generations, an average longevity of 3 years, reproductive maturity at 1 year, sex ratio of 1 male for every 2 females (Stiver et al. 2008), a single male per lek reproduced each year (male-dominant polygyny), and population size fluctuated proportionally to yearly population estimates for years 2005 to 2014 (as listed in United States Fish and Wildlife Service 2014). I acknowledge that a single mating male per lek is likely an underestimate of the amount of reproduction (Semple et al. 2001, Bush et al. 2011, Bird et al. 2013). However, the simulation also assumes equal reproduction at all leks, which would be an overestimate of reproduction because leks vary in the number of individuals attending and reproducing. I chose to use the simulations that balanced these two oversimplifications of diversity loss as my expectation of the effect of drift in the absence of translocation. A detailed discussion and testing of my assumptions for the simulated diversity loss is included in Appendix I. Diversity metrics were calculated for simulated data and used as the expectation of no effect from the translocated individuals (predicted data). I tested pre-, post-, and predicted estimates for differences in a non-parametric Wilcoxon paired signed-rank test in R (Hothorn and Hornik 2015). If the post-translocation data were different from the simulated data but not the pre-translocation data, I considered this evidence of a slowing of the effects of genetic drift and a positive effect of translocation on the genetic diversity of the satellite population.

Genetic Differentiation

Genetic differentiation analyses are sensitive to oversampling of family groups and uneven sampling effort (Peterman et al. 2016, Puechmaille 2016). I used COLONY (Jones and Wang 2010) to identify full siblings in all populations, and removed all but one full sibling. Because Gunnison Basin has a much larger sample size than other populations, I also created 10 replicate data sets by random sub-sampling at each lek within Gunnison Basin. Differentiation values reported are averages of 10 replicates. The STRUCTURE analysis required sub-sampling and full siblings removed; remaining differentiation analyses required only sub-sampling.

I used the 'diveRsity' (Keenan et al. 2013) package in R to calculate F_{ST} (Weir and Cockerham 1984) with confidence intervals based on 1,000 bootstraps. Significance (probability (random ≥ data) < 0.019) of F_{ST} values was evaluated with Genalex (Peakall and Smouse 2006, 2012) based on 999 permutations. Significance threshold was based on a Benjamini-Yekutieli multiple comparison adjustment (Benjamini and Yekutieli 2001; Narum 2006). Analogous metrics were also calculated and found to be highly correlated. Only F_{ST} is presented here.

I used the Bayesian clustering program STRUCTURE (Pritchard et al. 2000), with an admixture model, and a burn-in of 250,000 and 300,000 Markov chain Monte Carlo (MCMC) iterations testing 20 replicates of each hypothetical number of populations from K=1 to K=10 to further examine clustering of individuals into distinct groups before and after translocation. Barplots of individual ancestry coefficients for hypothesized values of K were created and customized using DISTRUCT (Rosenberg 2004). The 10 data sets were analyzed in STRUCTURE as above, but with the number of repetitions per hypothetical number of groups reduced to 5. The optimal number of groups for each data set was determined by the Evanno method (Evanno et al. 2005) and mean likelihood method plots.

I created population graphs using 'Gstudio' with 100 permutations to ensure topological stability for each data set. Population graphs are a graph-theoretical representation of the genetic covariance among populations. In these graphs, populations are represented as nodes, and gene flow is represented as edges between nodes. This approach allows genetic data to describe the statistical relationships among all populations simultaneously, as opposed to pair-wise metrics of distance that give an average effect (Dyer et al. 2011, Dyer 2015). Each population graph was quantified by calculating closeness (weighted distance from one node to all other nodes), betweenness (rank of the number of shortest paths through the graph that go through a specific node), and degree (the number of edges attached to a node). Population graphs created for the pre- and post-translocation data sets were checked for similarity with tests of correlation and structural congruity with the *test_congruence* function and using the 'combinatorial' and 'structural' methods.

Reproduction

I tested for evidence of reproduction between translocated individuals and resident satellite population individuals in two ways. First, I simulated data sets of 50 individuals each using Hybridlab (Nielsen et al. 2006) based on the pre-translocation genotypes to represent each population, F1 individuals between each satellite population and Gunnison Basin, a backcross to the satellite population (BC1 to satellite population), and a backcross to Gunnison Basin (BC1 to Gunnison Basin). I then used STRUCTURE (K = 6 because this was optimal for the pre-translocation data, a burn-in of 250,000, and 500,000 iterations) to identify thresholds of population ancestry (5^{th} and 95^{th} percentiles of the Q values) within which hybrids in the post-translocation data for each population would be expected to fall (Appendix II Table S2.1). I then

combined the pre- and post-translocation data for a STRUCTURE analysis using the POPFLAG option for all Gunnison Basin and pre-translocation satellite population birds as recommended for identifying hybrids (Pritchard et al. 2000), setting K = 5 (identified from STRUCTURE), and using a burn-in of 250,000 over 500,000 iterations. I assumed correlated allele frequencies and used an admixture model and allowed for independent estimation of the relative admixture levels between populations, or the alpha prior, as recommended by Wang (2017). *Q* value thresholds identified with simulated data were used to identify F1 individuals between a particular satellite population and the Gunnison Basin, BC1 to the satellite population, BC1 to Gunnison Basin, and individuals belonging to either the Gunnison Basin or the satellite population. Second, I used Genalex to identify private (or unique) alleles in each population before and after translocation. Alleles unique to the Gunnison Basin and a satellite population prior to translocation, but present in a single individual within a satellite population post-translocation would indicate reproduction between a translocated individual and a local satellite population individual.

Results

Examination of Data

Violations of the assumptions of HWE within all populations were minimal, ranging between 13 and 30 percent of loci in each population. No locus deviated from HW expectation and no pair of loci were in linkage disequilibrium in all populations, and therefore all loci were retained for analysis. Individuals within populations were generally highly related. Percentage of full and half siblings in each population ranged between 37% and 94% (Appendix II Table S2.2). The sex ratio in each data set was only slightly biased toward males as determined by the sexing locus. The pre-translocation data set was composed of 58.0% males, 41.3% females, and 0.7%

undetermined individuals. The post-translocation data set was composed of 59.2% males, 39.3% females, and 1.4% undetermined individuals. Males and females were translocated to satellite populations in approximately equal proportions (55.5 % female of 176 genotyped translocated individuals, 9% did not amplify; unpublished data). All estimates of sex ratio are reflective of the composition of the samples used and not a true estimate of the species sex ratio.

Genetic Diversity

Cimarron, Crawford, Dove Creek, Piñon Mesa, and San Miguel all showed a significant increase in heterozygosity compared to predicted values based on simulated loss from pre-translocation data (Figure 2.2). Gunnison Basin remained constant. Notably, heterozygosity in Dove Creek and Piñon Mesa showed a significant increase from pre-translocation, not just from the predicted level. Crawford, Dove Creek, and Piñon Mesa show a significantly higher number of alleles post translocation, while all remaining satellite populations were significantly higher than the expected number of alleles with continued drift. The Gunnison Basin population maintained a constant level of allelic diversity.

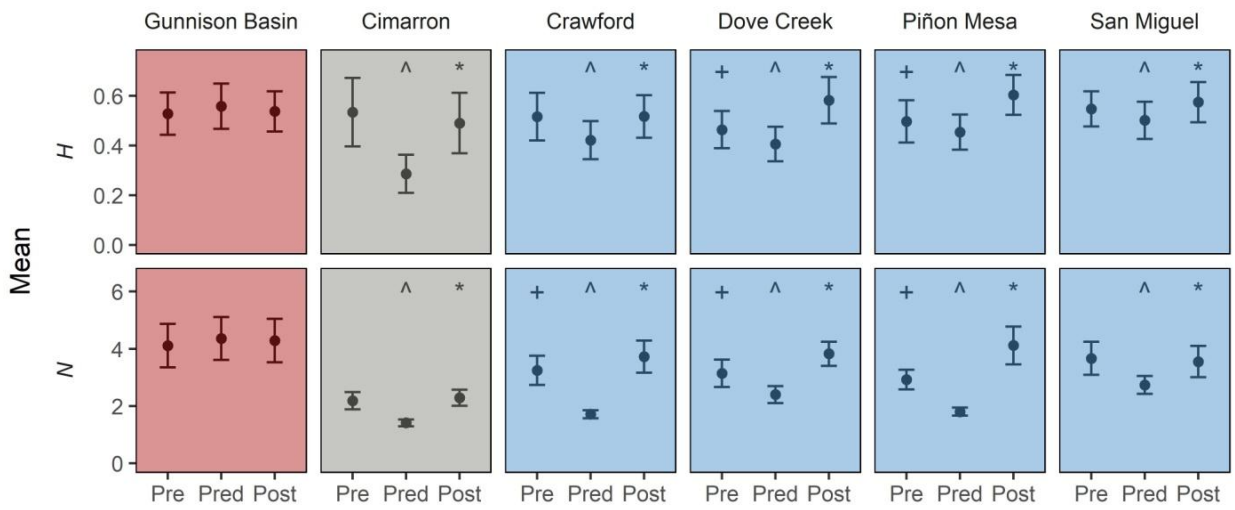

Figure 2. 2- Estimates (mean and 95% confidence intervals) of heterozygosity (*H*) and number of alleles per locus (*N*) for each population prior to translocation (pre), after translocation (post), and as predicted with simulated data (pred). Plus signs (+) indicate the pre- and post-translocation estimates were different, carrots (^) indicate the predicted value was different from the pre-translocation estimates, and stars (*) indicate post-translocation values were significantly increased from expected values due to drift ($P<0.05$, Wilcoxon paired signed-rank test). Shaded backgrounds indicate populations which received no contemporary translocated individuals (gray), were the recipient of translocation efforts (blue), or were the source population (red).

Prior to translocation, there were 32 private alleles (17.2% of the total alleles) identified in Gunnison Basin. After translocation, only 5 of those alleles remained private, meaning the rest were now found in 1 or more of the satellite populations. Two of the private alleles were not identified in any population in the post-translocation data, though these alleles were present at low frequencies prior to translocation (Appendix II Table S2.3). The number of alleles previously private to Gunnison Basin varied by population: 1 in Cimarron, 6 in Dove Creek, 7 in San Miguel, 11 in Crawford, and 20 in Piñon Mesa. The single allele formerly private to Gunnison Basin found in Cimarron post-translocation was low frequency in Gunnison Basin prior to translocation (0.009), probably representing a rare allele rather than a private allele.

Genetic Differentiation

Pair-wise F_{ST} values showed a downward trend in all population comparisons with Gunnison Basin following translocation, except Cimarron (Figure 2.3). Only the comparison between Gunnison Basin and Piñon Mesa showed a significant decrease in F_{ST} (i.e., non-overlapping confidence intervals).

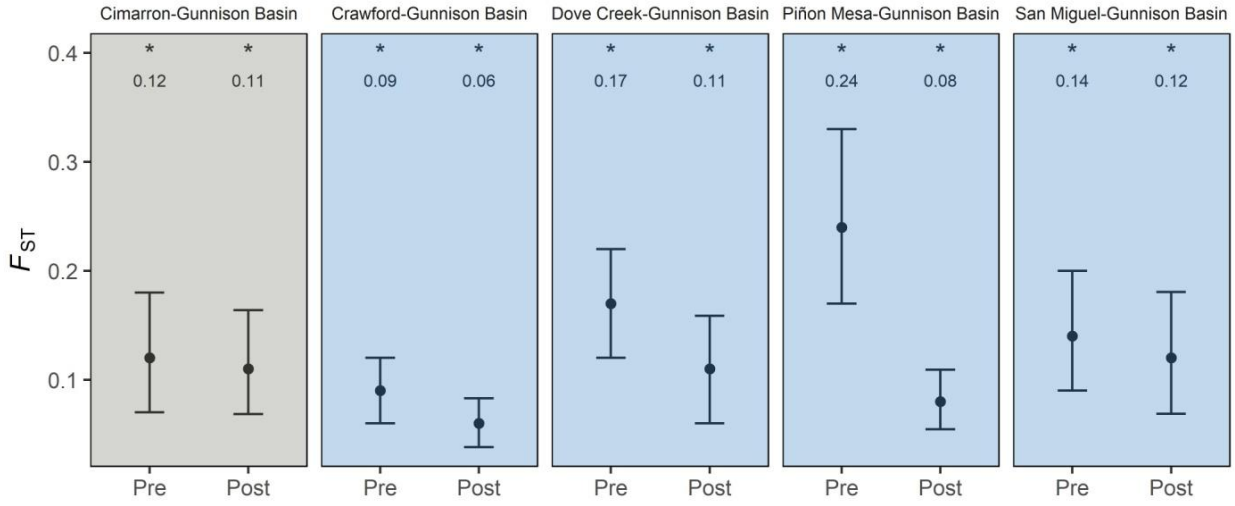

Figure 2. 3- Mean pair-wise F_{ST} and 95% confidence intervals from 1000 bootstraps in the R package diveRsity; values are listed along the top of the plot. Stars (*) indicate a significant pair-wise F_{ST} value as calculated by Genalex with 999 permutations at the 0.019 Benjamini-Yekutieli adjusted significance level. Population comparisons are listed along the top. Shaded backgrounds indicate populations that received no contemporary translocated individuals (gray) and were the recipient of translocation efforts (blue).

Estimates of the optimal number of populations pre- and post-translocation indicated K=6 before translocation and K=5 after translocation in both the Evanno method (Appendix II Figure S2.1A) and the mean likelihood of K method (Appendix II Figure S2.1B). In both the pre- and post-translocation STRUCTURE analyses the Cimarron samples do not show substantial amounts of shared ancestry with the Gunnison Basin cluster, supporting our assumption that early translocation to the Cimarron population from Gunnison Basin did indeed fail (Appendix II

Figure S2.2). Comparison of population graphs is consistent with other genetic structure metrics; post-translocation the graph has more connections between populations (Figure 2.4). Graph congruence tests yielded a correlation of -0.34 (*CI*: -0.72, 0.20), an insignificant *P*-value (0.21), and a 0.74 probability that there are more nodes and edges in the congruence graph than would be expected if the two individual graphs were randomly associated, indicating the network has significantly changed post-translocation. There was no change in closeness (weighted measure of distance from one population to all other populations) post translocation. I would have predicted a decrease in the closeness metric if translocated individuals were persisting in the satellite populations. Betweenness was largely unchanged, although it decreased from 1 to 0 in Gunnison Basin and San Miguel, and increased from 0 to 2 in Piñon Mesa (Table 2.2).

Table 2. 2- Population graph metrics for Gunnison sage-grouse pre- and post-translocation. Betweenness = number of shortest paths going through a node/edge; Degree = number of adjacent edges. Gunnison Basin was the source population for all translocation efforts. Cimarron did not receive contemporary translocations.

Population	Betweenness		Degree	
	Pre	Post	Pre	Post
Gunnison Basin	1	0	4	3
Cimarron	0	0	4	4
Crawford	0	0	5	5
Dove Creek	0	0	5	4
Piñon Mesa	0	2	4	5
San Miguel	1	0	4	5

This change corresponds to an increase in the number of shortest paths through Piñon Mesa, and a decrease in the shortest paths through Gunnison Basin and San Miguel. Degree remained constant for Cimarron and Crawford, showing no change in the number of edges, or dispersal routes, for both populations. Degree for Dove Creek and Gunnison Basin decreased by 1, indicating 1 route connecting Dove Creek and Gunnison Basin is no longer intact (Figure 2.4).

Lastly, degree for Piñon Mesa and San Miguel both increased, indicating an increase in the number of genetic connections between populations. The additional connection for Piñon Mesa is to Gunnison Basin and for San Miguel is to Cimarron (Figure 2.4).

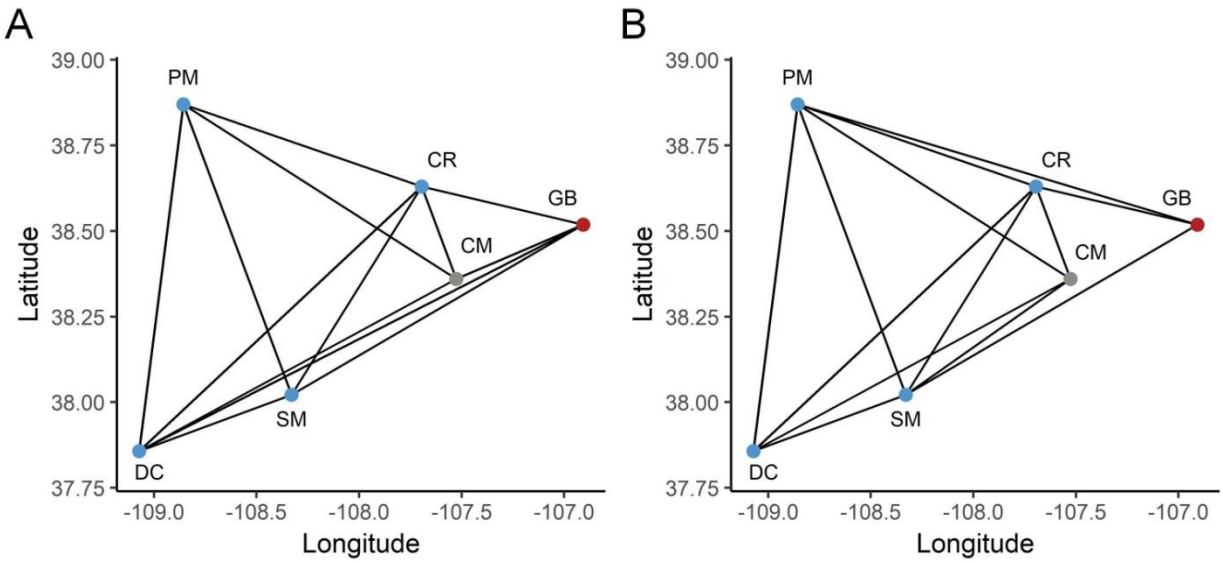

Figure 2. 4- Population graphs for the Gunnison sage-grouse pre- (A) and post-translocation (B) data. Populations are abbreviated as follows: CM = Cimarron, CR = Crawford, DC = Dove Creek, GB = Gunnison Basin, PM = Piñon Mesa, SM = San Miguel. Nodes are plotted at the geographic coordinates of each population center and color coded to indicate populations which received no contemporary translocated individuals (gray), were the recipient of translocation efforts (blue), or were the source population (red).

Reproduction

All populations where individuals were translocated showed evidence of reproduction between Gunnison Basin birds and resident satellite population birds post translocation (Figure 2.5). The amount of reproduction detected was variable. In Crawford, Dove Creek, Piñon Mesa, and San Miguel 16.1%, 37.5%, 37.8%, and 10.0% of the collected samples were assigned to a category indicating reproduction with translocated Gunnison Basin birds (Appendix II Table S2.4). Crawford and Piñon Mesa had 12.9% and 12.2% of samples assigned to the Gunnison

Basin group. All four populations had samples assigned to the resident satellite population category, though in differing percentages: Crawford with 61.3%, Dove Creek with 25.0%, Piñon Mesa with 25.7% and San Miguel with 82.5%. Some individuals remained unassigned: 3 in Crawford, 3 in Dove Creek, 18 in Piñon Mesa, and 3 in San Miguel.

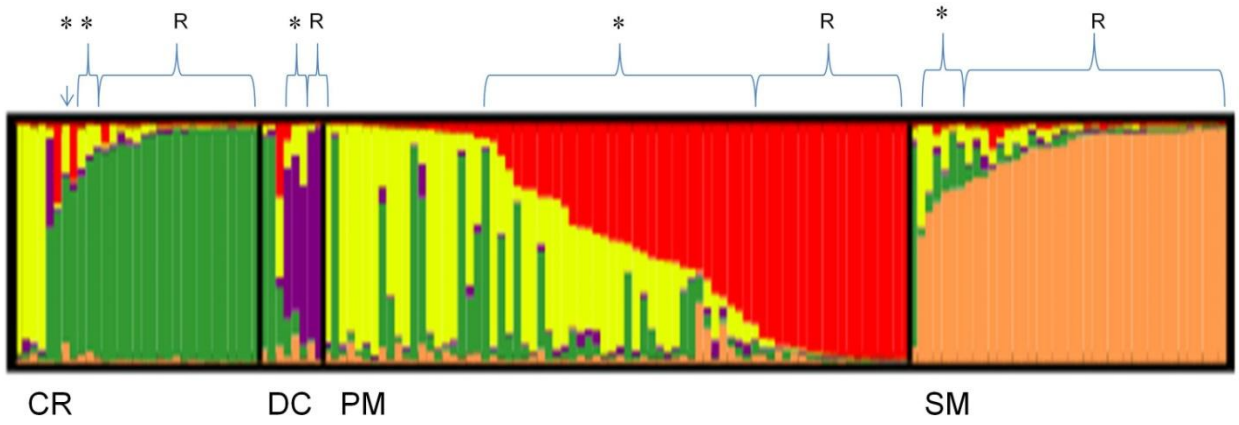

Figure 2. 5- Identification of reproduction between translocated Gunnison Basin individuals and satellite populations using STRUCTURE. Each vertical bar represents an individual Gunnison sage-grouse that is color coded by the proportion of genetic inheritance each individual has from one of the 5 distinct clusters (K = 5 was optimal for the post-translocation data set). Stars (*) above the plot indicate individuals that represent reproduction between resident individuals and a translocated Gunnison Basin individual. Vertical bars labeled with an "R" indicate resident satellite population individuals. Vertical bars without a label are either translocated individuals from Gunnison Basin (majority yellow), or unassigned. See Appendix II Table S2.1 for *Q* value thresholds. Green = Cimarron/Crawford (CR), purple = Dove Creek (DC), red = Piñon Mesa (PM), orange = San Miguel (SM), and yellow = Gunnison Basin. Total N = 153; CR = 31, DC = 8, PM = 74, SM = 40.

Eleven individuals from all post-translocation satellite populations that received translocated individuals were identified as having alleles that were formerly private to Gunnison Basin, in addition to private alleles from the satellite population where the individual was sampled. All but 2 of the 11 individuals (PMS04 and WF02) were also identified as having mixed ancestry (Appendix II Table S2.5). Both samples, PMS04 and WF02, were identified as Gunnison Basin individuals (Appendix II Table S2.5) and private alleles from Gunnison Basin

and satellite populations were of low frequency, making it possible that these were instances of rare alleles rather than private alleles (Appendix II Table S2.5). The remaining 9 birds with private alleles from 2 populations strongly indicate reproductive events between local and translocated individuals.

Discussion

Although the magnitude varied, I detected genetic change in all recipient populations consistent with my expectations of translocated individuals surviving and integrating into recipient populations. The frequent use of translocation in North American grouse species (Reese and Connelly 1997, Bouzat et al. 1998, Snyder et al. 1999, Hoffman et al. 2015) has led to detailed recommendations on evaluating success. Baxter et al. (2008) recommend tracking several metrics to evaluate sage-grouse translocation efforts including annual survival rates, distance moved from release site, nesting propensity, nest survival, chick survival, flocking, and attendance at leks. Efforts may be considered successful when translocated individuals are indistinguishable from resident birds in behavior and demographic rates are comparable to resident birds (Baxter et al. 2008). My evaluation of translocation success using genetic sampling addresses several of the evaluation metrics suggested by Baxter et al. (2008) because detection of reproducing individuals implies that translocated individuals are surviving, integrating into the resident population, attending leks, nesting, and recruiting offspring. My results indicate some degree of translocation success was attained in all recipient populations.

While translocation efforts have increased genetic diversity and decreased the amount of genetic differentiation in satellite populations, relocation efforts must continue indefinitely to maintain the observed changes in the absence of restored habitat corridors and increased natural

dispersal. The small size of satellite populations is presumably a result of local habitat loss and/or fragmentation. Without increasing available habitat, or connectivity between populations, Gunnison sage-grouse satellite populations may remain limited in size and the forces of genetic drift may remain strong (Caughley 1994, Fischer and Lindenmayer 2000).

Despite my detection of genetic change in recipient satellite populations, not all of my predictions were realized. Consideration of additional sources of information helped me identify some potential explanations for the observed deviations from my expectations. I predicted satellite populations receiving translocated individuals would increase in genetic diversity, decrease in genetic differentiation, and some subset of individuals would have a higher than expected proportion of Gunnison Basin ancestry post-translocation. I expected populations not receiving translocated individuals would not show indications of increased genetic diversity or decreased differentiation. The Crawford, Dove Creek, Piñon Mesa, and San Miguel satellite populations all showed varying degrees of increased diversity, decreased differentiation compared to Gunnison Basin, and evidence of reproduction with translocated birds. Gunnison Basin fit our expectation as a null model for diversity metric changes, with no observed change in heterozygosity and allelic diversity. Greater subdivision was apparent in Gunnison Basin post-translocation (Appendix II Figure S2.3), potentially a result of sampling methods or reduced gene flow between leks, which is the subject of a separate investigation (See Chapter III). Cimarron diversity and differentiation metrics remained constant, contrary to a large predicted diversity loss, which should have been detectable with the eight samples collected post-translocation (See Appendix III). There are two possible reasons for the maintenance of diversity in Cimarron. First, the simulation may be overestimating the amount of diversity loss expected because only four samples were used as an initial diversity estimate. Four samples may not be an

adequate number to estimate actual population diversity. I was limited in the availability of samples for the Cimarron population. Future studies could evaluate how well collected samples refelect true diversity through simulation techniques (e.g., Miyamoto et al. 2008). Second, natural dispersal to Cimarron might be occurring. The longest distance from Cimarron to Gunnison Basin, San Miguel, Crawford, or the 2000 translocation release site is 50 km, just beyond the longest known dispersal for Gunnison sage-grouse (~39 km; Doug Ouren, personal communication), yet well within known dispersal distances for greater sage-grouse (120-240 km; Tack et al. 2011, Cross et al. 2017, Newton et al. 2017). Translocated adults are known to make large movements (Letty et al. 2007), and on at least one occasion a GPS collared Crawford individual temporarily moved to near Cimarron (Doug Ouren, personal communication). A previous genetic study on Gunnison sage-grouse indicated low levels of gene flow between Cimarron and San Miguel (Oyler-McCance et al. 2005). Tripling of population size (see Appendix III) and increased genetic diversity in Cimarron indicate natural dispersal from any population in relatively close proximity could be occurring. However, known movement from Crawford, and clustering of Cimarron samples with Crawford samples (Appendix II Figure S2.3) indicate natural dispersals from Crawford to Cimarron might be more common than originally thought. The appearance of shared ancestry with San Miguel in Cimarron individuals both before (Appendix II Figure S2.2A) and after (Appendix II Figure S2.3) translocation, as well as the presence of Dove Creek ancestry in other populations further supports that long-distance natural dispersal is occurring to some degree. Detecting genetic signals of long-distance dispersal is particularly interesting because the populations of Gunnison sage-grouse are arranged within a matrix of landscape features known to impede dispersal or movement in sage-grouse, such as fragmented or reduced habitat, potential for predator pressure, rough terrain and mountain

passes, and human impacts (Hagen et al. 2011, Aldridge et al. 2012, Row et al. 2015, Green et al. 2017, Rice et al. 2017, Row et al. 2018).

The differing amounts of genetic change observed in each population was not particularly surprising given the known differences in local environmental conditions, though many additional factors are likely contributing to differing success of translocation efforts. First, more translocated individuals often correspond to higher impact (Fischer and Lindenmayer 2000). An asymptotic relationship between number of individuals translocated and success rates suggest a minimum number of individuals is required for intended impact (Griffith et al. 1989, Wolf et al. 1996). Generally, the populations that received more translocated birds (Crawford and Piñon Mesa) showed a corresponding increase in population size (Appendix III Figure S3.2A) suggesting the number of individuals translocated might be impacting the amount of change detected. Second, higher quality habitat typically indicates higher degrees of translocation impact (Griffith et al. 1989, Wolf et al. 1996). Habitat quality and quantity vary among Gunnison sage-grouse populations (Gunnison sage-grouse Range-wide Steering Committee 2005). Dove Creek and San Miguel both have subpopulations, potentially from fragmented habitat in Dove Creek and natural fragmentation in San Miguel, and little impact from translocation was detected in both populations. In greater sage-srouse, survival rates have been linked to habitat quality (Aldridge and Boyce 2007), suggesting the documented difference in survival for Gunnison sage-grouse populations (United States Fish and Wildlife Service 2014, Davis et al. 2015) may also be linked to the differences in habitat quality in each satellite population. Third, seasonal timing of translocation matters (Letty et al. 2007). For sage-grouse, survival rates from spring translocations tend to be higher relative to fall (Reese and Connelly 1997, United States Fish and Wildlife Service 2014). Higher spring survival rates might be a result of habitat breadth. That is,

fall habitat requirements are less specialized than requirements for spring habitat, potentially resulting in large movements and delayed population integration in fall and encouraging integration into the population more quickly through lek attendance during spring (Berry and Eng 1985, Bell and George 2012). Fourth, individuals vary in overall contribution to translocation success (Letty et al. 2007). The Gunnison sage-grouse has a male dominant polygynous mating system where females are more likely to mate and relatively few males participate in the majority of copulations (Patterson 1952, Wiley 1973). If a male becomes dominant at a lek, however, the genetic impact will be greater than that of a single female. Similarly, if the size of the recipient population is small, the genetic impact on the population from a single translocated individual would be greater than if the population was large. All satellite populations are small, however, the two populations with the strongest signal of genetic change (Crawford and Piñon Mesa) had relatively smaller population estimates prior to the start of translocation efforts than the two populations which showed little genetic change (2004 population estimates: Crawford = 128, Piñon Mesa = 142, Dove Creek = 162, San Miguel = 255; United States Fish and Wildlife Service 2014). Lastly, the age of translocated individuals matters. Translocated adults are known to make large movements and may be less malleable to new social and environmental conditions (Letty et al. 2007). In contrast, younger birds may have a lower breeding propensity and smaller clutches, as has been shown for greater sage-grouse (Eng 1963, Taylor et al. 2012), which may affect their genetic contributions when translocated.

Considering population trends can provide insight into the benefits of translocation beyond the detection of genetic change. Increased population size and expanding occupation post translocation could be evidence of genetic rescue (Fredrickson et al. 2007). In addition to increased genetic diversity, Piñon Mesa and Crawford appear to have approximately tripled in

population size since 2011 (United States Fish and Wildlife Service 2014), and three new leks were located in Piñon Mesa (Dan Neubaum, personal communication). Observed occupied range and population increases occurred without efforts to increase available habitat. These observations are confounded with increased efforts to monitor population trend and changes in counting procedure, as well as the addition of individuals to populations via translocation. However, increases in population size from 2012 to 2014 in Crawford and 2011 to 2014 in Piñon Mesa, are greater than would be expected by the addition of translocated individuals alone in that time period (Appendix III Figure S3.2B). During the time period in which translocation occurred, San Miguel and Dove Creek experienced population estimate declines. Population cycling in sage-grouse could be an alternative explanation for population estimate increases in satellite populations (Patterson 1952, Rich 1985, Fedy and Aldridge 2011), though there is some evidence cyclic population dynamics may be more likely to be disrupted in isolated populations separated by fragmented habitat (Moss and Watson 2001). Allee effects may also be impacting local population demographics via improved group vigilance, increased reproduction from higher male lek attendance, or a buffering of the population to individual stochasticity through translocation (Stephens et al. 1999). We are unable to separate the relative contributions of genetic and demographic effects to observed population increases, however, experimental evidence suggests genetic effects can positively impact population size faster than demographic effects (Hufbauer et al. 2015).

Habitat fragmentation has resulted in many species of conservation concern acquiring complicated dispersal patterns (Hanski 1994, Sweanor et al. 2000, Gamble et al. 2007) consistent with metapopulation dynamics, or stepping stone dispersal (Hanski and Gilpin 1991). Historically, Gunnison sage-grouse is thought to have persisted as population centers connected

by dispersal in a metapopulation configuration (Braun et al. 2014). The current inhabited range is thought to be the result of loss and degradation of habitat and reduced dispersal and subsequent gene flow, ultimately forming isolated populations. In addition to detecting gene flow between translocated and resident birds, I also identified changes in genetic connections among populations, some of which were contrary to my expectations. My population graphs indicate there was restoration of a direct genetic connection between Gunnison Basin and Piñon Mesa as expected. However, despite observed increases in genetic diversity and evidence of reproduction between resident and translocated birds, a direct genetic connection between Gunnison Basin and Dove Creek was lost (Figure 2.4). The loss of this connection could be a result of genetic drift in Dove Creek as population estimates show a substantial decline since the early 2000s, to fewer than 100 birds in 2014, despite translocation efforts to increase population numbers (United States Fish and Wildlife Service 2014). There is also the possibility that I am detecting average genetic change in Dove Creek, resulting from an individual(s) from another satellite population making long-distance movements in search of habitat in response to increased population size or continued loss of locally available habitat (Pulliam 1988). The STRUCTURE plot indicates that even before translocations were implemented, a few individuals appeared to have the genetic characteristics of a population other than their own (Appendix II Figure S2.2A), suggesting that rare dispersal among populations may be occurring. Satellite populations may play an important role in facilitation of range-wide gene flow for this species if any amount of natural gene flow is occurring among them.

Though translocation of individuals to satellite populations has been halted, my results provide an indication of the relative impact on each satellite population and could be used to prioritize which populations may benefit most from any future translocation efforts. At the time

translocation efforts were implemented, the fear was loss of small, isolated populations. Colorado Parks and Wildlife opportunistically captured and relocated individuals with the goal of augmenting the small populations and increasing genetic diversity within them. My results suggest that multiple interacting factors impact detectable change from translocation efforts for Gunnison sage-grouse. If future translocation efforts were to occur, it could be beneficial to evaluate the relative genetic effect of sex, age, and season to obtain information to further tune and prioritize efforts.

LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: Habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–26.

Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for Gunnison sage-grouse: A spatially explicit hierarchical approach. Journal of Wildlife Management 76:391–406.

Allendorf, F. W., G. Luikart, and S. N. Aitken. 2013. Conservation and the Genetics of Populations. 2nd edition. Wiley-Blackwell, New York.

Bateson, Z. W., P. O. Dunn, S. D. Hull, A. E. Henschen, J. A. Johnson, and L. A. Whittingham. 2014. Genetic restoration of a threatened population of Greater Prairie-Chickens. Biological Conservation 174:12–19.

Baxter, R. J., J. T. Flinders, and D. L. Mitchell. 2008. Survival, movements, and reproduction of translocated greater sage-grouse in Strawberry Valley, Utah. Journal of Wildlife Management 72:179–186.

Bell, C. B., and T. L. George. 2012. Survival of translocated greater sage-grouse hens in northeastern California. Western North American Naturalist 72:369–376.

Benjamini, Y., and D. Yekutieli. 2001. The control of the false discovery rate in multiple testing under dependency. The Annals of Statistics 29:1165–1188.

Berry, J. D., and R. L. Eng. 1985. Interseasonal movements and fidelity to seasonal use areas by female sage-grouse. Journal of Wildlife Management 49:237–240.

Bird, K. L., C. L. Aldridge, J. E. Carpenter, C. A. Paszkowski, M. S. Boyce, and D. W. Coltman.

2013. The secret sex lives of sage-grouse: Multiple paternity and intraspecific nest parasitism revealed through genetic analysis. Behavioral Ecology 24:29–38.

Blomqvist, D., A. Pauliny, M. Larsson, and L. Flodin. 2010. Trapped in the extinction vortex? Strong genetic effects in a declining vertebrate population. BMC Evolutionary Biology 10:1–9.

Bouzat, J. L., H. H. Cheng, H. A. Lewin, R. L. Westemeier, D. Jeffrey, and K. N. Paige. 1998. Genetic evaluation of a demographic bottleneck the Greater Prairie Chicken. Conservation Biology 12:836–843.

Boyce, M. S.. 1990. The red queen visits sage-grouse leks. American Zoologist 30:263–270.

Braun, C. E., S. J. Oyler-McCance, J. A. Nehring, M. L. Commons, J. R. Young, and K. M. Potter. 2014. The historical distribution of Gunnison sage-grouse in Colorado. The Wilson Journal of Ornithology 126:207–217.

Bush, K. L., M. D. Vinsky, C. L. Aldridge, and C. A. Paszkowski. 2005. A comparison of sample types varying in invasiveness for use in DNA sex determination in an endangered population of greater sage-grouse (*Centrocercus uropihasianus*). Conservation Genetics 6:867–870.

Bush, K. L., C. L. Aldridge, J. E. Carpenter, C. A. Paszkowski, M. S. Boyce, and D. W. Coltman. 2010. Birds of a feather do not always lek together : Genetic diversity and kinship structure of greater sage-grouse (*Centrocercus urophasianus*) in Alberta. The Auk 127:343–353.

Bush, K. L., C. K. Dyte, B. J. Moynahan, C. L. Aldridge, H. S. Sauls, A. M. Battazzo, B. L.

Walker, K. E. Doherty, J. Tack, J. Carlson, D. Eslinger, J. Nicholson, M. S. Boyce, D. E. Naugle, C. A. Paszkowski, and D. W. Coltman. 2011. Population structure and genetic diversity of greater sage-grouse (*Centrocercus urophasianus*) in fragmented landscapes at the northern edge of their range. Conservation Genetics 12:527–542.

Caizergues, A., O. Rätti, P. Helle, L. Rotelli, L. Ellison, and J. Y. Rasplus. 2003. Population genetic structure of male Black Grouse (*Tetrao tetrix* L.) in fragmented vs. continuous landscapes. Molecular Ecology 12:2297–2305.

Carden, R. F.. 2009. Genetic structure of, and hybridisation between, Red (*Cervus elaphus*) and Sika (*Cervus nippon*) deer in Ireland. Mammalian Biology 74:263–273.

Caughley, G.. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Cross, T. B., D. E. Naugle, J. C. Carlson, and M. K. Schwartz. 2016. Hierarchical population structure in greater sage-grouse provides insight into management boundary delineation. Conservation Genetics 17:1417-1433.

Cross, T. B., D. E. Naugle, J. C. Carlson, and M. K. Schwartz. 2017. Genetic recapture identifies long-distance breeding dispersal in greater sage-grouse (*Centrocercus urophasianus*). The Condor 119:155–166.

Davis, A. J., M. L. Phillips, and P. F. J. Doherty. 2015. Survival of Gunnison sage-grouse *Centrocercus minimus* in Colorado, USA. Journal of Avian Biology 45:186–192.

Dyer, R. J., D. M. Chan, V. A. Gardiakos, and C. A. Meadows. 2011. Pollination graphs: Quantifying pollen pool covariance networks and the influence of intervening landscape on genetic connectivity in the North American understory tree, *Cornus florida* L. Landscape

Ecology 27:239–251.

Dyer, R. J.. 2014. Gstudio: Analyses and functions related to the spatial analysis of genetic marker data. R pakcage version 1.3.

Dyer, R.J.. 2015. Population graphs and landscape genetics. Annual Review of Ecology Evolution and Systematics 46: 327-342.

Eng, R. L.. 1963. Observations on the breeding biology of male sage-grouse. Journal of Wildlife Management 27:841–846.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. Molecular Ecology 14:2611–2620.

Ewen, J. G., D. P. Armstrong, K. A. Parker, and P. J. Seddon (Editors). 2012. Reintroduction Biology: Integrating Science and Management. Wiley-Blackwell, Hoboken, New Jersey, USA.

Ezard, T. H. G., and J. M. J. Travis. 2006. The impact of habitat loss and fragmentation on genetic drift and fixation time. Oikos 2:367–375.

Fahrig, L.. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Fedy, B. C., and C. L. Aldridge. 2011. The importance of within-year repeated counts and the influence of scale on long-term monitoring of sage-grouse. Journal of Wildlife Management 75:1022–1033.

Fike, J. A., S. J. Oyler-McCance, S. J. Zimmerman, and T. A. Castoe. 2015. Development of 13

microsatellites for Gunnison sage-grouse (*Centrocercus minimus*) using next-generation shotgun sequencing and their utility in greater sage-grouse (*Centrocercus urophasianus*). Conservation Genetics Resources 7:211–214.

Fischer, J., and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. Biological Conservation 96:1–11.

Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation : A synthesis. Global Ecology and Biogeography 16:265–280.

Frankham, R.. 2005. Genetics and extinction. Biological Conservation 126:131–140.

Fredrickson, R. J., P. Siminski, M. Woolf, and P. W. Hedrick. 2007. Genetic rescue and inbreeding depression in Mexican Wolves. Proceedings of the Royal Society of London, Series B 274:2365–2371.

Galpern, P., M. Manseau, P. Hettinga, K. Smith, and P. Wilson. 2012. Allelematch: An R Package for identifying unique multilocus genotypes where genotyping error and missing data may be present. Molecular Ecology Resources 12:771-778.

Gamble, L. R., K. McGarigal, and B. W. Compton. 2007. Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: Implications for spatio-temporal population dynamics and conservation. Biological Conservation 139:247–257.

Gibson, D., E. J. Blomberg, G. L. Patricelli, A. H. Krakauer, M. T. Atamian, and J. S. Sedinger. 2013. Effects of radio collars on survival and lekking behavior of male greater sage-grouse. The Condor 115:769–776.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1992. Methods for trapping sage-grouse in

Colorado. Wildlife Society Bulletin 10:224–231.

Green, A. W., C. L. Aldridge, and M. S. O'Donnell. 2017. Investigating impacts of oil and gas development on greater sage-grouse. Journal of Wildlife Management 81:46–57.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: Status and strategy. Science 245:477–479.

Gunnison sage-grouse Rangewide Steering Committee. 2005. Gunnison sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado, USA.

Hagen, C. A., M. J. Willis, E. M. Glenn, and R. G. Anthony. 2011. Habitat selection by greater sage-grouse during winter in southeastern Oregon. Western North American Naturalist 71:529–538.

Hanski, I.. 1994. A practical model of metapopulation dynamics. The Journal of Animal Ecology 1:151–162.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: Brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

Heber, S., A. Varsani, S. Kuhn, A. Girg, B. Kempenaers, and J. Briskie. 2013. The genetic rescue of two bottlenecked South Island Robin populations using translocations of inbred donors. Proceedings of the Royal Society of London, Series B 280:20122228.

Hoffman, R. W., K. A. Griffin, J. M. Knetter, M. A. Schroeder, A. D. Apa, J. D. Robinson, S. P. Espinosa, T. J. Christiansen, R. D. Northrup, D. A. Budeau, and M. J. Chutter. 2015. Guidelines for the management of Columbian Sharp-Tailed Grouse populations and their habitats. Sage and Columbian Sharp-tailed Grouse Technical Committee, Western

Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Hothorn, T., and K. Hornik. 2015. exactRankTests: Exact distributions for rank and permutation tests. R package version 0.8-28.

Hufbauer, R. A., M. Szűcs, E. Kasyon, C. Youngberg, M. J. Koontz, C. Richards, T. Tuff, and B. A. Melbourne. 2015. Three types of rescue can avert extinction in a changing environment. Proceedings of the National Academy of Sciences 112:10557–10562.

IUCN/SSC. 2013. Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0. *Gland, Switzerland: IUCN Species Survival Commission*.

Johnson, W. E., D. P. Onorato, M. E. Roelke, E. D. Land, M. Cunningham, R. C. Belden, R. McBride, D. Jansen, M. Lotz, D. Shindle, J. Howard, D. E. Wildt, L. M. Penfold, J. A. Hostetler, M. K. Oli, and S. J. O'Brien. 2010. Genetic restoration of the Florida panther. Science 329:1641–1645.

Jones, O. R., and J. Wang. 2010. COLONY: A program for parentage and sibship inference from multilocus genotype data. Molecular Ecology Resources 10:551–555.

Kahn, N. W., J. St. John, and T. W. Quinn. 1998. Chromosome-specific intron size differences in the Avian CHD gene provide an efficient method for sex identification in birds. The Auk 115:1074–1078.

Kahn, N. W., C. E. Braun, J. R. Young, S. Wood, D. R. Mata, and T. W. Quinn. 1999. Molecular analysis of genetic variation among large- and small-bodied sage-grouse using mitochondrial control-region sequences. The Auk 116:819–824.

Keenan, K., P. McGinnity, T. F. Cross, W. W. Crozier, and P. A. Prodohl. 2013. diveRsity: An R

package for the estimation of population genetics parameters and their associated errors. Methods in Ecology and Evolution 4:782–788.

Kuo, C. H., and F. J. Janzen. 2003. BOTTLESIM: A bottleneck simulation program for long-lived species with overlapping generations. Molecular Ecology Notes 3:669–673.

Lank, D. B., C. M. Smith, O. Hanotte, A. Ohtonen, S. Bailey, and T. Burke. 2002. High frequency of polyandry in a lek mating system. Behavioral Ecology 13:209–215.

Letty, J., S. Marchandeau, and J. Aubineau. 2007. Problems encountered by individuals in animal translocations: Lessons from field studies. Ecoscience 14:420–431.

McKelvey, K. S., and M. K. Schwartz. 2005. DROPOUT: A program to identify problem loci and samples for noninvasive genetic samples in a capture-mark-recapture framework. Molecular Ecology Notes 5:716–718.

Miller, J. M., J. Poissant, J. T. Hogg, and D. W. Coltman. 2012. Genomic consequences of genetic rescue in an insular population of Bighorn Sheep (*Ovis canadensis*). Molecular Ecology 21:1583–1596.

Miyamoto, N., J. F. Fernández-Manjarrés, M.-E. Morand-Prieur, P. Bertolino, and N. Frascaria-Lacoste. 2008. What sampling is needed for reliable estimations of genetic diversity in *Fraxinus excelsior* L. (Oleaceae)? Annals of Forest Science 65:403–403.

Moss, R., and A. Watson. 2001. Population cycles in birds of the grouse family (Tetraonidae). Advances in Ecological Research 32:53–111.

Narum, S. R.. 2006. Beyond Bonferroni : Less conservative analyses for conservation genetics. Conservation Genetics 7:783–787.

Nehring, J. A., and C. E. Braun. 2000. Gunnison sage-grouse investigations: Poncha Pass area, Colorado April- December 1999. Colorado Division of Wildlife, Fort Collins, Colorado, USA.

Newton, R. E., J. D. Tack, J. C. Carlson, M. R. Matchett, P. J. Fargey, and D. E. Naugle. 2017. Longest sage-grouse migratory behavior sustained by intact pathways. Journal of Wildlife Management 81:962-971.

Nielsen, E. E., L. A. Bach, and P. Kotlicki. 2006. HYBRIDLAB (version 1.0): A program for generating simulated hybrids from population samples. Molecular Ecology Notes 6:971–973.

Oyler-McCance, S. J., and J. St. John. 2010. Characterization of small microsatellite loci for use in non invasive sampling studies of Gunnison sage-grouse (*Centrocercus minimus*). Conservation Genetics Resources 2:17–20.

Oyler-McCance, S. J., and J. A. Fike. 2011. Characterization of small microsatellite loci isolated in endangered Indiana Bat (*Myotis sodalis*) for use in non-invasive sampling. Conservation Genetics Resources 3:243–245.

Oyler-McCance, S. J., J. St. John, S. E. Taylor, A. D. Apa, and T. W. Quinn. 2005. Population genetics of Gunnison sage-grouse: Implications for management. Journal of Wildlife Management 69:630–637.

Oyler-McCance, S. J., R. S. Cornman, K. L. Jones, and J. A. Fike. 2015. Genomic single-nucleotide polymorphisms confirm that Gunnison and greater sage-grouse are genetically well differentiated and that the bi-state population is distinct. The Condor 117:217–227.

Patterson, R. L.. 1952. The Sage-Grouse in Wyoming. Wyoming Game and Fish Commission Sage Books, Inc., Denver, CO.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Peakall, R., and P. E. Smouse. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research - an update. Bioinformatics 28:2537–2539.

Peterman, W., E. R. Brocato, R. D. Semlitsch, and L. S. Eggert. 2016. Reducing bias in population and landscape genetic inferences: The effects of sampling related individuals and multiple life stages. PeerJ 4:e1813.

Piertney, S. B., and J. Hoglund. 2001. Polymorphic microsatellite DNA markers in Black Grouse (*Tetrao tetrix*). Molecular Ecology Resources 1:303–304.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–59.

Puechmaille, S. J.. 2016. The program STRUCTURE does not reliably recover the correct population structure when sampling is uneven: Subsampling and new estimators alleviate the problem. Molecular Ecology Resources 16:608–627.

Pulliam, H. R.. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652–661.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Raymond, M., and F. Rousset. 1995. GENEPOP (Version 1.2): Population genetics software for exact tests and ecumenicism. The Journal of Heredity 86:248–249.

Reed, D. H.. 2004. Extinction risk in fragmented habitats. Animal Conservation 7:181–191.

Reese, K. ., and J. W. Connelly. 1997. Translocations of sage-grouse *Centrocercus urophasianus* in North America. Wildlife Biology 6:235–241.

Rice, M. B., A. D. Apa, and L. A. Wiechman. 2017. The importance of seasonal resource selection when managing a threatened species: Targeting conservation actions within critical habitat designations for the Gunnison sage-grouse. Wildlife Research 44:407–417.

Rich, T.. 1985. Sage grouse population fluctuations: Evidence for a 10-year cycle. Technical Bulletin 85-1. Idaho State Office, USDI Bureau of Land Management. 28 pp.

Rosenberg, N. A.. 2004. distruct: A program for the graphical display of population structure. Molecular Ecology Notes 4:137–138.

Rousset, F.. 2008. GENEPOP'007: A complete re-implementation of the GENEPOP software for Windows and Linux. Molecular Ecology Resources 8:103–106.

Row, J. R., S. J. Oyler-McCance, J. A. Fike, M. S. O'Donnell, K. E. Doherty, C. L. Aldridge, Z. H. Bowen, and B. C. Fedy. 2015. Landscape characteristics influencing the genetic structure of greater sage-grouse within the stronghold of their range: A holistic modeling approach. Ecology and Evolution 5:1955–1969.

Row, J. R., K. E. Doherty, T. B. Cross, M. K. Schwartz, S. J. Oyler-Mccance, D. E. Naugle, S. T. Knick, and B. C. Fedy. 2018. Quantifying functional connectivity: The role of breeding habitat, abundance, and landscape features on range-wide gene flow in sage-grouse.

Evolutionary Applications 11:1305–1321.

Sala, O. E., F. S. C. Iii, J. J. Armesto, E. Berlow, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, B. Robert, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, D. H. Wall, O. E. Sala, F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. The Condor 106:363–376.

Segelbacher, G., R. J. Paxton, G. Steinbruck, P. Tronteljs, and I. Storch. 2000. Characterization of microsatellites in Capercaillie *Tetrao urogallus* (AVES). Molecular Ecology 9:1934–1935.

Semple, K., R. K. Wayne, and R. M. Gibson. 2001. Microsatellite analysis of female mating behaviour in lek-breeding sage-grouse. Molecular Ecology 10:2043–2048.

Snyder, J. W., E. C. Pelren, and J. A. Crawford. 1999. Translocation histories of prairie grouse in the United States. Wildlife Society Bulletin 27:428–432.

Stephens, A. P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? Oikos 87:185–190.

Stiver, J. R., A. D. Apa, T. E. Remington, and R. M. Gibson. 2008. Polygyny and female breeding failure reduce effective population size in the lekking Gunnison sage-grouse. Biological Conservation 141:742–781.

Sweanor, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulations dynamics, and conservation. Conservation Biology 14:798–808.

Taberlet, P., L. P. Waits, and G. Luikart. 1999. Noninvasive genetic sampling: Look before you leap. Trends in Ecology & Evolution 14:323–327.

Tack, J. D., D. E. Naugle, J. C. Carlson, and P. J. Fargey. 2011. Greater sage-grouse *Centrocercus urophasianus* migration links the USA and Canada: A biological basis for international prairie conservation. Oryx 46:64–68.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336–347.

Taylor, S. E., S. J. Oyler-McCance, and T. W. Quinn. 2003. Isolation and characterization of microsatellite loci in greater sage-grouse (*Centrocercus urophasianus*). Molecular Ecology Notes 3:262–264.

United States Fish and Wildlife Service. 2014. Endangered and Threatened Wildlife and Plants;Threatened Status for Gunnison sage-grouse, 79 Fed. Reg. ss 224 (final rule Nov. 20, 2014) (to be codified at 50 C.F.R. part 17).

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighing technique for capturing sage-grouse. Wildlife Society Bulletin 20:425–426.

Wang, J.. 2017. The computer program structure for assigning individuals to populations: Easy to use but easier to misuse. Molecular Ecology Resources 17:981-990.

Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370.

Whiteley, A. R., S. W. Fitzpatrick, W. C. Funk, and D. A. Tallmon. 2015. Genetic rescue to the rescue. Trends in Ecology & Evolution 30:42–49.

Wiley, R. H.. 1973. Territoriality and non-random mating in sage-grouse, *Centrocercus urophasianus*. Animal Behaviour Monographs 6:85–109.

Wolf, C. M., B. Griffith, and C. Reed. 1996. Avian and mammalian translocations : Update and reanalysis of 1987 survey data. Conservation Biology 10:1142–1154.

Young, J. R., J.W. Hupp, J.W. Bradbury, and C.E. Braun. 1994. Phenotypic divergence of secondary sexual traits among sage-grouse, *Centrocercus urophasianus*, populations. Animal Behaviour 47:1353-1362.

Young, J. R., C. E. Braun, S. J. Oyler-McCance, J. W. Hupp, and T. W. Quinn. 2000. A new species of sage-grouse (Phasianidae: *Centrocercus*) from southwestern Colorado. The Wilson Bulletin 112:445–453.

CHAPTER III. LANDSCAPE GENETIC CONNECTIVITY OF GUNNISON SAGE-GROUSE AT TWO SCALES: RANGE-WIDE AND WITHIN THE LARGEST POPULATION

Summary

Habitat fragmentation and degradation is an ongoing process impacting a species ability to move through the landscape, ultimately resulting in decreased gene flow and increased risk of extinction. Understanding how natural and anthropogenic landscape features impact species movement is essential to making decisions about conservation. The Gunnison sage-grouse is a species of conservation concern with a historically naturally fragmented distribution that persists now as a network of discrete populations with low levels of gene flow. The largest population (~85-90% of remaining birds) occurs in a relatively contiguous patch of native habitat, though several human-created (i.e., agriculture, development) and naturally occurring (i.e., coniferous forests, rugged terrain) features disrupt the landscape. Here, I use a landscape genetics approach to identify the ecological processes underlying connectivity at two scales: among populations and within the largest population among leks. I found that while presence of habitat is important at both scales, connectivity within a population is more a function of habitat structure and quality than presence of sagebrush habitat. My findings also support the previous assumptions that the formation of isolated populations of Gunnison sage-grouse is largely a result of conversion of habitat for anthropogenic use. In addition to providing insight into how the landscape impacts effective dispersal, estimation of the impact different landscape components have on connectivity can be used in conservation planning. Identification of specific impediments or facilitators of gene flow and locating them on the landscape can help identify areas which might be protected for habitat, restored as a potential dispersal route, or considered when making land-use change decisions. For example, if increased connectivity among populations was a desired

outcome, conservation actions may want to include re-establishing sagebrush habitat on the landscape.

Introduction

Alteration of landscape composition can fragment habitat and create population structure. The genetic impact of fragmentation will depend on a species ability to navigate the landscape (Frankham 2003, Epps et al. 2005), which in turn depends on its interactions with a complex environment (Fahrig and Merriam 1985). The degree to which the landscape facilitates or impedes movement among resource patches across a species range is known as connectivity (Taylor et al. 1993). Connectivity (or lack thereof) can impact access to resources through dispersal limitations (Pulliam 1988, Dunning et al. 1992), as well as the biophysical composition of the landscape impeding movement (Henein and Merriam 1990). Reduced connectivity can negatively affect gene flow (Frankham 2003) potentially influencing evolutionary processes such as adaptation, inbreeding, genetic drift (Wiens 2001), and can ultimately increase extinction risk (Burkey 1989, Soule et al. 1992). An understanding of how a species interacts with the landscape can provide insights into which features influence gene flow (Manel et al. 2003, Storfer et al. 2007, Holderegger and Wagner 2008) and can help identify the ecological processes influencing connectivity, aiding in subsequent design of movement corridors, identification of potential habitat reserves, or even predicting impacts of future environmental change on gene flow (Spear et al. 2010). Connectivity has recently become a focus of research for conservationists, ecologists, and biologists given the distribution of many wildlife species are increasingly becoming fragmented.

Landscape genetics is an integrative field that combines population genetics, landscape ecology, and statistics to infer the ways gene flow is affected by the landscape (Manel et al. 2003, Holderegger and Wagner 2006, Storfer et al. 2007). Some of the most popular ways to represent the landscape include the development of resistance surfaces, or raster layers, representing hypothetical relationships between landscape features and gene flow (Spear et al. 2010). Circuit theory is often used as a model for gene flow, which simultaneously integrates all possible pathways connecting populations, and improving gene flow predictions (McRae and Beier 2007), without assuming an organism has complete knowledge of the landscape (McRae et al. 2008). The analogy relates movement to circuit theory using random walk theory, where populations (i.e., nodes) are connected by dispersal (i.e., edges) in a landscape (i.e., graph) and dispersal events between populations are dependent upon the ease with which an individual can disperse along edges (i.e., edge weight) (McRae et al. 2008).

The last decade has seen numerous applications of landscape genetics to wildlife species (e.g., Gerlach and Musolf 2000, Murphy et al. 2010, Garroway et al. 2011, Row et al. 2015), though limitations in many of the most common methods employed have been noted. One of the major critiques of landscape genetics is the lack of estimates of uncertainty in the inferred relationships which make them difficult to incorporate into management or conservation actions (Keller et al. 2015). Another critique is the reliance on expert opinion to parameterize landscape resistance models, which can be unreliable (Koen et al. 2012, Shirk et al. 2015) or overly influential (Koen et al. 2012). Expert opinion is typically based on a measure of dispersal (i.e., telemetry, GPS) which cannot distinguish between exploratory movements versus effective dispersal (Koenig et al. 1996, Bohonak 1999). Furthermore, dispersal and gene flow can be correlated, though in practice it is often not a one-to-one relationship (Bohonak 1999),

suggesting connectivity based on telemetry as opposed to genetic data may ultimately capture entirely different biological processes (Shirk et al. 2015). The use of the Mantel test, one of the most common methods to evaluate relationships between genetic distance and resistance distance (Lichstein 2006, Wagner and Fortin 2012), can result in misleading results with limited power to detect relationships when a lag effect in landscape change and genetic change is strong (Landguth et al. 2010), in addition to difficulties detecting non-linear relationships (Zeller et al. 2016). Extensions of the Mantel test provide some improvements (Legendre et al. 1994, Cushman and Landguth 2010a) but often fail to recover the true model in simulations (Graves et al. 2013, Zeller et al. 2016) leading some to question the use of the method in multi-model inference (Legendre et al. 2015, Wagner and Fortin 2015). Use of linear mixed-models in a model selection framework has provided some improvement over the Mantel test (Row et al. 2015), specifically allowing the development of competing hypotheses (Cushman et al. 2006, Cushman and Landguth 2010a), though the approach still requires multivariable models to be created post-hoc.

Recent advancements in the use of spatially structured ecological networks in landscape genetics has improved the modeling of genetic variation across space (Hanks and Hooten 2013, Hanks et al. 2016, Peterson et al. in revision). One of the recently developed statistical models to evaluate connectivity overcomes many of these hurdles and addresses some of the suggested improvements by modeling circuits explicitly through linking Gaussian Markov random fields and circuit theory with a covariance structure that allows direct estimation of the resistance coefficients (Hanks and Hooten 2013). The model is an improvement because it eliminates use of expert opinion to infer resistance, incorporates estimates of uncertainty for each landscape variable, and provides a statistically supported framework for model selection. To date, this

model has not been widely implemented by the landscape genetics community, likely due to the computational requirements and mathematical complexity. Here I utilize the the Hanks and Hooten (2013) connectivity model to evaluate competing hypotheses of connectivity as measured by gene flow (connectivity hereafter) for a species of conservation concern at two spatial scales.

The Gunnison sage-grouse (*Centrocercus minimus*) is a sagebrush (*Artemisia spp*.) obligate avian species historically inhabiting ~46,500 km^2 of sagebrush habitat in Colorado, Utah, New Mexico, and Arizona (Schroeder et al. 2004). The American West has seen widespread development and land degradation in the twentieth century (Bock and Webb 1984, Braun 1998, Beck and Mitchell 2000, Knick et al. 2003, Holloran 2005) leaving sagebrush (*Artemisia* sp.) communities and the species that depend on them imperiled (Anderson and Inouye 2001). Continued development of land for human use in southwestern Colorado and southeastern Utah has resulted in additional fragmentation, habitat loss, and degradation (Primack 1993, Theobald et al. 1996). Sagebrush habitat is also likely to be negatively impacted by climate change through drought (Karl et al. 2009, Miller et al. 2011) and decreased fire return intervals (United States Fish and Wildlife Service 2014). Land-use changes in sagebrush-steppe communities have occurred within the species range (Oyler-McCance et al. 2001) reducing the species distribution to just 8% of the historical extent (Schroeder et al. 2004, Braun et al. 2014). The species persists as a network of populations with a single, relatively large and stable population in the Gunnison Basin with ~85-90% of the remaining birds, surrounded by six much smaller satellite populations: Poncha Pass to the east, and Cimarron, Crawford, Dove Creek, Piñon Mesa, and San Miguel Basin to the west (United States Fish and Wildlife Service 2014) (Figure 3.1). Although the species has low genetic diversity range-wide (Oyler-McCance et al.

2005, 2015) the Gunnison Basin population has the highest genetic diversity in addition to having the most individuals (Oyler-McCance et al. 2005). Natural migration between populations is low, resulting in significant genetic differentiation (Oyler-McCance et al. 2005).

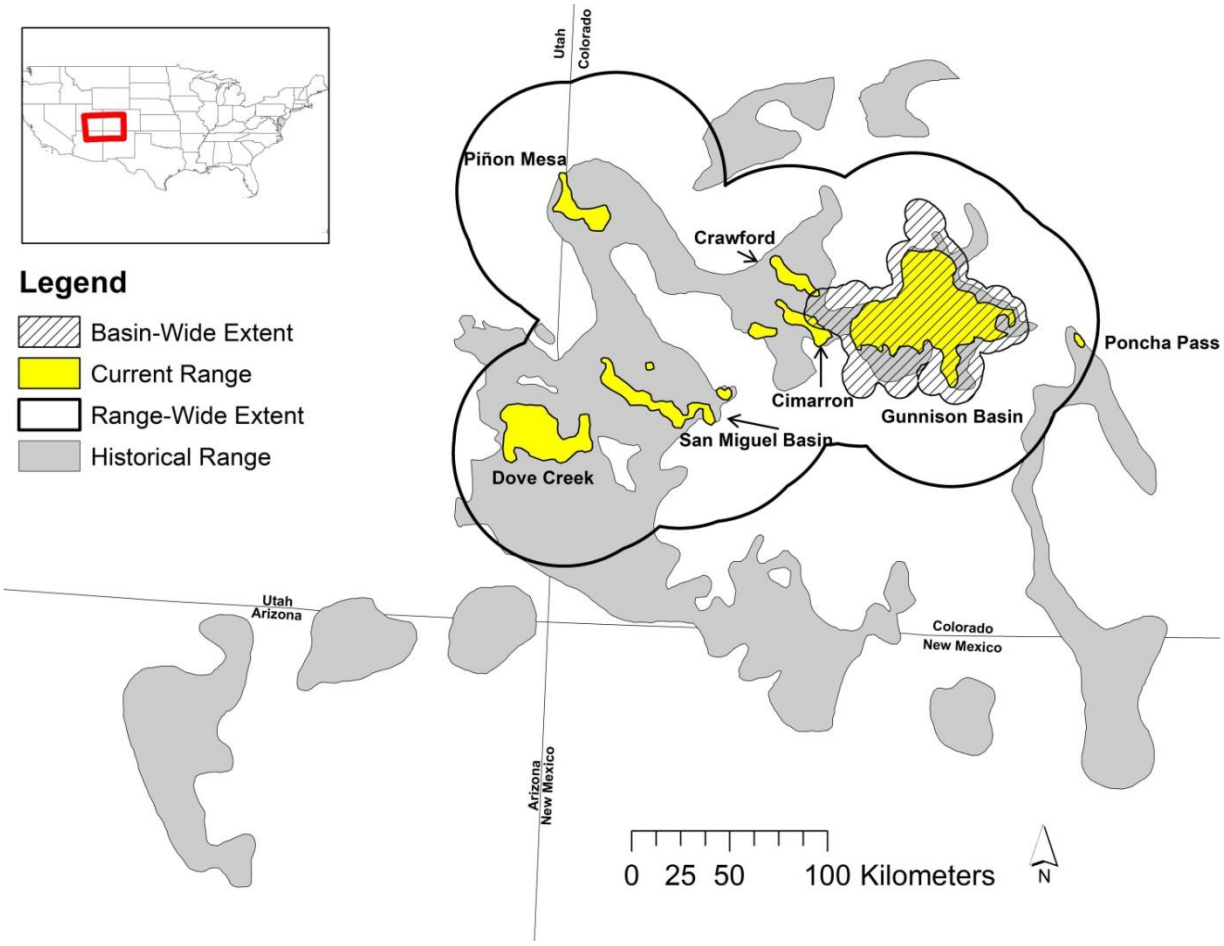

Figure 3. 1- Historical (gray) and current (yellow) distribution of Gunnison sage-grouse in the southwestern United States. Populations are labeled with respective names. Black polygon designates the range-wide study area and the hatched polygon delineates the Gunnison Basin study area. The historical range map is as described by Braun et al. (2014); the two northernmost portions of the historical range correspond to an unknown species of sage-grouse and are not verified by Colorado Parks and Wildlife (Gunnison sage-grouse Rangewide Steering Committee, 2005).

Gunnison sage-grouse has been of conservation concern to local working groups and state management agencies prior to its designation as a distinct species from greater sage-grouse

in 2000 (Young et al. 2000), and was listed as threatened under the federal Endangered Species Act in 2014 (United States Fish and Wildlife Service 2014). Gunnison Basin individuals were translocated to satellite populations by Colorado Parks and Wildlife (CPW) between 2005 and 2014 to augment small populations and to attempt to overcome the genetic consequences of population fragmentation. Modest gains in genetic diversity were observed in two of the satellite populations (Piñon Mesa and Crawford; Chapter 2), which will require continued supplementation from Gunnison Basin to maintain in lieu of creating corridors for connectivity. Though the Gunnison Basin population is considered stable and estimated to support ~4,000 birds (United States Fish and Wildlife Service 2014) across 76 active leks, these leks exist within significant amounts of development and agriculture. The human population within the Gunnison Basin is projected to continue growing (2.3 times by 2050; Colorado Water Conservation Board 2009) and subsequently bring more land development and conversion (Theobald et al. 1996, United States Fish and Wildlife Service 2014).

A great deal of information is available on the way sage-grouse (*Centrocercus* spp.) select habitat, or move through the landscape in the short-term, which can provide some insights into the way in which gene flow might be impacted by the landscape. It is known that sagebrush habitat is important for diet and cover from predators (Patterson 1952, Braun et al. 1977, 2005, Schoenberg 1982, Barnett and Crawford 1994, Sveum et al. 1998), and that high density or close proximity to conifer cover is generally avoided (Hagen et al. 2011, Baruch-Mordo et al. 2013) and can result in lower survival (Severson et al. 2017). The timing of the available resources can also be important to sage-grouse, where high quality forbs and grasses are necessary during brood rearing for a nutritious diet (Barnett and Crawford 1994, Aldridge and Brigham 2002) and concealment (Aldridge and Brigham 2002, Watters et al. 2002, Webb et al. 2012). Sage-grouse

respond negatively to increased density of or proximity to anthropogenic features (Knick et al. 2003, Aldridge et al. 2008, 2012, Tack et al. 2011, Blickley et al. 2012, Copeland et al. 2013), which likely reduces available habitat, and provides more movement corridors or perch sites for predators. The Gunnison sage-grouse populations are located within an inhospitable range of climatic and topographic features, both of which are known to impact habitat use and movement (Aldridge and Boyce 2008, Blomberg et al. 2012, Harju et al. 2013, Knick et al. 2013).

My objectives were to use a landscape genetics approach to investigate the degree to which different components of the landscape facilitate or impede gene flow of the Gunnison sage-grouse in a spatial context. My analysis was conducted at two scales: 1) among leks within the Gunnison Basin, and 2) among populations range-wide. I implemented the Hanks and Hooten (2013) connectivity model in a Bayesian framework to test ecological hypotheses of impacts to connectivity as meausured by gene flow: temperature-moisture regimes, habitat composition and configuration, terrain morphology, anthropogenic change, habitat selection (within the Gunnison Basin only), and phenology. I also wanted to create an overall model of connectivity, incorportating all ecological hypotheses, at both scales. I predicted that areas with high densities of, or close proximity to, anthropogenic features, rough terrain, and low precipitation would negatively impact connectivity, while sites with high percentages of sagebrush cover, low percentages of conifer cover, and more moisture would positively impact connectivity.

Methods

Study Area

My two study areas were delineated using lek location and buffers based on known movement distances for Gunnison sage-grouse. First, I used the Gunnison Basin extent covering ~6,282 km^2 which was previously developed for creating resource selection functions (Aldridge et al. 2012). Connectivity across the Gunnison Basin evaluated connectivity among the leks within native sagebrush-steppe (dominated by big sagebrush, *Artemisia tridentata* ssp.) interrupted by anthropogenic features and variable topography, including the Curecanti National Recreation Area along the western side (Gunnison sage-grouse Rangewide Steering Committee 2005). The Gunnison Basin is a subset of the range-wide extent (Figure 3.1).

For the range-wide analysis, I buffered each active lek by twice the maximum distance a collared bird moved during the resource selection function study (D.J. Saher, unpublished data; 2 x 17.34 km) in addition to the maximum radius covariates were averaged over (20,000 m) to include all potential accessible habitat and account for edge effects during spatial smoothing using moving averaging (see *Spatial Covariates* section below). Range-wide connectivity was based on population comparisons across ~56,818 km^2 of the species range which includes frequent changes in cover type, including anthropogenic features, land conversions, mountains, and natural land cover patches (Gunnison sage-grouse Rangewide Steering Committee 2005).

Genetic Samples

For the range-wide connectivity analysis, I used 254 genetic samples collected from birds captured using spotlight trapping methods (Giesen et al. 1992, Wakkinen et al. 1992) between 1996 and 2004 as part of a previous study (Oyler-McCance et al. 2005) to avoid confounding effects of translocations from the Gunnison Basin to the satellite populations that began in 2005.

Samples were distributed across populations as follows: Cimarron = 4, Crawford = 21, Dove Creek = 43, Gunnison Basin = 116, Piñon Mesa = 19, San Miguel = 51. The Poncha Pass population was excluded because it is believed to have been extirpated in the 1950s and re-established in the 1970s with Gunnison Basin birds, and therefore would not provide biologically meaningful inference on connectivity (Nehring and Apa 2000). For the analysis within the Gunnison Basin, I used a data set composed of 624 unique feathers non-invasively collected basin-wide from 49 of the 70 active leks between 2006 and 2014 in the spring after lekking had ceased for the season. These samples also included mortalities, mark-recapture individuals, and many individuals which were trapped in the Gunnison Basin and transported to a satellite population. Samples were not obtained from leks which had no public access. Some leks yielded no feathers when searched and were, therefore, also not included in the analysis. Sample collection was accomplished in cooperation with state and federal agencies (CPW, Western State College, Bureau of Land Management, U.S. Fish and Wildlife Service, National Park Service, Forest Service, U.S. Geological Survey, Colorado State University, Utah Division of Wildlife Resources). The number of samples collected at a lek ranged from 1 to 57 (See Appendix IV for the number of samples included in the Gunnison Basin data from each lek). Variability in the number of samples collected at each node could result in a large degree of uncertainty in areas that are represented by few samples. However, leks or populations with low sample size were typically leks or populations that support fewer individuals (either population estimates or as estimated by high male lek counts), and therefore fewer samples may be needed to accurately capture genetic diversity. The majority (92%) of the Gunnison Basin samples were collected between 2011 and 2014.

Samples were genotyped with 22 microsatellite loci, using the Polymerase Chain Reaction (PCR) with components and concentrations as described in Oyler-McCance and Fike (2011) and thermal profiles as originally published. Microsatellite primers used included: MSP11, MSP18, reSGCA5, reSGCA11, SG21, SG23, SG24, SG28, SG29, SG30, SG31, SG33, SG36, SG38, SG39, SGCTAT1, SGMS06.4, SGMS06.8, TTT3, TUT3, TUT4, and WYBG6 (Segelbacher et al. 2000, Piertney and Höglund 2001, Caizergues et al. 2003, Taylor et al. 2003, Oyler-McCance and St. John 2010, Fike et al. 2015). A sexing locus (Kahn et al. 1998) was used to evaluate sex-ratio of samples in each data set. Duplicate non-invasive samples (Gunnison Basin only) were identified using a combination of the R package 'allelematch' (Galpern et al. 2015) and the stand-alone program Dropout (McKelvey and Schwartz 2005) and removed. See Chapter 2 for details on DNA extraction, microsatellite characterization, and duplicate sample elimination. I calculated a pairwise genetic distance matrix for individuals using GenAlEx (Peakall and Smouse 2006, 2012; sum of the individual based allelic differences across all loci) range-wide and for the Gunnison Basin data for use in our connectivity analyses. Individuals sampled within the same population (range-wide analysis) or from the same lek (Gunnison Basin analysis) were treated as repeated samples at a location in my connectivity analyses.

Spatial Covariates

I reviewed existing literature for both greater (*C. urophasianus*) and Gunnison sage-grouse, to identify spatial covariates that might impact the ability of a Gunnison sage-grouse to navigate the landscape. I considered an impact anything that affects dispersal, resource selection, survival, fecundity, occupancy, avoidance, or behavior. The landscape components identified include the following: habitat structure and sagebrush cover (Oyler-McCance et al. 2001,

Aldridge and Boyce 2007, Aldridge et al. 2008, 2012, Doherty et al. 2010, Baruch-Mordo et al. 2013, Harju et al. 2013, Knick et al. 2013, Rice et al. 2017), conifer cover (Commons et al. 1999, Hagen et al. 2011, Baruch-Mordo et al. 2013, Knick et al. 2013, Severson et al. 2017), conifer configuration (a measure of conifer cover aggregation; Baruch-Mordo et al. 2013), normalized difference vegetation index (NDVI; here I used the green-up, brown-down, green-up rate, brown-down rate, and season length variables derived from NDVI using Talbert et al. 2013; Aldridge and Boyce 2007, Aldridge et al. 2012), soil wetness as indicated by compound topographic index (CTI; Aldridge and Boyce 2007, Carpenter et al. 2010), seasonal habitat models for Gunnison sage-grouse (Aldridge et al. 2012, Aldridge et al. unpublished data), agricultural cover (Beck and Maxfield 2003, Aldridge et al. 2008, Bush et al. 2011, Knick et al. 2013), development cover (Aldridge et al. 2012, Knick et al. 2013, Rice et al. 2017), distance to development (Aldridge and Boyce 2007, Aldridge et al. 2012), human population density (Aldridge et al. 2008), distance to human population density (Aldridge and Boyce 2007, Aldridge et al. 2008), road density (Aldridge and Boyce 2007, Aldridge et al. 2012, Knick et al. 2013), distance to roads (Aldridge et al. 2012, Rice et al. 2017), oil and gas well density (Aldridge and Boyce 2007, Tack et al. 2011, Blickley et al. 2012, Copeland et al. 2013, Smith et al. 2014, Green et al. 2017), distance to gas wells (Aldridge and Boyce 2007, Tack et al. 2011, Blickley et al. 2012, Copeland et al. 2013), slope (Harju et al. 2013, Knick et al. 2013), topographic roughness as indicated by the terrain ruggedness index (TRI; Harju et al. 2013, Knick et al. 2013), annual rainfall (Blomberg et al. 2012), mean max temperature (Blomberg et al. 2012), growing degree days (Aldridge and Boyce 2008), and a dryness index (Aldridge and Boyce 2008). I divided these covariates into hypotheses based on ecological processes which could drive gene flow: temperature-moisture regimes, habitat composition and configuration,

terrain morphology, anthropogenic change, habitat selection, and phenology (see Table 3.1 for spatial variables included in each hypothesis). Wind energy infrastructure can also impact movement and survival of sage-grouse (LeBeau et al. 2013, Lebeau et al. 2017), however there currently are no major existing wind energy developments within the Gunnison sage-grouse range (United States Fish and Wildlife Service 2014). Although all identified landscape components are candidate drivers, the ecological and biological processes which identified them is fundamentally different from gene flow and components that drive habitat selection and effective dispersal may differ (Roffler et al. 2016).

Table 3. 1- Variables and their abbreviations (Abv.) that were used to model connectivity of Gunnison sage-grouse range-wide and within the Gunnison Basin. Top univariable form (Q = quadratic, L = linear) and moving window radius (MW) are included for both extents. Predicted impact (Pred) of each variable on connectivity is also included. See Appendix V for complete details on covariates.

			Gunnison Basin		Range-wide		
Abv.	Variables	Source	MW	Form	MW	Form	Pred
Habitat Composition and Configuration							
AS	Proportion of all sagebrush cover	Landfire	3000	Q	1000	Q	+
BS	Proportion of big sagebrush cover	Landfire	3000	L	1000	L	+
CON	Proportion of conifer cover	Landfire	20000	Q	3000	L	-
LS	Proportion of low sagebrush cover	Landfire	6400	Q	1000	L	+
CC	Conifer configuration	Derived from Landfire	20000	Q	3000	Q	-
PBS	Percentage big sagebrush cover	Sagebrush product (USGS; Xian et al. 2015)	3000	L	1000	L	+
PSB	Percentage all sagebrush cover	Sagebrush product (USGS; Xian et al. 2015)	3000	L	1000	L	+
SBHT	Shrub height	Sagebrush product (USGS; Xian et al. 2015)	3000	L	1000	Q	+
Phenology							
BD	Brown Down	Phenology tool (MODIS; Talbert et al. 2013)	1000	L	1000	L	-
BDR	Brown Down Rate	Phenology tool (MODIS; Talbert et al. 2013)	1000	Q	20000	L	-
GU	Green Up	Phenology tool (MODIS; Talbert et al. 2013)	1000	Q	1000	L	+
GUR	Green-up Rate	Phenology tool (MODIS; Talbert et al. 2013)	3000	Q	20000	Q	+
SL	Season Length	Phenology tool (MODIS; Talbert et al. 2013)	1000	L	1000	L	+
Habitat Selection							
N	Nest habitat RSF	Aldridge et al. (2012)	564	L			+
W	Winter habitat RSF	Aldridge et al. unpublished	564	Q			+
B	Brood habitat RSF	Aldridge et al. unpublished	564	L			+
Temperature-moisture Regimes							
MMT	Mean Maximum Temp.	PRISM	15000	L	1000	L	-
MAR	Mean Annual Rainfall	PRISM	3000	L	20000	L	+
DRI	Dryness Index	Dayment derived	10000	L	3000	Q	-
GDD	Growing Degree Days	Dayment derived	15000	L	1000	L	+
Null							

			Gunnison Basin		Range-wide		
Abv.	Variables	Source	MW	Form	MW	Form	Pred
PAS	Presence/absence of sagebrush cover	Landfire	564	Q	1000	Q	+
Terrain Morphology							
CTI	Compound Topo. Index	USGS	20000	Q	20000	Q	+
S	Slope	DEM derived	20000	L	20000	L	-
TRI	Terrain Ruggedness Index	USGS	6400	L			-
Anthropogenic Change							
DI14	Dist. To Class 1 - 4 Roads	USGS for Aldridge et al. (2012)	564	Q	1000	L	-
DI12	Dist. To Class 1 & 2 Roads	USGS for Aldridge et al. (2012)	564	L	1000	Q	-
DI47	Dist. To Class 4-7 Roads	USGS for Aldridge et al. (2012)	564	L			-
DIA	Dist. To All Roads	USGS for Aldridge et al. (2012)TIGER	564	Q	1000	Q	-
DIB	Dist. To BLM Roads	USGS for Aldridge et al. (2012)	564	L			-
DID	Dist. To Development	NLCD	564	Q	1000	L	-
DIOG	Dist. To Oil & Gas Wells	States of CO & UT	564	L	1000	L	-
DIP	Dist. To Pop. Dens.	LandScan	564	Q	1000	L	-
DOG	Dens. Of Oil & Gas Wells	States of CO & UT			1000	L	-
DAG	Proportion Of Agriculture	NLCD	3000	Q	20000	L	-
DA	Dens. Of All Roads	USGS for Aldridge et al. (2012)/TIGER	20000	Q	10000	L	-
DB	Dens. Of BLM Roads	USGS for Aldridge et al. (2012)	564	Q			-
DD	Dens. Of Development	NLCD	564	Q	20000	L	-
DP	Dens. Of Population	LandScan	1000	Q	1000	L	-
D14	Dens. Of Roads Class 1 - 4	USGS for Aldridge et al. (2012)/TIGER	15000	Q	1000	L	-
D12	Dens. Of Roads Class 1 & 2	USGS for Aldridge et al. (2012)/TIGER	3000	L	1000	L	-
D2	Dens. Of Roads Class 2	TIGER			1000	L	-
D47	Dens. Of Roads Class 4 - 7	USGS for Aldridge et al. (2012)	564	Q			-
DLD	Dens. Of Light Duty Roads	USGS digitized from USFS, TIGER, & BLM			10000	Q	-

Sage-grouse respond to different landscape components and characteristics in different ways and at different scales (Wiens 1989, Wiens and Milne 1989, Aldridge et al. 2012), thus I performed spatial smoothing using moving averaging in a circular moving window for all variables with radii of 564 m, 1 km, 3 km, 6.4 km, 10 km, 15 km, and 20 km. In a spatial circular moving window analysis each pixel of the resulting raster is the average value within a cicular window with a center at a given pixel and with a specified radius. Evaluated radii had some support in the sage-grouse literature up to 6.4 km. Additional radii were included in attempt to capture the appropriate scale of connectivity because I was uncertain of the maximum scale that might influence connectivity processes. I resampled (decreased pixel size) all spatial layers using a bilear interpolation after calculating moving window averages to 600-m grain size for the Gunnison Basin analyses due to computational limitations. For the range-wide analysis all variables were resampled to 1-km grain size after application of the moving window average for computational efficiency and because I was interested in broad scale patterns. All spatial data processing was performed in ArcMap 10.1 (ESRI). For details on how covariates vary by study area extent and population, and a complete accounting for the spatial data processing see Appendix V. The range-wide model also differed from the basin-wide model in the unit which represents a node; instead of a lek representing a node, the range-wide analysis uses population centers as nodes because range-wide sample location information is limited to the population where the sample was collected. Multiple samples collected within a population or at a lek were treated as repeated samples at a node and the analysis was based on individual genetic distances.

Model Fitting

I implemented a model based on circuit theory to induce resistance developed by Hanks and Hooten (2013) in a Bayesian framework. Our model was as follows:

$$-\mathbf{D} \sim GW(1, 2\boldsymbol{\Psi})$$

$$\alpha_{ij} = \begin{cases} exp\left[\frac{1}{d_{ij}}\left(\frac{\mathbf{x}_i + \mathbf{x}_j}{2}\right)\boldsymbol{\beta}\right] & j \in \mathcal{N}(i) \\ 0 & j \notin \mathcal{N}(i) \end{cases}$$

$$\boldsymbol{\beta} \sim N(\boldsymbol{\mu}_{\boldsymbol{\beta}}, \Sigma_{\boldsymbol{\beta}})$$

$$\log(\tau) \sim N(0,1)$$

where **D** is the genetic distance matrix for individuals, **Ψ** is the covariance matrix of the observed nodes accounting for variability in repeated measures at a node. The graph structure of the populations/leks (nodes) connected by dispersal/gene flow (edges) can be used to define the correlation structure of the measured genetic distances (**D**) between nodes, which is represented by **Σ.** The covariance matrix **Σ** is obtained by calcualting edge weights (α_{ij}) for each pair of nodes for a spatial covariate (i.e., raster layer) for the whole grid, and then finding the inverse to account for the influence of intervening nodes on the correlation structure. In the calcualation of each $\alpha_{ij,}$ i and j are locations of two nodes, $\mathbf{x}_i$ is the vector of values of all spatial covariates at location i, $\mathbf{x}_j$ is the vector of values of all spatial covariates at location j, and d_{ij} is the distance between location i and j. The edge weights (α_{ij}) are the conductances between locations (nodes) and are proportional to the transition rate from one location (i) to another (j). The exponential link function ensures coefficients less than zero are interpreted as increased resistance with an increase in the landscape feature, and coefficients greater than zero decrease in resistance with an increase in the landscape feature. The covariance matrix of the observed nodes **Ψ** is calculated as $\mathbf{K\Sigma K}^{\mathrm{T}} + \tau\mathbf{I}$, where **K** is a matrix relating each sample to the location where it was sampled (nodes), **I** is the identity matrix, and τ is a spatial nugget parameter representing the variability in repeated observations (individual birds) obtained from the same location (node in the graph). The

transformation of $\boldsymbol{\Sigma}$ into $\boldsymbol{\Psi}$ is necessary to incorporate variability in multiple samples at a single population or lek. I used the generalized Wishart probability density function and as well as functions to relate sample locations to raster grids and calculate covariance structure in the 'rwc' R package developed by Hanks (2018).

Model fitting for both extents was performed with the same three steps. First, I fit univariable models for each covariate, at each moving window extent, as both a linear and quadratic relationship. Each covariate was optimized for moving window extent and form with model comparison using the deviance information criterion (DIC; Spiegelhalter et al. 2002). Each model fit included two independent chains and 50,000 Markov chain Monte Carlo (MCMC) iterations (the first 5,000 discarded as a burn-in period) to check consistency of results across chains, in a random walk Metropolis-Hastings sampler. Convergence of independent chains was evaluated through visual inspection of trace and density plots and formally with calculation of the Gelman-Rubin diagnostic (Gelman and Rubin 1992). A simulation based evaluation of my model to identify univariable covariate form and multivariable models is included in Appendix VI. All model fitting was accomplished in R.

Second, multivariable models representing each category (anthropogenic change, moisture-temperature regimes, phenology, habitat composition and configuration, terrain morphology, habitat selection) were created in all possible combinations of the top ranked form of each uncorrelated covariate (Pearson's $r < |0.70|$). I determined the top model for each category through DIC rank. As in step 1, each model fit included two independent chains and 50,000 MCMC iterations (the first 5,000 discarded as a burn-in period) to check consistency of results in a random walk Metropolis-Hastings sampler. Convergence of independent chains was evaluated through visual inspection of trace and density plots and formally with calculation of

the Gelman-Rubin diagnostic. I also compared the top univariable models in each category to the top multivariable model using DIC. If the top univariable model ranked higher than the top multivariable model for each hypothesis, the univariable model was considered the top multivariable model.

Third, all top multivariable hypothesis models were combined in all combinations to describe connectivity across the landscape as facilitated or impeded by landscape components overall. When a multivariable hypothesis was included in a model, it was represepresented by all covariates identified in the top multivariable model. As in previous steps, we used two independent chains and 50,000 MCMC iterations (the first 5,000 discarded as a burn-in period) to check consistency of results in a random walk Metropolis-Hastings sampler. Convergence was again evaluated through visual inspection of trace and density plots and formally with calculation of the Gelman-Rubin diagnostic. The top model was chosen through DIC rank.

At all stages of model fitting I compared models representing hypotheses to three null models, which were fit as described above: intercept only, isolation by Euclidean distance (Wright 1943), and presence-absence of sagebrush cover.

Results

Genetic data and differentiation

Sex-ratio in each data set was only slightly biased toward males as determined by the sexing locus. The range-wide data set was composed of 58.0% males, 41.3% females, and 0.7% individuals that did not amplify. The Gunnison Basin data set was composed of 59.8% males,

40.2% females, and 1.6% individuals that did not amplify. Pair-wise genetic distance for individuals used in our connectivity analyses in the Gunnison Basin ranged between 3 and 68. Individual pairwise genetic distance across populations ranged between 4 and 71.

Gunnison Basin

Univariable models

Univariable optimization identified variables at different scales, from 564 m to 20 km, and with both a linear and a quadratic relationship (Table 3.1; Appendix VII for complete list). In general, habitat components were important at the 3 km (AS, BS, PSB, PBS, SBHT) to 6.4 km (LS) scale, while the arrangement and cover of conifer forest was important at a larger scale (CON, CC). Phenology metrics showed the best fit at smaller scales, from 1 km (BD, BDR, GU, SL) to 3 km (GUR). In contrast, topography metric models showed the best fit at larger scales, from 6.4 km (TRI) to 20 km (CTI, S). Climate variables generally showed a large-scale relationship with 10 km (DRI) to 15 km (MMT, GDD) being optimal, though mean annual rainfall (MAR) showed the best fit at 3 km. Most anthropogenic variables showed the best fit at smaller scales, with density of two-tracks/trails (DLD), residential roads (D47), and proportion of development (DD) showing a best fit at 564 m, human population density at 1 km (DP), proportion of agriculture (DAG), and density of main roads at 3 km (D12). Larger geographic scales showed the best fit with density of main and residential roads at 15 km (D14) and density of all roads at 20 km (DA).

Multivariable models

Several variables were highly correlated, thus I retained the variable with the lowest univariable DIC for combination into multivariable hypotheses (See Appendix VIII for highly correlated variables and DIC comparisons). Top multivariable models for each category are displayed in Table 3.2 (see Appendix IX for complete list). The habitat composition and configuration model was identified as the top model across the categories and included shrub height (SBHT) and low sagebrush cover (LS) (DIC = -12604.15). In general gene flow was higher when shrubs were relatively tall (β_{SBHT} = 3.60 [2.16 – 5.08]) and the proportion of low sagebrush cover is low (β_{LS} = -1.07 [-4.46 – 2.60]) (Table 3.3; Figure 3.2 & 3.3). The top anthropogenic change model included proportion of development (DD), density of main and residential roads (D14), and density of agriculture (DAG) (DIC = -11715.84). The top temperature-moisture regime model included growing degree day (GDD) and mean annual rainfall (MAR) (DIC = -11539.43). Phenology and terrain morphology did not have a multivariable model which ranked higher than a top univariable model; although some predictive ability was gained by adding more variables to the model, it was not enough to overcome the penalty component within the DIC estimation. All multivariable and top univariable models ranked higher than all three null hypotheses: isolation by distance (DIC = -1.88), presence absence of sagebrush habitat (DIC = -11150.29), and the intercept only model (DIC = -11234.87).

Table 3. 2- Comparison of the models representing hypotheses of landscape components impacting connectivity of the Gunnison sage-grouse within the Gunnison Basin. See Appendix IX for complete list of competing multivariable models. Int = intercept. NH1, NH2, NH3 = null hypotheses. MW = moving window. Form: L= linear, Q=quadratic. k= number of parameters estimated. DIC= deviance information criterion. ΔDIC= difference from the top model.

Hypothesis	Model	k	MW	Form	DIC	ΔDIC
Habitat comp. & Config.	int + SBHT + LS	4			-12604.15	0.00
Anthropogenic Change	int + DD + D14 + DAG	5			-11715.84	888.32
Temp.-moist. Regime	int + GDD + MAR	4			-11539.43	1064.73
Phenology	int + GUR	3	3000	Q	-11465.67	1138.49
Resource Selection	int + N	3			-11450.70	1153.45
Terrain Morphology	int + TRI	3	6400	L	-11272.28	1331.87
NH2: Intercept only	int	2			-11234.90	1369.28
NH3: Presence-Absence	int + PAS	3			-11150.30	1453.87
NH1: Geographic Distance	Euclidean Distance	3			1.88	12606.03

Table 3. 3- Posterior means for parameters with 80% CIs in the top hypothesis of connectivity across the Gunnison Basin. Values were calculated as the 10, 50, & 90% quantiles from a chain of 50,000 values after discarding the first 5,000 values as a burn-in period. τ corresponds to the residual variance unaccounted for by the spatial covariates.

Variable	Mean [80% CI]
intercept	-0.12 [-1.02 – 0.77]
SBHT	3.60 [2.19 – 5.08]
LS	-1.07 [-4.46 – 2.60]
τ	1.46 [1.43 – 1.48]

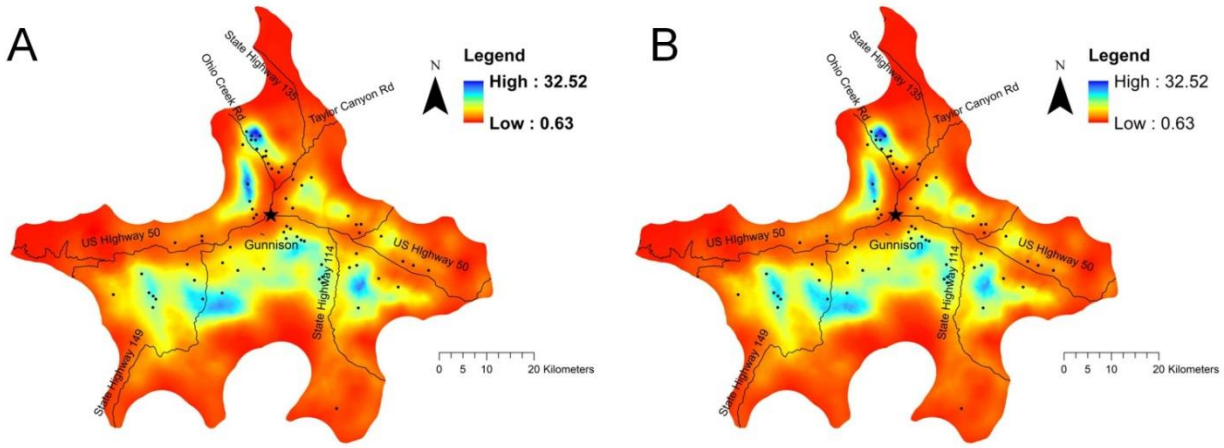

Figure 3. 2- Average conductance (gene flow) across the Gunnison Basin for the top multivariable habitat model (A) and top overall model (B). For reference major roads, the city of Gunnison (★), and active lek locations (•) are included. The habitat model contained shrub height (SBHT) and low sagebrush cover (LS), and the top overall model included shrub height (SBHT), low sagebrush cover (LS), and nesting habitat (N).

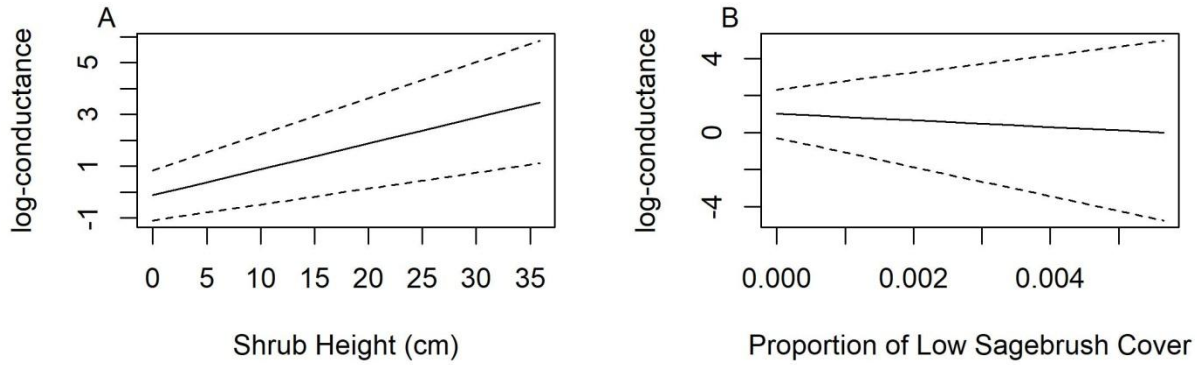

Figure 3. 3- Functional response for each covariate in the top Gunnison Basin multivariable model: (A) shrub height (cm), (B) proportion of low sagebrush cover. The dashed lines correspond to the 80% credible intervals calculated as the 10^{th} and 90^{th} quantiles of the posterior distribution for each variable.

Top multiple hypothesis models

The top multiple hypothesis model included habitat composition and configuration and resource selection variables (DIC = -12642.39) and ranked higher than the top multivariable hypothesis model. All of the top 10 overall multiple hypothesis models included habitat composition and configuration, 5 included resource selection, 5 included temperature-moisture regimes, 4 included phenology, and anthropogenic change variables (Table 3.4; see Appendix X for complete list). Generally, connectivity was high across areas with relatively tall shrub cover (β_{SBHT} = 3.47 [1.97 – 5.08]), low proportion of low sagebrush cover (β_{LS} = -1.00 [-4.38 – 2.82]), and where nesting habitat is high quality (i.e., areas with habitat components selected for during nesting season) (β_{NEST} = 0.22 [-0.52 – 1.00]). The pattern observed in the top multiple hypothesis model largely mimics that of the top multivariable habitat composition and configuration model (Table 3.5; Figure 3.2).

Table 3. 4- Comparison of the top 10 multiple hypothesis models of connectivity for the Gunnison sage-grouse within the Gunnison Basin as determined by DIC rank. See Appendix X for complete list of competing multiple hypothesis models. k= number of parameters estimated. DIC= deviance information criterion. ΔDIC= difference from the top model.

Model	k	DIC	ΔDIC
int + SBHT + LS + N	5	-12642.39	0.00
int + SBHT + LS + GDD + MAR	5	-12627.86	14.53
int + SBHT + LS + GUR + GDD + MAR	6	-12583.42	58.97
int + SBHT + LS + N + GDD + MAR	6	-12576.49	65.90
int + SBHT + LS + GUR	5	-12512.66	129.72
int + SBHT + LS + N + GUR	6	-12510.58	131.80
int + SBHT + LS + N + GUR + GDD + MAR	7	-12484.99	157.40
int + DD + D14 + DAG + SBHT + LS + GDD + MAR	8	-12350.39	292.00
int + DD + D14 + DAG + SBHT + LS + GUR	8	-12278.29	364.10
int + DD + D14 + DAG + SBHT + LS	7	-12273.12	369.27

Table 3. 5- Posterior means for parameters with 80% CIs in the top overall model of connectivity for the Gunnison sage-grouse within the Gunnison Basin. Values were calculated as the 10, 50, & 90% quantiles from a chain of 50,000 values after discarding the first 5,000 values as a burn-in period. τ corresponds to variance in observations obtained from the same location.

Variable	Mean [80% CI]
intercept	-0.08 [-1.03 – 0.81]
SBHT	3.47 [1.97 – 5.08]
LS	-1.00 [-4.38 – 2.82]
N	0.22 [-0.52 – 1.00]
τ	1.46 [1.43 – 1.48]

Range-Wide

Univariable models

Univariable optimization identified variables at all evaluated scales and as a linear or quadratic form (Table 3.1; see Appendix XI for a complete list). Habitat composition and configuration variable scale was either 1 km (LS, BS, AS, PSB, PBS, SBHT) or 3 km (CC, CON). Temperature-moisture regime variables were optimal at either a small scale (DRI = 3 km, GDD, MMT = 1 km) or a broad scale (MAR = 20 km). Similarly, phenology variables were optimal at either a small scale (BD, GU, SL = 1 km) or a large scale (BDR, GUR = 20 km). Topography variables (CTI, S) were optimal only at a broad scale (20 km). Anthropogenic change variables varied in optimal scale. Human population density (PD), density of oil and gas wells (DOG), and density of higher traffic roads (D2, D12, D124) were optimal at the 1 km scale. Density of features likely to cover more area, were optimal at a broader scale: DA (10 km), DLD (10 km), DD (20 km), and DAG (20 km).

Multivariable models

As in the Gunnison Basin models, several variables were highly correlated and the variable with the lowest univariable DIC was retained for combination into multivariable hypotheses (see Appendix VIII for highly correlated variables and DIC comparisons). The top range-wide multivariable models are listed in Table 3.6 (see Appendix XII for a complete list). Similar to the Gunnison Basin, all multivariable models ranked above the null model of isolation by distance (DIC = 1.93). However, distance to anthropogenic features (DIC = -47300.88) ranked below the intercept only null model (DIC = -47344.93), and both temperature-moisture regimes (DIC = -48055.12) and terrain morphology (DIC = -47373.90) ranked below presence-absence of sagebrush cover null model (DIC = -48257.43). Density of anthropogenic variables ranked at the top (DIC = -48476.15) and was composed of the variables density of oil and gas wells (DOG), density of light duty roads (DLD), proportion of agriculture (DAG), and human population density (DP). However, the coefficents indicate small and insiginificant (credible intervals overlapping zero) effects for two included variables variables (β_{DOG} = 0.53 [-0.57 – 1.67], β_{DP} = 0.09 [-4.02 – 4.14]; Table 3.7; Figure 3.5). On average, connectivity was low near cities, along main roads, and high predominantly in the east, across the Gunnison Basin (Figure 3.4A).

Table 3. 6- Comparison of the models representing hypotheses of landscape components impacting connectivity of the Gunnison sage-grouse range-wide. See Appendix XII for complete list of competing multivariable models. Int = intercept. NH1, NH2, NH3 = null hypotheses. MW = moving window. Form: L= linear, Q=quadratic. k= number of parameters estimated. DIC= deviance information criterion. ΔDIC= difference from the top model.

Hypothesis	Model	k	MW	Form	DIC	ΔDIC
Anthropogenic Change	int + DOG + DLD +AG + DP	6			-48476.15	0.00
Phenology	int + BDR	3	20000	L	-48421.41	54.74
Habitat Comp. & Config.	int + AS	3	10000	Q	-48258.84	217.31
NH3: Presence-absence Sagebrush	int + PAS	3			-48257.43	218.72
Temp.-moist. Regime	int + MAR	3	20000	L	-48055.12	421.03
Terrain Morphology	int + CTI	3	20000	Q	-47373.90	1102.25
NH2: Intercept only	int	2			-47344.93	1131.22
Anthropogenic Distance	int + DID + DIA	4			-47300.88	1175.27
NH1: Euclidean Distance		3			1.93	48478.08

Table 3. 7- Posterior means for parameters with 80% CIs in the top hypothesis of range-wide connectivity range-wide. Values were calculated as the 10, 50, & 90% quantiles from a chain of 50,000 values after discarding the first 5,000 values as a burn-in period. τ corresponds to variance in observations obtained from the same location.

Variable	Mean [80% CI]
intercept	0.73 [0.06 – 1.37]
DOG	0.53 [-0.57 – 1.67]
DLD	-1.79 [-4.88 – 1.32]
DAG	1.56 [-0.43 – 3.89]
DP	0.09 [-4.02 – 4.14]
τ	1.29 [1.24 – 1.33]

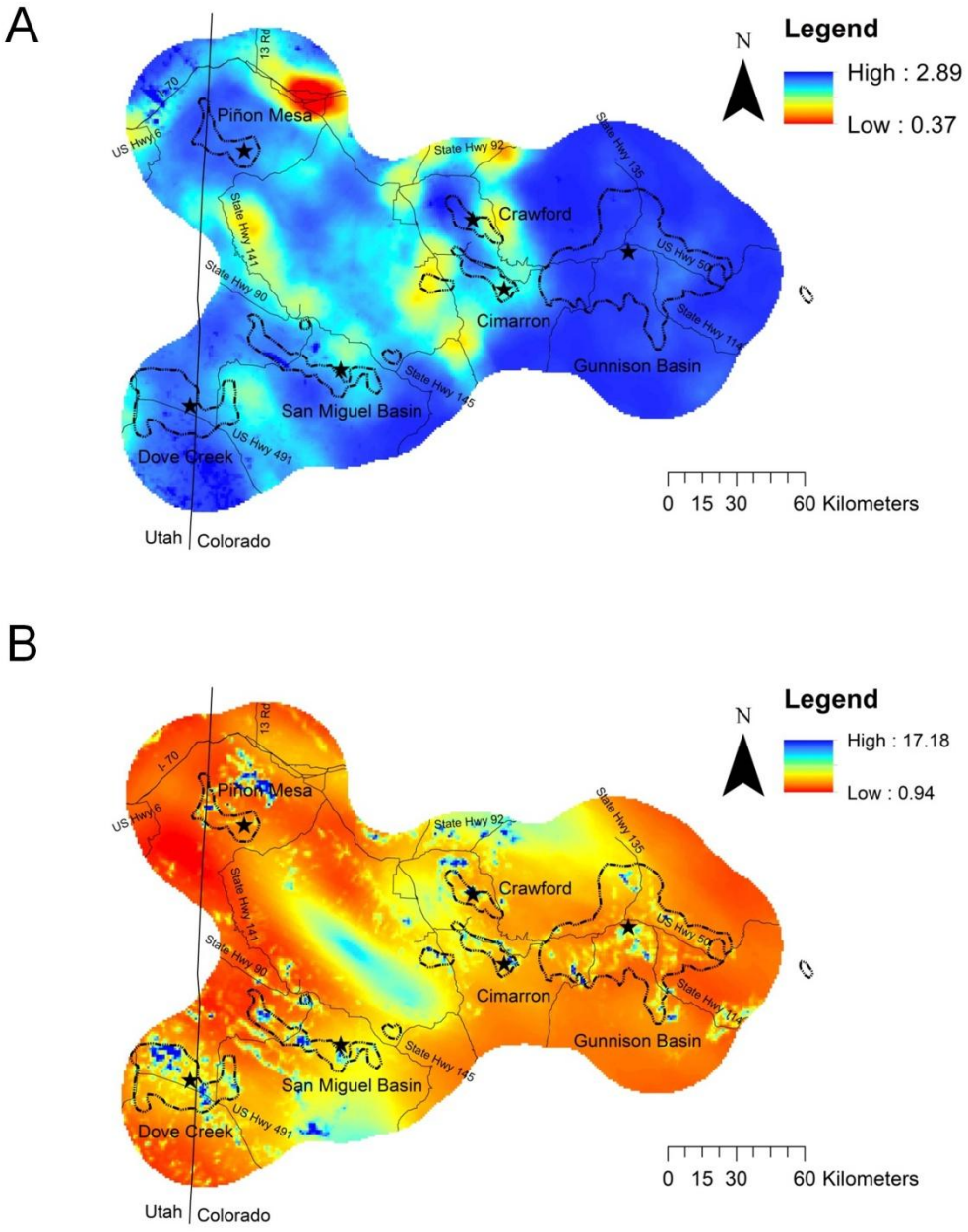

Figure 3. 4- Average conductance (gene flow) across the landscape for the top range-wide multivariable anthropogenic change model (A), and the top overall model (B). For reference major roads, population centers (★), and population boundaries are included. The top multivariable anthropogenic change model includes distance to oil and gas wells (DOG), distance to light duty roads (DLD), proportion of agriculture (AG), and population density (DP). The top overall model includes proportion of sagebrush cover (AS), brown-down rate (BDR), and compound topographic index (CTI). Note the different scales between model A and model B.

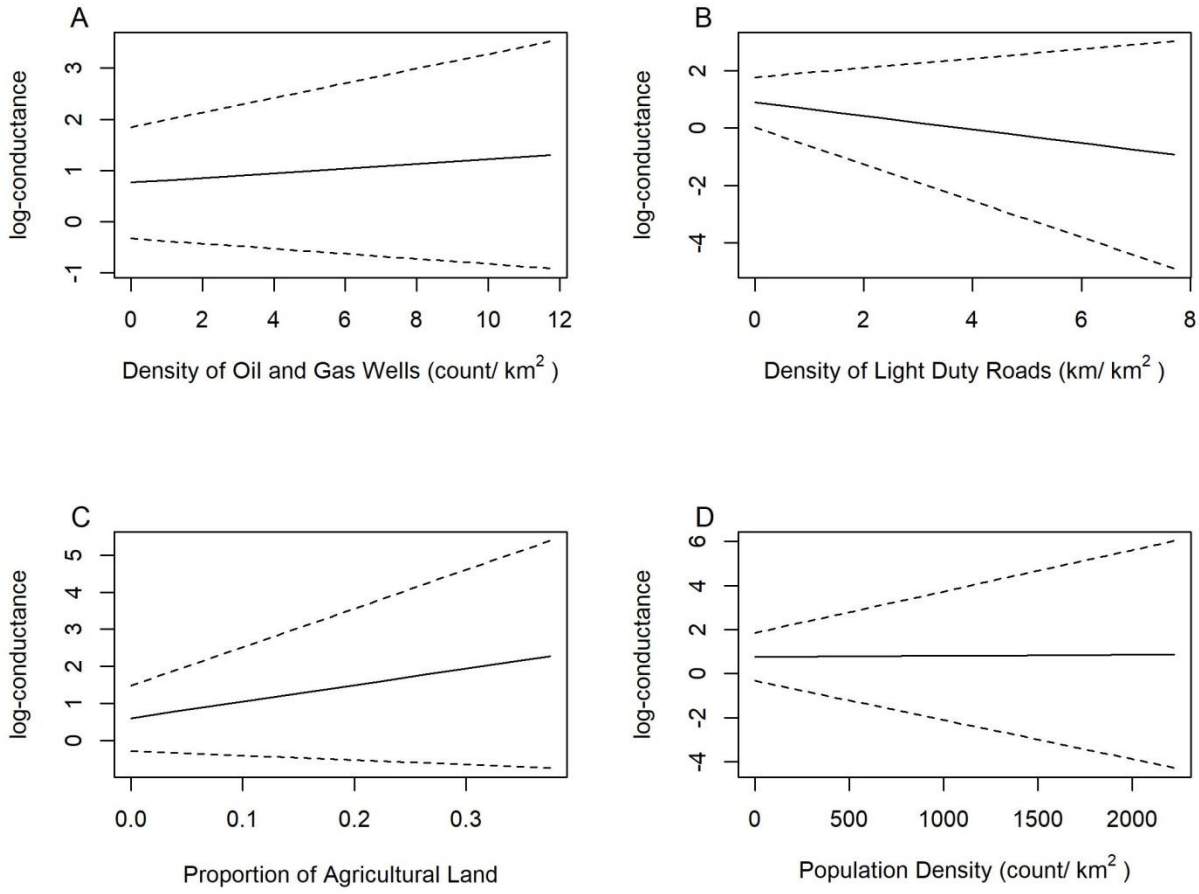

Figure 3. 5- Functional response for each covariate in the top range-wide multivariable anthropogenic change model: (A) density of oil and gas wells, (B) density of light duty roads, (C) proportion of agricultural land, (D) population density. The dashed lines correspond to the 80% credible intervals calculated as the 10^{th} and 90^{th} quantiles of the posterior distribution for each variable.

Multiple hypothesis models

The top multiple hypothesis model included habitat composition and configuration, phenology, and terrain morphology (DIC = -49265.71) and ranks higher than the top multivariable model. Nine of the top 10 models include all sagebrush cover and either BDR or CTI, both of which correspond to presence of habitat and some proxy for vegetation quality

(Table 3.8; see Appendix XIII for complete list). Generally, connectivity was high across areas with a relatively high proportion of sagebrush cover (β_{AS} = 2.45 [-0.54 – 5.84]), higher brown-down rate (i.e., proxy for the rate of vegetative senescence; β_{BDR} = 1.66 [-0.60 – 3.94], and higher CTI (β_{CTI} = 0.94 [-0.44 – 2.45]). The pattern observed in the top multiple hypothesis model shows that connectivity was relatively high between small patches, mostly near population centers and relatively low between populations (Table 3.9; Figure 3.4B).

Table 3. 8- Comparison of the top 10 multiple hypothesis models as determined by DIC rank for overall connectivity of the Gunnison sage-grouse range-wide. See Appendix XIII for complete list of competing models. k= number of parameters estimated. DIC= deviance information criterion. ΔDIC= difference from the top model.

Model	k	DIC	ΔDIC
int + AS + BDR + CTI	5	-49265.71	0.00
int + DIA + DID + AS + BDR + CTI	7	-48799.38	466.34
int + AS + CTI	4	-48727.23	538.48
int + DIA + DID + CTI	5	-48700.89	564.82
int + DAG + DP + DLD + DOG + AS + BDR + CTI	9	-48538.68	727.04
int + DIA + DID + AS + CTI	6	-48341.79	923.92
int + DAG + DP + DLD + DOG + AS + CTI	8	-48309.58	956.13
int + DIA + DID + AS + BDR	6	-48306.38	959.33
int + DIA + DID + AS	5	-48239.13	1026.58
int + AS + BDR	4	-47990.13	1275.58

Table 3. 9- Posterior means for parameters with 80% CI's in the top overall model range-wide connectivity. Values were calculated as the 10, 50, & 90% quantiles from a chain of 50,000 values after discarding the first 5,000 values as a burn-in period. τ corresponds to variance in observations obtained from the same location.

Variable	Mean [80% CI]
intercept	-0.29 [-1.53 – 0.89]
AS	2.45 [-0.54 – 5.84]
BDR	1.66 [-0.60 – 3.94]
CTI	0.94 [-0.44 – 2.45]
τ	1.29 [1.25 – 1.32]

Discussion

The way the landscape interacts with a species behavior and physical movement capabilities to impact ecological processes ultimately dictates the connectivity across that species' range. Drivers of ecological processes can act differently at difference scales (Wiens 1989) and identification of the appropriate scale of impact is crucial to understanding the underlying ecological processes of connectivity (Cushman and Landguth 2010b). Yet few studies have attempted to evaluate how different landscape variables may impact gene flow at different scales (though see Anderson et al. 2010, Murphy et al 2010, Angelone et al 2011, Galpern et al. 2012, Keller et al. 2013). In this study, I used genetic information to evaluate landscape components contributing to landscape resistance among geographically distinct populations and among leks within the largest population of Gunnison sage-grouse. I add to the current understanding of how scale interacts with landscape heterogeneity and gene flow by demonstrating that connectivity as measure by gene flow is impacted by different features at different spatial scales, but also that different ecological processes are underlying connectivity at different spatial scales. For Gunnison sage-grouse, a more complicated interaction of ecological processes appears to underlie connectivity among populations than the ecological processes underlying connectivity among leks within the Gunnison Basin.

Scale of Landscape Features Impact on Connectivity

I found that most habitat, phenology, and most anthropogenic features were best fit at smaller scales (564 m– 6.4 km) while topography and climate were important at larger scales (6.4 km – 20 km) both within the Gunnison Basin and range-wide. Range-wide, however, the top

ecological hypothesis model includes two large scale variables (density of light duty roads 10 km and proportion of agriculture 20 km) and two small scale variables (density of oil and gas wells 1 km and population density 1 km), suggesting connectivity also occurs through hierarchical decision making, similar to previous findings (Aldridge et al. 2012). For connectivity, it appears that hierarchical decision making might play a larger role in interpopulation movements than with interlek movements. Interlek gene flow, in particular, was influenced more by small-scale patterns on the landscape given the top two ecological hypothesis models in the Gunnison Basin (habitat composition and configuration and anthropogenic change) contained variables averaged over a smaller circular radius. Small scale drivers of Gunnison sage-grouse gene flow is contrary to previous studies of greater sage-grouse gene flow (variables in top model averaged at ~17.33 km circular radius; Row et al. 2015) and sage-grouse habitat selection (Doherty et al. 2010, Aldridge et al. 2012, Fedy et al. 2014). Large observed interseasonal movement distances of some greater sage-grouse from studies in relatively contiguous habitat have also been used as evidence to suggest small scale differences in habitat are less likely to impact dispersal at a large spatial scale (Fedy et al. 2012, Taylor et al. 2012). My top range-wide models suggest that long range movements of Gunnison sage-grouse are indeed impacted by small scale habitat differences. While the two species of sage-grouse have many things in common, the distribution of Gunnison sage-grouse has historically been described as naturally patchy, encompassing mountain ranges and deep canyons of decidedly non-habitat regions (Gunnison sage-grouse Rangewide Steering Committee 2005, Braun et al. 2014). Perhaps the naturally patchy habitat of Gunnison sage-grouse has resulted in an effective dispersal behavior that relies on successive short range movements within patches of favorable conditions.

Interaction of Ecological Processes at Different Scales

Range-wide, I found the most support for anthropogenic change as the primary driver of gene flow (top ecological hypothesis DIC = -48476.15), although phenology, habitat composition and configuration, and topography in combination provided the best model fit (top multiple hypothesis model DIC = -49265.71). The fragmentation of Gunnison sage-grouse into isolated populations has previously been attributed to habitat removal and degradation, which is consistent with identifying anthropogenic change as a main driver of gene flow. Specifically, the anthropogenic change model indicates, on average, gene flow increases as density of light duty roads decrease, and oil and gas well density, proportion of agriculture and human population density increased (Table 3.7), although all positive relationships here are relatively weak (Figure 3.5) and two significantly overlap zero suggesting little to no effect on gene flow despite improved model fit (i.e., oil and gas well density and human population density). Roads are generally avoided by many wildlife species (Gerlach and Musolf 2000). High density of light duty roads likely corresponds to reduced natural habitat cover and higher human presence, particularly use of motor vehicles. The positive relationship between agricultural land and gene flow is counterintuitive given that agriculture typically removes sagebrush habitat and some studies have shown that agriculture is negatively associated with habitat selection (Aldridge and Boyce 2007, Walker et al. 2007, Fedy et al. 2014) and gene flow in greater sage-grouse (Row et al. 2018). However, one greater sage-grouse study showed a positive relationship between gene flow and agricultural land (Row et al. 2015), and several studies have shown that sage-grouse may use agricultural fields in some cases (Lupis et al. 2006, Connelly et al. 2011, Knapp et al. 2013). Much of the agricultural land within the Gunnison sage-grouse range is irrigated for crops like alfalfa, and may provide a source of food (Patterson 1952). Individuals may be using

agricultural fields as a more favorable stop-over site to make long-distance dispersal movements, and therefore, perhaps the presence of agricultural land on the landscape acts to facilitate gene flow between populations.

The top multiple hypothesis model describing interpopulation gene flow included relatively strong positive relationships with proportion of sagebrush cover, brown-down rate (the rate at which vegetation senesces from peak physiological activity in a growing season), and CTI (soil moisture retention as a result of microtopography; DIC = -49265.71). Generally, gene flow increased as the proportion of sagebrush on the landscape, CTI, and the brown-down rate increased. Interpopulation effective dispersal appears to require sagebrush habitat, but also appears to include a timing element. The positive relationship between gene flow and the brown-down rate might suggest that locations which senesce more rapidly encourage birds to move on quickly during long-distance movements, while sites with slower rates of senescence might stay productive longer and be more attractive for birds to remain. Even though my top range-wide ecological hypothesis model is not included in the top multiple hypothesis model, both of my top models are still consistent with previous assumptions that connectivity among populations is primarily driven by the presence of sagebrush habitat (positive association with proportion of sagebrush on the landscape in the top multiple hypothesis model, negative association with density of light duty roads in the top ecological hypothesis) but is moderated by additional local processes (positive relationship with CTI and BDR in the top multiple hypothesis model, positive association with proportion of agriculture in the top ecological hypothesis model).

Among leks within the Gunnison Basin, connectivity was best described by habitat composition and configuration (top ecological hypothesis DIC = -12604.15), however a better model fit was obtained by including the nesting habitat RSF covariate (top multiple hypothesis

model DIC = -12642.38). In general, the coefficients for each variable indicate taller shrubs (including sagebrush), less low sagebrush cover, and higher quality nesting habitat result in higher gene flow. However, included in the development of the nesting habitat layer was avoidance of roads and residential areas indicating that these variables impact gene flow as well although they did not improve model fit when included as an additional covariate (Aldridge et al. 2012). Protecting the remaining sagebrush habitat is thought to be essential to the survival of the species (Oyler-McCance et al. 2001). It was somewhat surprising that shrub height and not sagebrush cover was directly indicated as important to gene flow, especially since sagebrush cover was important in greater sage-grouse genetic connectivity (Row et al. 2015). However, sagebrush cover and height are correlated, so increasing amounts of tall sagebrush will likely correspond to increased sagebrush cover. Features that are abundant on the landscape may impact movement or be important to the species but may not directly influence gene flow. For example, in mountain goat (*Oreamnos americanus*) populations in the Cascade mountain range, escape terrain was abundant and essential for the species, but was not important for gene flow (Shirk et al. 2010). The Gunnison Basin has some of the most contiguous sagebrush habitat within the species range (Oyler-McCance et al. 2001). While the shrub-steppe plant community is essential for the species, variables included in the top models suggest that habitat quality and structure is important for interlek movement within a relatively contiguous habitat patch.

Conifer Cover & Gene Flow

Conifer removal has recently been suggested as a method for habitat improvement for sage-grouse (i.e., Doherty et al. 2018), in large part because of the previously identified negative

population level impacts for both greater (Coates et al. 2016, Severson et al. 2017) and Gunnison sage-grouse (Commons et al. 1999, Aldridge et al. 2012, Doherty et al. 2018). However, none of my top models included conifer variables, suggesting presence of conifer is not a main driver of gene flow. In addition, top univariable models for conifer variables showed a relatively flat relationship with gene flow (see Appendix XIV Figure S14.1A-D). While conifer cover has always been part of the naturally fragmented landscape within the Gunnison sage-grouse range, conifer encroachment has contributed to the displacement of sagebrush cover in recent decades (Bukowski and Baker 2013). Productive, early-phase woodland sites, such as those formed by encroachment, may be attractive to sage-grouse despite the potential negative effects on vital rates, and may act as an ecological trap (Coates et al. 2016). Interlek connectivity within the satellite populations was not evaluated here due to data limitations, though may be important to consider given the known hazards of conifer encroachment and known presence of pinyon-juniper woodlands in some satellite populations.

Conservation Applications

Development of conservation planning tools is a goal of many landscape genetic analyses (Keller et al. 2015). The relationships identified in the work presented here, could provide insight into identification of high connectivity areas that might be considered dispersal corridors or areas which have low gene flow that might benefit from some habitat improvement or restoration. For example, in the Gunnison Basin, gene flow according to my top overall model appears to be low around roads and agriculture, but predominantly north of State Highway 50 (Figure 3.2B). While we know higher shrub height corresponds to high gene flow, this appears to be less of a problem

south of State Highway 50. The distribution of areas of reduced gene flow might suggest prioritizing restoration of habitat north of the highway and conservation of the habitat south of the highway. Additionally, predicted changes to the landscape, either from further anthropogenic alteration or from climate change, could be used to evaluate a predicted response in connectivity. For example, this could be accomplished through altering potential future landscapes (e.g., remove development of coniferous forest, or restore habitat), and using simulation techniques to find the predicted change in gene flow based on the estimates of facilitation present in this chapter (see Doherty et al. 2018 and Peterson et al. in review). Similar approaches have been utilized to prioritize habitat for conservation using greater sage-grouse population size instead of genetic change (see Heinrichs et al. 2017).

From a conservation prioritization perspective, it is also important to consider the magnitude of differentiation before making conservation recommendations (Richardson et al. 2016). The pairwise F_{ST} (Weir and Cockerham 1984) among leks (represented by >1 sample) ranged between 0.00 and 0.18, while the values among populations ranged between 0.09 and 0.29, suggesting there are limitations to gene flow both among populations and among leks within the Gunnison Basin (see Appendix XV for all lek and population comparison F_{ST} values). However, differentiation is not necessarily an indicator of risk to the species (Hedrick 1999) and there is no consensus on what level of differentiation would correspond to a conservation concern at present. Given what we know about population size and diversity loss in the satellite populations, the lack of gene flow is undoubtedly problematic range-wide. Within the Gunnison Basin, it is less clear whether the amount of differentiation is significant enough to warrant some action.

The relationships we present between landscape features and gene flow may require additional consideration before used to identify specific locations for management or conservation actions. First, our top range-wide multiple hypothesis model indicates a region with intermittent sagebrush cover, mountain tops, and canyons as having relatively high gene flow potential from Piñon Mesa to San Miguel Basin and Crawford (Figure 3.4B), features that in reality are unlikely to facilitate gene flow. Second, the relatively wide 80% Bayesian credible intervals (CRIs) result in considerable uncertainty about the facilitation of gene flow. When the top relationships are applied to the landscape (range-wide or within the Gunnison Basin), on average there are areas of higher and lower gene flow (Figure 3.6B & 3.7B), though when compared directly to the lower bound (10% CRI; Figure 3.6B & 3.7B) and at the upper bound (90% CRI: Figure 3.6D & 3.7D) it is hard to distinguish between areas of high and low gene flow with much certainty. Our models were fit with relatively short algorithm runs (50,000 MCMC iterations) as a result of time and computing limitations. Longer algorithm runs would likely improve certainty in restistance estimates associated with landscape features. Future analyses could attempt to firther reduce variability by potentially accounting for impacts of lag effects in genetic signal from landscape change (Epps and Keyghobadi 2015), relaxing the assumption of symmetric gene flow (Hanks 2017), or allowing the coefficient to vary across the landscape using splines (Hanks and Hooten 2013). Nevertheless, I provide a first evaluation of the impact of landscape features on connectivity for Gunnison sage-grouse.

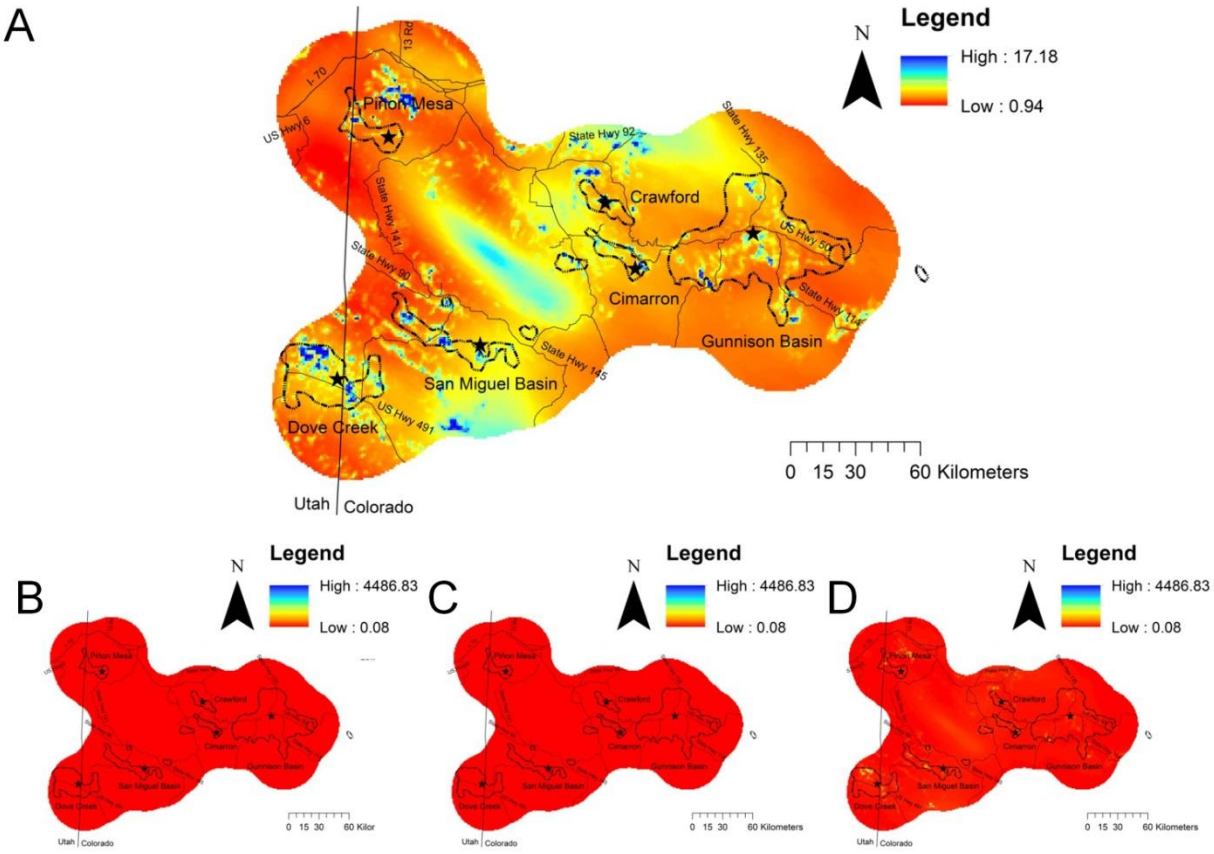

Figure 3. 6- Conductance (gene flow) across the landscape for the top multiple hypothesis range-wide model (A), and the 10% (B), 50% (C), and 90% (D) quantiles shown with a common scale. Top multiple hypothesis model includes proportion of distance to all roads, distance to development, sagebrush cover and brown-down rate. For reference major roads, population centers (★),and population boundaries are included.

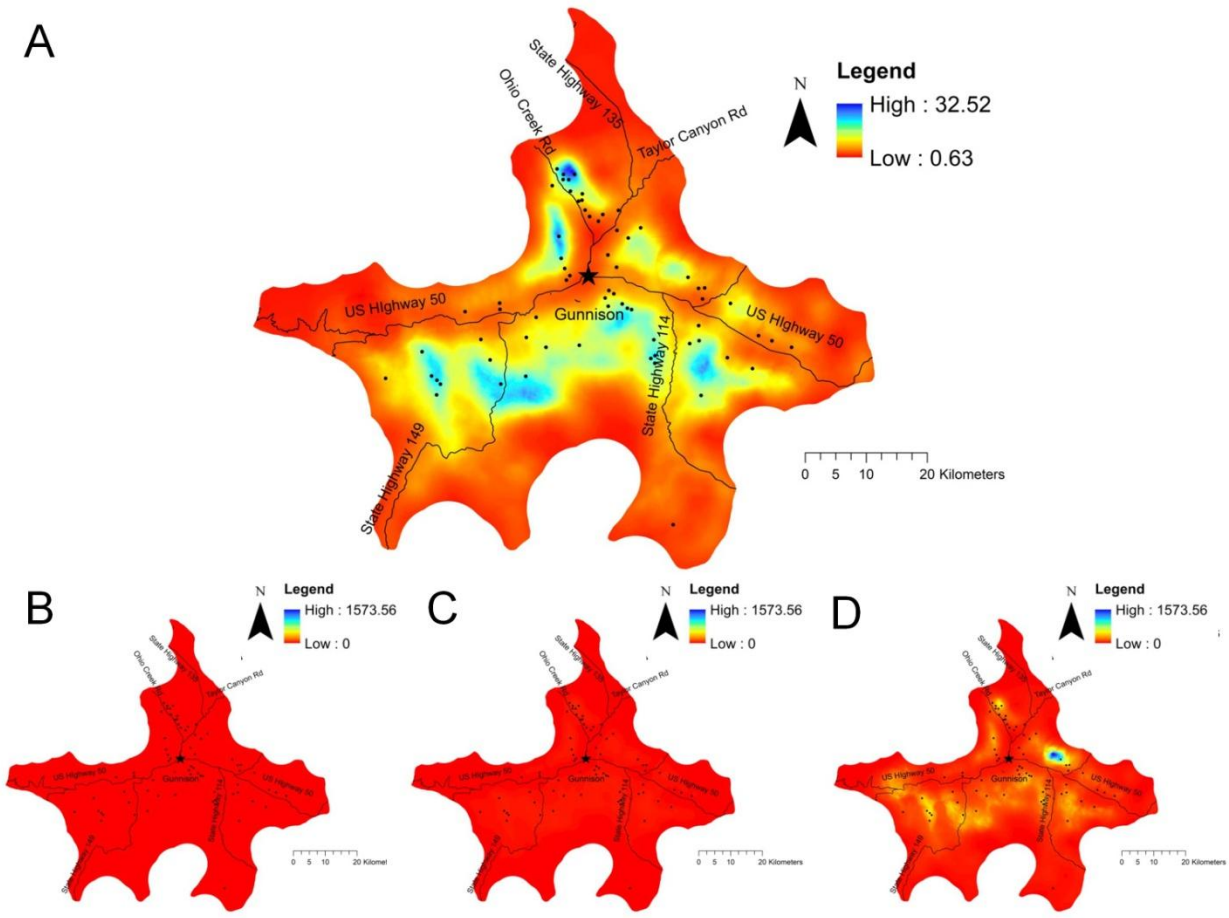

Figure 3. 7- Conductance (gene flow) across the Gunnison Basin for the top multiple hypothesis model (A), and the 10% (B), 50% (C), and 90% (D) quantiles shown with a common scale. Top multiple hypothesis model includes proportion of shrub height, low sagebrush cover, and nesting habitat. For reference major roads, the city of Gunnison (★), and active lek locations (•) are included.

Conclusions

My analyses provide insight into the landscape features and ecological processes that explain Gunnison sage-grouse connectivity as measured by gene flow at two scales: among populations range-wide and among leks within the Gunnison Basin. Contrary to previous studies for greater sage-grouse gene flow and habitat selection, I found that connectivity is impacted by

landscape features at smaller spatial scales. I found that the interaction of ecological processes underlying connectivity at a broad geographic scale (range-wide) were more complex than the processes underlying connectivity at a finer geographic scale (among leks). Importantly, with the landscape genetics approach I implemented, I was able to directly estimate resistance coefficients for landscape components without use of expert opinion, I was also able to obtain an estimate of uncertainty, and formally compare competing hypotheses of ecological processes in a statistical framework which can include multiple variables in a single hypothesis; significant improvements to previous landscape genetic analyses. My findings indicate that, while habitat is important, Gunnison sage-grouse individuals are interacting with the landscape differently at different scales. Among populations the top ecological hypothesis of connectivity included the presence of sagebrush cover, which is in contrast to the findings in Gunnison Basin that included shrub height. While the structure of the habitat (i.e., shrub height) might be important within a population, longer effective dispersal events appear to be governed more by the presence or absence of sagebrush habitat in general. My findings support previous assumptions that land alteration which degrades, and in particular removes, sagebrush cover has contributed to the formation of distinct populations. My findings also provide support for the need to restore sagebrush patches between populations if connectivity is to be increased

LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: Habitat-based approach for endangered greater sage-grouse. Ecological Applications 17:508–26.

Aldridge, C. L., and M. S. Boyce. 2008. Accounting for fitness: Combining survival and selection when assessing wildlife-habitat relationships. Israel Journal of Ecology and Evolution 54:389–419.

Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. Journal of Wildlife Management 66:433–444.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983–994.

Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for Gunnison sage-grouse: A spatially explicit hierarchical approach. Journal of Wildlife Management 76:391–406.

Anderson, C. D., B. K. Epperson, M.-J. Fortin, R. Holderegger, P. M. A. James, M. S. Rosenberg, K. T. Scribner, and S. Spear. 2010. Considering spatial and temporal scale in landscape-genetic studies of gene flow. Molecular Ecology 19:3565–3575.

Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecological Monographs 71:531–556.

Angelone, S., F. Kienast, and R. Holderegger. 2011. Where movement happens: scale-dependent landscape effects on genetic differentiation in the European tree frog. Ecography 34:714–

722.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage-grouse hens in Oregon. Journal of Range Management 47:114–118.

Baruch-Mordo, S., J. S. Evans, J. P. Severson, D. E. Naugle, J. D. Maestas, J. M. Kiesecker, M. J. Falkowski, C. A. Hagen, and K. P. Reese. 2013. Saving sage-grouse from the trees: A proactive solution to reducing a key threat to a candidate species. Biological Conservation 167:233–241.

Beck, J. L., and B. D. Maxfield. 2003. Changes in the distribution and status of sage-grouse in Utah. Western North American Naturalist 63:203–214.

Beck, J. L., and D. L. Mitchell. 2000. Influences of livestock grazing on sage-grouse habitat. Wildlife Society Bulletin 28:993–1002.

Blickley, J. L., D. Blackwood, and G. L. Patricelli. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conservation Biology 26:461–71.

Blomberg, E. J., J. S. Sedinger, M. T. Atamian, and D. V. Nonne. 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. Ecosphere 3:1–20.

Bock, C. E., and B. Webb. 1984. Birds as grazing indicator species in southeastern Arizona. Journal of Wildlife Management 48:1045–1049.

Bohonak, A. J. 1999. Dispersal, gene flow, and population structure. The Quarterly Review of Biology 74:21–45.

Braun, C. E. 1998. Sage-grouse declines in western North America: What are the problems? Proceedings, Western Association of Fish and Wildlife Agencies 78:139–156.

Braun, C. E., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage-grouse habitats. Wildlife Society Bulletin 5:99–106.

Braun, C. E., J. W. Connelly, and M. A. Schroeder. 2005. Seasonal habitat requirements for sage-grouse : Spring , summer, fall, and winter. USDA Forest Service Proceedings RMRS-P-9-38 38–42.

Braun, C. E., S. J. Oyler-McCance, J. A. Nehring, M. L. Commons, J. R. Young, and K. M. Potter. 2014. The historical distribution of Gunnison sage-grouse in Colorado. The Wilson Journal of Ornithology 126:207–217.

Burkey, T. V. 1989. Extinction in nature reserves : The effect of fragmentation and the importance of migration between reserve fragments. Oikos 55:75–81.

Bukowski, B. E., and W. L. Baker. 2013. Historical fire in sagebrush landscapes of the Gunnison sage-grouse range from land-survey records. Journal of Arid Environments 98:1–9.

Bush, K. L., C. K. Dyte, B. J. Moynahan, C. L. Aldridge, H. S. Sauls, A. M. Battazzo, B. L. Walker, K. E. Doherty, J. Tack, J. Carlson, D. Eslinger, J. Nicholson, M. S. Boyce, D. E. Naugle, C. A. Paszkowski, and D. W. Coltman. 2011. Population structure and genetic diversity of greater sage-grouse (*Centrocercus urophasianus*) in fragmented landscapes at the northern edge of their range. Conservation Genetics 12:527–542.

Caizergues, A., O. Rätti, P. Helle, L. Rotelli, L. Ellison, and J. Y. Rasplus. 2003. Population genetic structure of male black grouse (*Tetrao tetrix* L.) in fragmented vs. continuous

landscapes. Molecular Ecology 12:2297–2305.

Carpenter, J., C. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806–1814.

Coates, P. S., B. G. Prochazka, M. A. Ricca, K. Ben Gustafson, P. Ziegler, and M. L. Casazza. 2016. Pinyon and juniper encroachment into sagebrush ecosystems impacts distribution and survival of greater sage-grouse. Rangeland Ecology and Management 70:25–38.

Colorado Water Conservation Board. 2009. 2050 population projections for the state of Colorado municipal and industrial water use projections. Final report prepared for Colorado Water Conservation Board, Appendix B in Colorado's water supply future: State of Colorado 2050 municipal and industrial.

Commons, M. L., R. K. Baydack, and C. E. Braun. 1999. Sage-grouse response to pinyon-juniper management discussion. USDA Forest Service Proceedings RMRS-P-9 97: 238–239.

Connelly, J. W., E. T. Rinkes, and C. E. Braun. 2011. Characteristics of greater sage-grouse habitats: A landscape species at micro- and macro-scales. Pages 69–83 *in* S. T. Knick and J. W. Connelly, editors. Studies in Avian Biology; Greater Sage-grouse: Ecology and Conservation of a Landscape Species and its Habitats. University of California, Berkeley, CA.

Copeland, H. E., A. Pocewicz, D. E. Naugle, T. Griffiths, D. Keinath, J. Evans, and J. Platt. 2013. Measuring the effectiveness of conservation: A novel framework to quantify the benefits of sage-grouse conservation policy and easements in Wyoming. PloS one

8:e67261.

Cushman, S. A, and E. L. Landguth. 2010a. Spurious correlations and inference in landscape genetics. Molecular Ecology 19:3592–602.

Cushman, S. A., and E. L. Landguth. 2010b. Scale dependent inference in landscape genetics. Landscape Ecology 25:967–979.

Cushman, S. A, K. S. McKelvey, J. Hayden, and M. K. Schwartz. 2006. Gene flow in complex landscapes: Testing multiple hypotheses with causal modeling. The American naturalist 168:486–99.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat : The importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

Doherty, K.E., J.D. Hennig, J.B. Dinkins, K.A. Griffin, A.A. Cook, J.D. Maestas, D.E. Naugle, and J.L. Beck. 2018. Understanding biological effectiveness before scaling up range-wide restoration investments for Gunnison sage-grouse. Ecosphere 9(3): e02144.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169–175.

Epps, C. W., and N. Keyghobadi. 2015. Landscape genetics in a changing world: disentangling historical and contemporary influences and inferring change. Molecular Ecology 24:6021–6040.

Epps, C. W., P. J. Palsbøll, J. D. Wehausen, G. K. Roderick, R. R. Ramey, and D. R. McCullough. 2005. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8:1029–1038.

Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology 66:1762–1768.

Fedy, B. C., C. L. Aldridge, K. E. Doherty, M. O'Donnell, J. L. Beck, B. Bedrosian, M. J. Holloran, G. D. Johnson, N. W. Kaczor, C. P. Kirol, C. A. Mandich, D. Marshall, G. McKee, C. Olson, C. C. Swanson, and B. L. Walker. 2012. Interseasonal movements of greater sage-grouse, migratory behavior, and an assessment of the core regions concept in Wyoming. Journal of Wildlife Management 76:1062–1071.

Fedy, B. C., K. E. Doherty, C. L. Aldridge, M. O'Donnell, J. L. Beck, B. Bedrosian, D. Gummer, M. J. Holloran, G. D. Johnson, N. W. Kaczor, C. P. Kirol, C. A. Mandich, D. Marshall, G. Mckee, C. Olson, A. C. Pratt, C. C. Swanson, and B. L. Walker. 2014. Habitat prioritization across large landscapes, multiple seasons, and novel areas: An example using greater sage-grouse in Wyoming. Wildlife Monographs 190:1–39.

Fike, J. A., S. J. Oyler-McCance, S. J. Zimmerman, and T. A. Castoe. 2015. Development of 13 microsatellites for Gunnison sage-grouse (*Centrocercus minimus*) using next-generation shotgun sequencing and their utility in greater sage-grouse (*Centrocercus urophasianus*). Conservation Genetics Resources 7:211–214.

Frankham, R. 2003. Genetics and conservation biology. Comptes Rendus Biologies 326:S22–S29.

Galpern, P., M. Manseau, and P. Wilson. 2012. Grains of connectivity: analysis at multiple spatial scales in landscape genetics. Molecular Ecology 21:3996–4009.

Galpern, P., M. Manseau, P. Hettinga, K. Smith, and P. Wilson. 2015. The allelematch package

for R : Supplementary documentation with tutorials.

Garroway, C. J., J. Bowman, and P. J. Wilson. 2011. Using a genetic network to parameterize a landscape resistance surface for fishers, *Martes pennanti*. Molecular Ecology 20:3978–88.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–511.

Gerlach, G., and K. Musolf. 2000. Fragmentation of landscape as a cause for genetic subdivision in bank voles. Conservation Biology 14:1066–1074.

Gessler, P. E., I. D. Moore, N. J. McKenzie, and P. J. Ryan. 1995. Soil-landscape modelling and spatial prediction of soil attributes. International Journal of Geographical Information Systems 9:421–432.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1992. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Graves, T. A., P. Beier, and J. A. Royle. 2013. Current approaches using genetic distances produce poor estimates of landscape resistance to interindividual dispersal. Molecular Ecology 22:3888–3903.

Green, A. W., C. L. Aldridge, and M. S. O'Donnell. 2017. Investigating impacts of oil and gas development on greater sage-grouse. Journal of Wildlife Management 81:46–57.

Gunnison sage-grouse Rangewide Steering Committee. 2005. Gunnison sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado USA.

Hagen, C. A., M. J. Willis, E. M. Glenn, and R. G. Anthony. 2011. Habitat selection by greater

sage-grouse during winter in southeastern Oregon. Western North American Naturalist 71:529–538.

Hanks, E. M., and M. B. Hooten. 2013. Circuit theory and model-based inference for landscape connectivity. Journal of the American Statistical Association 108:22–33.

Hanks, E. M., M. B. Hooten, S. T. Knick, S. J. Oyler-McCance, J. A. Fike, T. B. Cross, and M. K. Schwartz. 2016. Latent spatial models and sampling design for landscape genetics. The Annals of Applied Statistics 10:1041–1062.

Hanks, E.M. 2017. Modeling spatial covariance using the limiting distribution of spatio-temporal random walks. Journal of the American Statistical Association 112(518): 497-507.

Hanks, E. M. 2018. rwc: random walk covariance models. R package version 1.11. https://CRAN.R-project.org/package=rwc.

Harju, S. M., C. V Olson, M. R. Dzialak, J. P. Mudd, and J. B. Winstead. 2013. A flexible approach for assessing functional landscape connectivity, with application to greater sage-grouse (*Centrocercus urophasianus*). PloS one 8:e82271.

Hedrick, P. W. 1999. Perspective: Highly variable loci and their interpretation in evolutation and conservation. Evolution 53:313–318.

Heinrichs, J. A., C. L. Aldridge, M. S. O'Donnell, and N. H. Schumaker. 2017. Using dynamic population simulations to extend resource selection analyses and prioritize habitats for conservation. Ecological Modelling 359:449–459.

Henein, K., and G. Merriam. 1990. The elements of connectivity where corridor quality is variable. Landscape Ecology 4:157–170.

Holderegger, R., and H. H. Wagner. 2006. A brief guide to landscape genetics. Landscape Ecology 21:793–796.

Holderegger, R., and H. H. Wagner. 2008. Landscape genetics. BioScience 58:199.

Holloran, M. J. 2005. Greater sage-grouse (*Centrocercus urophasianus*) population response to natural gas field development in western Wyoming. Phd Dissertation. University of Wyoming.

Jackson, M., and N. Seward. 2013. Gunnison Basin Gunnison sage-grouse lek count summary and population estimate, Final Report 22 March - 10 May lek season, Gunnison Basin, Colorado. Colorado Parks and Wildlife, Gunnison, Colorado, USA.

Kahn, N. W., J. St. John, and T. W. Quinn. 1998. Chromosome-specific intron size differences in the avian CHD gene provide an efficient method for sex identification in birds. The Auk 115:1074–1078.

Karl, T. R., J. M. Melillo, and T. C. Peterson. 2009. Global climate change impacts in the United States. Cambridge University Press, New York, New York.

Keller, D., R. Holderegger, and M. J. Van Strien. 2013. Spatial scale affects landscape genetic analysis of a wetland grasshopper. Molecular Ecology 33:2467–2482.

Keller, D., R. Holderegger, M. J. van Strien, and J. Bolliger. 2015. How to make landscape genetics beneficial for conservation management? Conservation Genetics 16:503–512.

Knapp, C. N., J. Cochran, F. S. Chapin, G. Kofinas, and N. Sayre. 2013. Putting local knowledge and context to work for Gunnison sage-grouse conservation. Human-Wildlife Interactions 7:195–213.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegan, and C. I. van Riper. 2003. Teetering on the edge of too late? Conservation and research issues for avifauna of sagebrush habitats. The Condor 105:611–634.

Knick, S. T., S. E. Hanser, and K. L. Preston. 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: Implications for population connectivity across their western range, U.S.A. Ecology and Evolution 3:1539–51.

Koen, E. L., J. Bowman, and A. A. Walpole. 2012. The effect of cost surface parameterization on landscape resistance estimates. Molecular Ecology Resources 12:686–96.

Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distance in vertebrates. Trends in Ecology and Evolution 11:514–517.

Landguth, E. L., S. A. Cushman, M. K. Schwartz, K. S. McKelvey, M. Murphy, and G. Luikart. 2010. Quantifying the lag time to detect barriers in landscape genetics. Molecular Ecology 4179–4191.

LeBeau, C. W., J. L. Beck, G. D. Johnson, and M. J. Holloran. 2013. Short-term impacts of wind energy development on greater sage-grouse fitness. Journal of Wildlife Management 78:522–530.

Lebeau, C. W., G. D. Johnson, M. J. Holloran, J. L. Beck, R. M. Nielson, M. E. Kauffman, E. J. Rodemaker, and T. L. McDonald. 2017. Greater sage-grouse habitat selection, survival, and wind energy infrastructure. Journal of Wildlife Management 81:690–711.

Legendre, P., M.-J. Fortin, and D. Borcard. 2015. Should the Mantel test be used in spatial

analysis? Methods in Ecology and Evolution 6(11):1239-1247.

Legendre, P., F.-J. Lapointe, and P. Casgrain. 1994. Modeling brain evolution from behavior : A permutational regression approach. Evolution 48:1487–1499.

Lichstein, J. W. 2006. Multiple regression on distance matrices: A multivariate spatial analysis tool. Plant Ecology 188:117–131.

Lupis, S. G., T. A. Messmer, and T. Black. 2006. Gunnison sage-grouse use of conservation reserve program fields in Utah and response to emergency grazing: A preliminary evaluation. Wildlife Society Bulletin 34:957–962.

Manel, S., M. K. Schwartz, G. Luikart, and P. Taberlet. 2003. Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology and Evolution 18:189–197.

McKelvey, K. S., and M. K. Schwartz. 2005. DROPOUT: A program to identify problem loci and samples for noninvasive genetic samples in a capture-mark-recapture framework. Molecular Ecology Notes 5:716–718.

McRae, B. H., and P. Beier. 2007. Circuit theory predicts gene flow in plant and animal populations. Proceedings of the National Academy of Sciences of the United States of America 104:19885–19890.

McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. . Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145–184 *in*. Greater sage-grouse: Ecology and conservation of a landscape species and its

habitats. Studies in Avian Biology (vol. 38). University of California Press, Berkeley, CA.

Murphy, M. A, J. S. Evans, and A. Storfer. 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. Ecology 91:252–61.

Nehring, J. A., and A. D. Apa. 2000. Gunnison sage-grouse population augmentation to Poncha Pass , Saguache County and Sims Mesa , Montrose County. Colorado Division of Wildlife, Fort Collins, CO, USA.

Oyler-McCance, S. J., K. P. Burnham, and C. E. Braun. 2001. Influence of changes in sagebrush on Gunnison sage-grouse in southwestern Colorado. The Southwestern Naturalist 46:323–331.

Oyler-McCance, S. J., R. S. Cornman, K. L. Jones, and J. A. Fike. 2015. Genomic single-nucleotide polymorphisms confirm that Gunnison and greater sage-grouse are genetically well differentiated and that the Bi-State population is distinct. The Condor 117:217–227.

Oyler-McCance, S. J., and J. A. Fike. 2011. Characterization of small microsatellite loci isolated in endangered Indiana bat (*Myotis sodalis*) for use in non-invasive sampling. Conservation Genetics Resources 3:243–245.

Oyler-McCance, S. J., and J. St. John. 2010. Characterization of small microsatellite loci for use in non-invasive sampling studies of Gunnison sage-grouse (*Centrocercus minimus*). Conservation Genetics Resources 2:17–20.

Oyler-McCance, S. J., J. St John, S. E. Taylor, A. D. Apa, and T. W. Quinn. 2005. Population genetics of Gunnison sage-grouse: Implications for management. Journal of Wildlife Management 69:630–637.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Wyoming Game and Fish Commission Sage Books, Inc., Denver, CO.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Peakall, R., and P. E. Smouse. 2012. GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research - an update. Bioinformatics 28:2537–2539.

Peterson, E.E., E.M. Hanks, M.B. Hooten, J.M. Ver Hoef, and M.-J. Fortin. In Revision. Estimating resistance parameters in spatially structured ecological network models. Methods in Ecology and Evolution.

Piertney, S. B., and J. Höglund. 2001. Polymorphic microsatellite DNA markers in black grouse (*Tetrao tetrix*). Molecular Ecology Resources 1:303–304.

Primack, R. B. 1993. Essentials of Conservation Biology. Sinauer Associates Inc, Sunderland, MA.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652–661.

Rice, M. B., A. D. Apa, and L. A. Wiechman. 2017. The importance of seasonal resource selection when managing a threatened species: Targeting conservation actions within critical habitat designations for the Gunnison sage-grouse. Wildlife Research 44:407–417.

Richardson, J. L., S. P. Brady, I. J. Wang, and S. F. Spear. 2016. Navigating the pitfalls and promise of landscape genetics. Molecular Ecology 25:849–863.

Roffler, G. H., M. K. Schwartz, K. L. Pilgrim, S. L. Talbot, G. K. Sage, L. G. Adams, and G. Luikart. 2016. Identification of landscape features influencing gene flow: How useful are habitat selection models? Evolutionary Applications 9:805–817.

Row, J. R., S. J. Oyler-McCance, J. A. Fike, M. S. O'Donnell, K. E. Doherty, C. L. Aldridge, Z. H. Bowen, and B. C. Fedy. 2015. Landscape characteristics influencing the genetic structure of greater sage-grouse within the stronghold of their range: A holistic modeling approach. Ecology and Evolution 5:1955–1969.

Schoenberg, T. J. 1982. Sage-grouse movements and habitat selection in North Park, Colorado. PhD disseration. Colorado State University.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. The Condor 106:363–376.

Segelbacher, G., R. J. Paxton, G. Steinbruck, P. Tronteljs, and I. Storch. 2000. Characterization of microsatellites in capercaillie *Tetrao urogallus* (AVES). Molecular Ecology 9:1934–1935.

Severson, J. P., C. A. Hagen, J. D. Tack, J. D. Maestas, D. E. Naugle, J. T. Forbes, and K. P. Reese. 2017. Better living through conifer removal : A demographic analysis of sage-grouse vital rates. PloS one 12:e0174347.

Shirk, A. J., M. A. Schroeder, L. A. Robb, and S. A. Cushman. 2015. Empirical validation of landscape resistance models: insights from the greater sage-grouse (*Centrocercus*

urophasianus). Landscape Ecology 30:1837–1850. Springer Netherlands.

Shirk, A. J., D. O. Wallin, S. A. Cushman, C. G. Rice, and K. I. Warheit. 2010. Inferring landscape effects on gene flow: A new model selection framework. Molecular Ecology 19:3603–19.

Smith, K. T., C. P. Kirol, J. L. Beck, and F. C. Blomquist. 2014. Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. Ecosphere 5:1–20.

Soule, M. E., A. C. Alberts, and D. T. Bolger. 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos 63:39–47.

Spear, S. F., N. Balkenhol, M.-J. Fortin, B. H. McRae, and K. Scribner. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular Ecology 19:3576–91.

Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. Journal of the Royal Statistical Society Series B 64:583–639.

Storfer, A., M. A. Murphy, J. S. Evans, C. S. Goldberg, S. Robinson, S. F. Spear, R. Dezzani, E. Delmelle, L. Vierling, and L. P. Waits. 2007. Putting the "landscape" in landscape genetics. Heredity 98:128–42.

Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998. Nesting habitat selection by sage-grouse in south-central Washington. Journal of Range Management 51:265–269.

Tack, J. D., D. E. Naugle, J. C. Carlson, and P. J. Fargey. 2011. Greater sage-grouse *Centrocercus urophasianus* migration links the USA and Canada: A biological basis for

international prairie conservation. Oryx 46:64–68.

Talbert, C., T. Kern, J. Morisette, D. Brown, and K. James. 2013. MODIS phenology image service ArcMap toolbox: U.S. Geological Survey Open-File Report 2013-1250.

Taylor, P. D., L. Fahrig, K. Heinein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. Journal of Wildlife Management 76:336–347.

Taylor, S. E., S. J. Oyler-McCance, and T. W. Quinn. 2003. Isolation and characterization of microsatellite loci in greater sage-grouse (*Centrocercus urophasianus*). Molecular Ecology Notes 3:262–264.

Theobald, D. M., H. Gosnell, and W. E. Riebsame. 1996. Land use and landscape change in the Colorado mountains II: A case study of the East River Valley. Mountain Research and Development 16:407–418.

United States Fish and Wildlife Service. 2014. Endangered and Threatened Wildlife and Plants;Threatened Status for Gunnison sage-grouse, 79 Fed. Reg. ss 224 (final rule Nov. 20, 2014) (to be codified at 50 C.F.R. part 17).

Wagner, H. H., and M.-J. Fortin. 2015. Basics of spatial data analysis: linking landscape and genetic data for landscape genetic studies. Pages 77–98 *in* N. Balkenhol, S. A. Cushman, A. T. Storfer, and L. T. Waits, editors. Landscape Genetics: Concepts, Methods, Applications. John Wiley and Sons, Chichester, UK.

Wagner, H. H., and M. Fortin. 2012. A conceptual framework for the spatial analysis of landscape genetic data. Conservation Genetics 14:253–261.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighing technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. Journal of Wildlife Management 71:2644–2654.

Watters, M. E., T. L. M. C. Lash, C. L. Aldridge, and R. M. Brigham. 2002. The effect of vegetation structure on predation of artificial greater sage-grouse nests. Ecoscience 9:314–319.

Webb, S. L., C. V Olson, M. R. Dzialak, S. M. Harju, J. B. Winstead, and D. Lockman. 2012. Landscape features and weather influence nest survival of a ground-nesting bird of conservation concern, the greater sage-grouse, in human-altered environments. Ecological Processes 1:4.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Wiens, J. A., and B. T. Milne. 1989. Scaling of "landscapes" in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology 3:87–96.

Wiens, J. J. 2001. Widespread loss of sexually selected traits: How the peacock lost its spots. Trends in Ecology and Evolution 16:517–523.

Wright, S. 1943. Isolation by Distance. Genetics 28:114–138.

Xian, G., C. Homer, M. Rigge, H. Shi, and D. Meyer. 2015. Characterization of shrubland

ecosystem components as continuous fields in the northwest United States. Remote Sensing of Environment 168:286–300.

Young, J. R., C. E. Braun, S. J. Oyler-McCance, J. W. Hupp, and T. W. Quinn. 2000. A new species of sage-grouse (Phasianidae: *Centrocercus*) from Southwestern Colorado. The Wilson Bulletin 112:445–453.

Zeller, K. A., T. G. Creech, K. L. Millette, R. S. Crowhurst, R. A. Long, H. H. Wagner, N. Balkenhol, and E. L. Landguth. 2016. Using simulations to evaluate Mantel-based methods for assessing landscape resistance to gene flow. Ecology and Evolution 6:4115–4128.

CHAPTER IV. SIGNATURES OF ADAPTIVE DIVERGENCE AMONG POPULATIONS OF GUNNISON SAGE-GROUSE

Summary

Understanding the genetic underpinning of adaptive divergence among populations is a key goal of evolutionary biology and conservation. Gunnison sage-grouse is a sagebrush obligate species with a restricted range consisting of seven populations, each with distinctly different habitat and climatic conditions. Though geographically close, populations have low levels of natural gene flow resulting in relatively high levels of differentiation. I used 15,033 SNP loci in genomic outlier analyses, genotype-environment association analyses, and gene ontology enrichment tests to examine patterns of putatively adaptive genetic differentiation in Gunnison sage-grouse. I found 191 genes associated with biological functions or pathways that were overrepresented in the assemblage of outlier SNPs. Four of these genes (TBXAS1, CYP2R1, CYP2C23B, CYP4B1) belong to the cytochrome P450 gene family and could impact metabolism of plant secondary metabolites, a critical challenge for sagebrush obligates. Additionally, SNPs in four genes (CYB5R4, DDX60, INPP5E, SETX) had non-synonymous variants predicted to moderately impact gene function. My results suggest adaptive divergence in multiple genes and in multiple metabolic and biochemical pathways, for isolated populations of a single species. In addition to providing insight into adaptive divergence in populations on a small geographic scale, this information can be useful in managing a species of conservation concern, e.g., identify unique populations to conserve, avoid translocation or release of individuals that may swamp locally adapted genetic diversity, or guide habitat restoration efforts.

Introduction

The investigation of adaption in populations and the underlying molecular mechanisms are key topics in ecology, evolutionary biology, and conservation. Groups within a species which can be used to guide management and conservation efforts, termed conservation units (Fraser and Bernatchez 2001), can be identified through characterization of adaptive divergence. For example, knowledge of adaptive variants in a population could determine which populations can serve as source and recipient for augmentation efforts (Sampson and Byrne 2016). Additionally, adaptive variation could inform whether augmentation should be done at all (Benedict et al. 2003), guide development of captive breeding programs (Williams and Hoffman 2009), aid in monitoring and maintaining locally adapted variation in populations, or used to identify evolutionarily significant units (ESUs; Funk et al. 2012). While diversity at putatively neutral genetic markers has long been used to characterize populations, advances in DNA sequencing technology (Mardis 2008, Metzker 2010, Shendure and Ji 2008) and methods to separate neutral and functional genetic variation (Allendorf et al. 2010) have facilitated a shift in focus to understanding the role genetic diversity plays in adaptation to local environments (De Wit and Palumbi 2013, Nielsen 2005, Schweizer et al. 2016, Wenzel and Piertney 2015). Genomic methods can be particularly valuable for characterizing adaptive divergence in species where traditional approaches to evaluate local adaptation (i.e. reciprocal transplant experiments) are not feasible, such as with federally protected species (Funk et al. 2012).

The Gunnison sage-grouse (*Centrocercus minimus*) is a sagebrush (*Artemisia spp*.) obligate avian species persisting as seven isolated populations with low gene flow and high genetic differentiation (Oyler-McCance et al. 2005). A single population supports the majority of the species (~85-90% of ~5,000 individuals) with the remaining birds residing in smaller satellite populations (United States Fish and Wildlife Service 2014). Historically, the species occurred

across ~46,521 km^2 of sagebrush habitat in Colorado, Utah, New Mexico, and Arizona (Schroeder et al. 2004). Land-use change in sagebrush habitat has reduced the species to just 8% of the historical range with birds remaining only in southwestern Colorado and southeastern Utah (Braun et al. 2014, Schroeder et al. 2004). As a sagebrush obligate, the species requires sagebrush cover for habitat during all life-stages (Patterson 1952, Wallestad and Eng 1975), and as a source of forage, with up to 99% of winter diet consisting of sagebrush leaves (Braun et al. 1977, Braun et al. 2005, Young 1994). Differences in local population environmental conditions also exist (Gunnison sage-grouse Rangewide Steering Committee 2005). Each population is centered in a relatively isolated area of the species range and has variable topography and environmental conditions covering a range of average annual precipitation, average annual temperature, and dominant vegetation (Gunnison sage-grouse Rangewide Steering Committee 2005; Table 4.1). Of particular interest to the species and local adaptation are the observed differences in local dominant sagebrush species: Cimarron is dominated by diverse sagebrush cover; Gunnison Basin is dominated by big sagebrush (*Artemisia tridentata* ssp.); Crawford is dominated by big sagebrush and black sagebrush (*A. nova*); Dove Creek has patchy big sagebrush and black sagebrush cover throughout; San Miguel is dominated by low sage (*A. arbuscula*) at low elevations and more contiguous low, black, and big sagebrush cover at higher elevations; Piñon Mesa is dominated by big and silver sagebrush (*A. cana*) at lower elevations and patchy big and silver sagebrush at high elevations.

Table 4. 1- Environmental characteristics of Gunnison sage-grouse populations. Pop. Est. = population estimates from 2005 (United States Fish and Wildlife Service 2014), Dom. Veg. = dominant vegetation cover type (sagebrush = *Artemisia tridentata* sp., oakbrush = *Quercus gambellii*, piñon pine = *Pinus edulis*, low sage = *Artemisia arbuscula*), Elev. = elevation range of population area (m), PPT = average annual precipitation (mm), TMP = average annual

temperature (°C), and to represent the extreme temperatures in each population TMAX = July maximum temperature (°C), TMIN = January minimum temperature (°C), and Ann. TMIN = annual average minimum temperature (°C).

Population	Pop. Est.	Dom. Veg.	Elev. (m)	PPT (mm)	TMP (°C)	TMAX (°C)	TMIN (°C)	Ann. TMIN (°C)
Cimarron	25	sagebrush, oakbrush, agriculture	2133-2743	478.05	5.3	24.32	-11.68	-1.46
Crawford	191	sagebrush, piñon pine, juniper	1549-2749	512.54	12.4	24.72	-10.52	-0.13
Dove Creek	196	sagebrush, agriculture	2011-2468	398.29	9.3	26.49	-9.36	0.96
Gunnison Basin	4763	sagebrush	2180-3100	376.61	3.2	22.32	-15.81	-4.53
Piñon Mesa	167	sagebrush, oakbrush	2438-2749	486.49	4.9	24.90	-10.22	0.18
San Miguel	334	sagebrush, low sage	1920-2164	479.18	8.6	25.49	-10.35	-0.22

Although populations are somewhat close in proximity (33.34 to 203.72 km apart) relative to observed dispersal capabilities (up to 120-240 km for greater sage-grouse in mostly contiguous habitat; Cross et al. 2017, Newton et al. 2017, Tack et al. 2011), genetic differentiation among populations is relatively high (Oyler-McCance et al. 2005), suggesting low levels of homogenizing gene flow which might otherwise limit local adaptation. The male dominant polygynous mating system of sage-grouse skews mating success among males (Wiley 1973, Young et al. 2000), and imposes strong sexual selection which could lead to rapid morphological and/or behavioral changes and further divergence among isolated groups (Ellsworth et al. 1995, Oyler-McCance et al. 2010, Spaulding 2007, Uy and Borgia 2000). The skew in mating success also decreases effective population size (Stiver et al. 2008). This mating skew, along with small population size, indicates genetic drift could overwhelm the the efficacy of selection for local adaptation.

Previous studies have found evidence for significant genetic divergence within some sage-grouse populations. Isolated populations of greater sage-grouse (*C. urophasianus*) are genetically distinct enough at neutral loci to warrant consideration for special protection (Benedict et al. 2003, Oh et al. in review). An evaluation of genetic variation at cytochrome P450 genes and additional candidate genes related to metabolism of PSMs in greater sage-grouse identified evidence for positive selection, potentially pointing to local dietary adaptation (Oh et al. in review). The cytochrome P450 superfamily of genes have broad roles in physiological and toxicological processes (Kubota et al. 2011). Importantly, some of the members of this gene family are involved in metabolism of plant secondary metabolites, or PSMs (Miyazawa et al. 2013), like the monoterpenes, sesquiterpene lactones, and phenolics found in sagebrush species (Kelsey et al. 1982). However, taken together with the relevant environmental variation among Gunnison sage-grouse populations, I became interested in whether there was evidence for adaptive divergence between the populations.

In this study, I examined SNP allele frequencies in six populations along with environmental covariates to address two main research questions about adaptive divergence at the genomic level. First, is there evidence of adaptive divergence among populations of Gunnison sage-grouse? Second, can I link signals of adaptive divergence to putative gene function? Identification of genes or groups or related genes potentially under adaptive divergence can help elucidate critical factors in the ecology of this threatened species, to be validated and elaborated with further targeted study.

Methods

Study System

My study area encompassed the entire species range excluding the eastern most population, Poncha Pass (Figure 4.1). The Poncha Pass population is thought to have been extirpated in the 1950s and re-sestablished with Gunnison Basin individuals beginning in the 1970s, persisting as a result of ongoing translocation (Nehring and Braun 2000). For these reasons, the Poncha Pass population was excluded from my analyses.

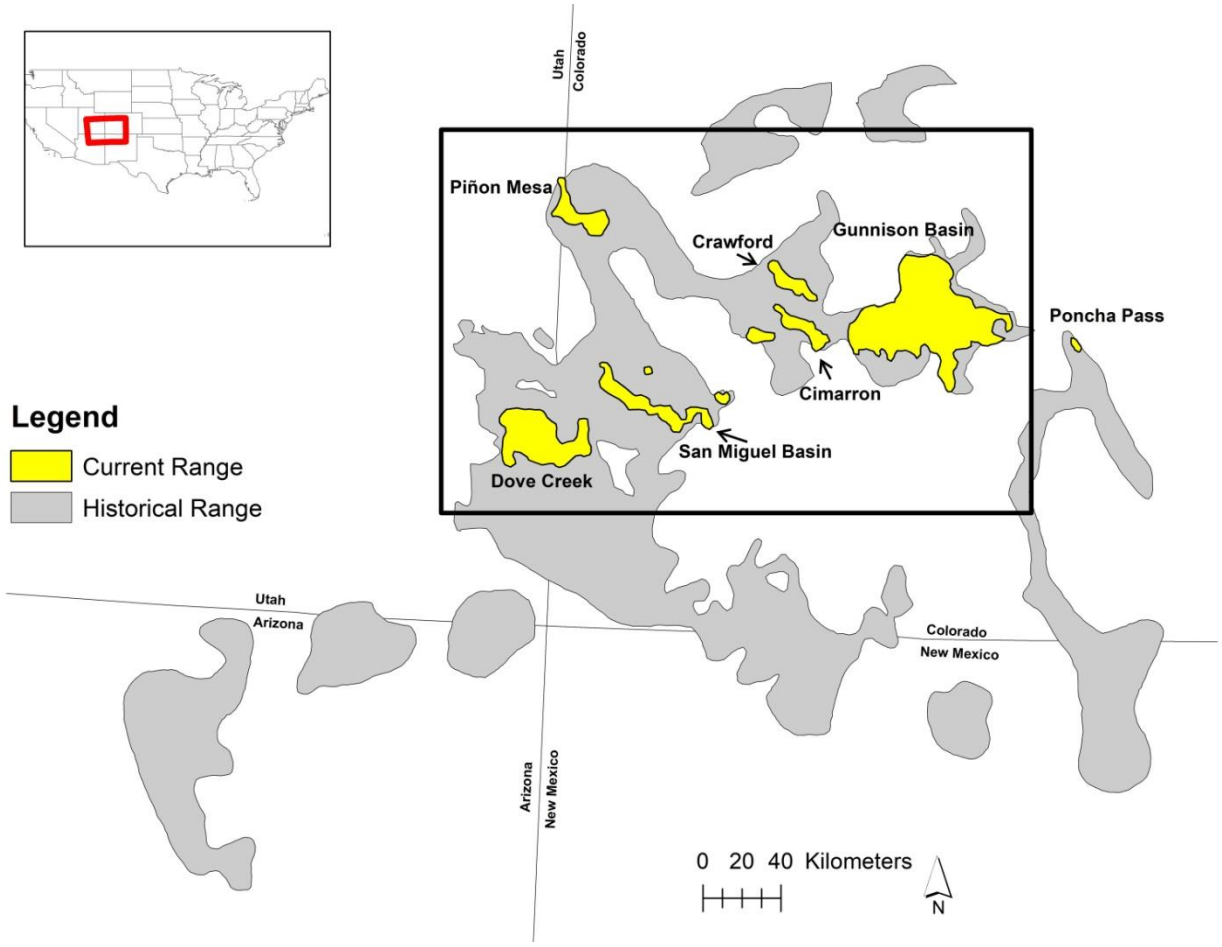

Figure 4. 1- Historical (gray) and current (yellow) distribution of Gunnison sage-grouse in the southwestern United States. Populations labeled with respective names. Black rectangle designates the study area. The historical range map is as described by Braun et al. (2014); the two northernmost portions of the historical range correspond to an unknown species of sage-grouse and are not verified by Colorado Parks and Wildlife (Gunnison sage-grouse Rangewide Steering Committee, 2005).

Genetic Samples

Blood samples were collected from 254 individuals captured using spotlight trapping methods (Giesen et al. 1992, Wakkinen et al. 1992) between 1996 and 2004 as part of a previous study (Oyler-McCance et al. 2005). DNA was extracted using either a phenol-chloroform method (Kahn et al. 1999) or the Genomic Prep Blood DNA Isolation Kit (Amersham Biosciences). From the 254 samples collected, a subset was chosen for reduced representation sequencing based on population of origin and relatedness. The goal was to obtain an equal number of individuals from each population that were minimally related according to Lynch and Ritland (1999) using the 22 microsatellite loci from Chapter 2. The exception to these requirements was the Cimarron population, which only had four samples in total; consequently, all Cimarron samples were included. All other populations had 12 samples included in the library preparation.

Library Preparation

I accomplished SNP identification using an adapted version of the ddRAD protocol as first described by Peterson et al. (2012). The double digestion utilizes two digestion enzymes that cut the DNA at different frequencies. I used Sau3AI (5,000 units ml^{-1}; New England BioLabs, Ipswich, Massachusetts, USA) as my common four cutter and SPEI (10,000 units ml^{-1}; New England BioLabs Ipswich, Massachusetts, USA) as my rare six cutter. The digestion reaction for each sample had a total volume of 20 µl: 2 µl T4 10x DNA ligase buffer (New England BioLabs, Ipswich, Massachusetts, USA), 0.2 µl Bovine Serum Albumin (BSA; New England BioLabs, Ipswich, Massachusetts, USA), 1 µl of each digestion enzyme, 2.8 µl of double-deionized water,

and 13 µl of whole genomic DNA adjusted to a concentration of 77 ng μl^{-1}. The digestion was accomplished by incubating all samples at 37 °C for 2 hours, then increasing the heat to 65 °C for 15 minutes to kill enzymes, and finally cooling the reaction back to 37 °C and holding at temperature. While at 37 °C, 1 µl of 10 µM stocks of P1 and P2 (individually barcoded) restriction site associated adaptors (Integrated DNA Technologies, Coralville, Iowa, USA) were added to each sample and left to equilibrate for 3 minutes to allow adapter dimers to separate. Additionally the P1/P2 adapter included a degenerate base region to identify PCR duplicates in the bioinformatics stage (Schweyen et al. 2014). After the reaction was in equilibrium, 1 µl of T4 ligase (400,000 units ml^{-1}; New England BioLabs, Ipswich, Massachusetts, USA) was added to each sample. For the adapters to ligate to the digested DNA, the temperature was then reduced to 16 °C and held for 30 minutes. The ligase was inactivated by holding the temperature at 65˚C for 20 minutes. The ligation reaction was then diluted with 80 µl of ddH_2O and then cleaned using 65 µl of SPRI beads (Applied Biological Materials inc., Richmond, British Columbia, Canada) to remove adapter dimers present in the reaction. To amplify DNA fragments I performed a 10 µl PCR reaction using 2 µl of cleaned ligation for each sample, 1 µl 10x Buffer (Fisher Scientific, Hampton, New Hampshire, USA), 1 µl dNTPs, 0.2 µl each of the forward and reverse primers, 0.2 µl Amplitag Gold (Fisher Scientific, Hampton, New Hampshire, USA), and 5.4 µl ddH_2O. The thermocycler protocol for the PCR consisted of 22 cycles of the following: 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 30 s. Each sample was amplified with 9 independent replicates, with all PCR replicates for a sample pooled into a single sample in an effort to identify and reduce the effects of PCR error. A 16 µl aliquot of the pooled PCR replicates for each sample were then pooled into a single Eppendorf tube creating a multi-sample pool, which was then cleaned with SPRI beads in a 1:1 ratio to remove PCR dimers and small size amplicons.

I performed a final size selection step using the Pippen Prep (Sage Science, Beverly, Massachusetts, USA) selecting for fragments between 300 and 500 base pairs. The final size selected library was sent to the Genomics and Cell Characterization Core Facility at the University of Oregon in Eugene, Oregon and was sequenced on the Illumina HiSeq 4000 platform (Illumina, San Diego, California, USA).

Sequence Data Processing and Genotyping

Raw sequencing reads were trimmed at a maximum error probability of 0.05 using CLC Genomics v. 9.5 (Qiagen, Hilden, Germany), allowing at most two ambiguous bases. Reads were mapped to a draft genome sequence of Gunnison sage-grouse (Oh et al. in review) with bowtie2 (Langmead and Salzberg 2012) using the "very-sensitive" and "end-to-end" parameter sets, and filtered on a mapping quality of 20 (Phred-scaled) with the samtools/bcftools package, v. 1.3 (Li et al. 2009). Potential PCR duplicates were removed by processing unique molecular identifiers with the UMI-tools package (Smith et al. 2017), using the "unique" identifier detection algorithm.

The samtools/bcftools package was used to merge alignments and identify variant sites in the reference genome. Base composition at sites was computed with the *mpileup* function using the recommended map-quality adjustment ("-C" set to 50) and base-alignment qualities recalculated from the combined data. Indels were called for the purposes of filtering nearby SNP sites (within 3 bp) that could be affected by local misalignment, but were not otherwise used. Genotype likelihoods were estimated with the bcftools *call* function using the multiallelic model, although only biallelic loci were retained. SNP loci were further filtered by requiring a minimum

coverage of 960X across all individuals (based on an average of 15X per sequenced individual) and called genotypes for at least 50 of the total 64 individuals. Loci potentially located on sex chromosomes were removed using both coverage and homology information: SNPs on scaffolds putatively homologous with the sex chromosomes of *Gallus gallus* (Oh et al. in review) were excluded, as were SNPs with unequal coverage in males and females (i.e., if the ratio of male to female mean coverage was outside the range 0.9-1.2). I excluded potentially sex-linked loci because the proportion of each sex sampled in each population was variable and I wanted to reduce the likelihood of false positives for adaptive divergence due to sampling bias at sex-linked loci. Sites with low-frequency minor alleles (below 5%) were also excluded. In addition to filtering variant sites based on these locus-based criteria, individual genotype calls were removed if coverage was less than 10X for an individual at a given location, regardless of whether a genotype was called by bcftools. After excluding four of the 64 sequenced individuals due to low coverage overall, the final data set included 15,033 loci across 35 "pseudo-chromosomes" (chromosome scaffolds inferred from synteny with chicken) for 60 individuals (four Cimarron, 12 Crawford, 12 Dove Creek, 12 Gunnison Basin, 10 Pinon Mesa, and 10 San Miguel). Because sample size in Cimarron is low, the power to detect unique outliers in this population is also low. However, inclusion of the Cimarron samples will still help estimate population structure and identify global outliers.

Genetic Data Analyses

Outlier locus analysis

I identified outlier SNPs using the BayPass core model (Gautier 2015). The core model expands on the approach implemented in BAYENV (Coop et al. 2010, Gunther and Coop 2013) by providing greater computational efficiency, flexibility, and a formal procedure for calculating outlier thresholds. As with BAYENV, this method incorporates a scaled covariance matrix accounting for background population structure that can confound analyses for adaptive variation (Meirmans 2012). The population covariance matrix was directly estimated with the core model, the Inverse-Wishart prior set to 1, and both hyperpriors for β (a_{pi}, b_{pi}) set to 1. Five-thousand MCMC iterations were performed after discarding a 5,000 iteration burn-in and thinning by a factor of 25. Twenty pilot runs of 1,000 MCMC iterations were performed to adjust the parameters in the proposal distribution of the Metropolis-Hastings algorithm so that an acceptance rate between 0.25 and 0.40 was achieved. The adjustment parameter (set to 1.25) was used in the pilot runs to adjust the range of possible values from the proposal distributions if the acceptance rate fell outside the desired window. Inference on the core model was through estimates of the *XtX* statistic. Allele counts were simulated with the *simulate.baypass* R function and the population covariance matrix to generate a pseudo-observed data set from the core model. Outliers were loci with *XtX* values exceeding the 99th quantile of the *XtX* distribution that resulted from the simulated pseudo-observed data set (false discovery rate (FDR) of 0.01). I verified that the scaled covariance matrix of population allele frequencies estimated from the simulated data was close to the matrix estimated from my data (FMD distance = 0.19, see Gautier 2015).

As an independent evaluation of the SNP data and the ability of BayPass to control for population structure, we compared pair-wise F_{ST} (as in Weir and Cockerham 1984) as calculated with the R package 'diveRsity' (Keenan et al. 2013) for the neutral SNPs (the SNP data with all

outliers removed) to values previously obtained using a microsatellite genotype data set created from the whole available sample set. If SNPs showed the same pattern of differentiation as microsatellite loci, I was confident in the ability of the SNP data and BayPass to estimate population structure (Figure 4.2A).

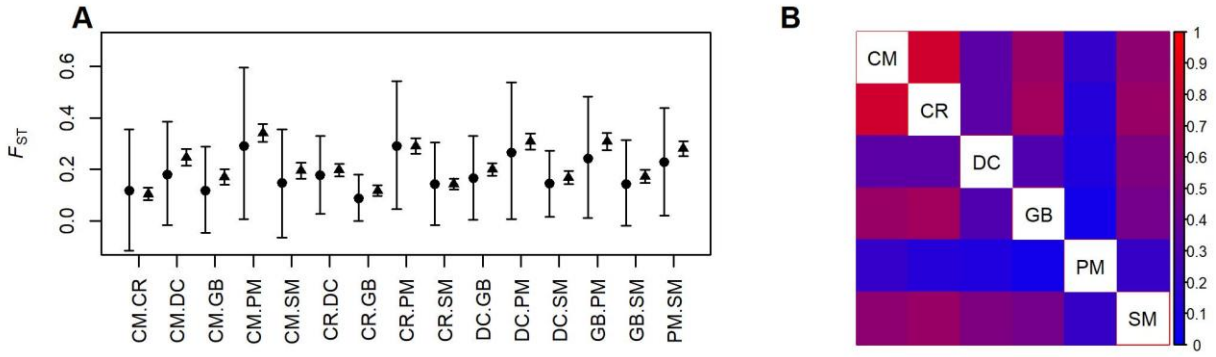

Figure 4. 2- (A) Comparison of F_{ST} values with confidence intervals from microsatellite and SNP loci. Values were estimated as in Weir and Cockerham (1984) for 254 Gunnison sage-grouse individuals and 22 microsatellites (●) and 60 individuals (a subset of the 254) with 11,282 SNP loci (▲). Populations in pair-wise comparisons are abbreviated along the x-axis: CM = Cimarron, CR = Crawford, DC = Dove Creek, GB = Gunnison Basin, PM = Piñon Mesa, SM = San Miguel; CM.CR = F_{ST} between Cimarron and Crawford. Pearson correlation and Spearman rank correlation of F_{ST} from the two marker sets = 0.961 and 0.911 respectively. (B) Heat map for the correlation between populations (low correlation = blue, high correlation = red) derived from the covariance matrix used in the BayPass program to account for demographic structure.

Genotype-environment association analyses

Environmental covariates tested for association with SNPs were selected based on previously documented effects on sage-grouse reported in the literature as well as environmental covariates that varied across the species range. Covariates used in model fits included sagebrush cover (Oyler-McCance et al. 2001, Aldridge et al. 2008, 2012, Doherty et al. 2010, Harju et al. 2013, Knick et al. 2013, Baruch-Mordo et al. 2013), conifer cover and configuration (clustered

versus dispersed trees; Baruch-Mordo et al. 2013, Doherty et al. 2018), dominant shrub type (Oyler-McCance et al. 2001, Aldridge et al. 2008, 2012, Doherty et al. 2010, Harju et al. 2013, Knick et al. 2013, Baruch-Mordo et al. 2013), a dryness index (Aldridge and Boyce 2008), growing degree days (Aldridge and Boyce 2008), seasonal and annual precipitation (Blomberg et al. 2012), seasonal and annual temperature (Blomberg et al. 2012), seasonal and annual humidity, and phenology metrics derived from NDVI (Aldridge et al. 2012). A total of 72 covariates were initially considered (Appendix XVI Table S16.1). I reduced this set to eight minimally correlated (Pearson r <0.7) covariates for my analyses that included spring and fall precipitation, spring maximum temperature, winter vapor pressure deficit (i.e., evapotranspiration), compound topographic index (CTI; a wetness index), green-up rate, big sagebrush cover, and a dryness index (Appendix XVI Table S16.2 and Appendix XVI Figure S16.1). I also used the loadings of the first three principal components (PCs) of the eight minimally correlated variables as a covariate in attempt to incorporate multiple covariates in a single model. The principal component analysis was performed with the *prcomp* function in R (see Appendix XVI for full details on covariates).

I then evaluated correlation of environmental covariates with SNP loci. I incorporated covariates with the auxiliary covariate model in BayPass that uses a binary indicator variable to identify whether each variable is associated with each SNP or not. The model was implemented as in the core model, although including the population covariance matrix estimated with the core model and the addition of regression coefficients which had a uniform prior bounded between -0.3 and 0.3. Covariates with a Bayes Factor (*BF*) greater than the 99th quantile of the *BF* distribution (FDR of 0.01) from the simulated data were considered significantly associated. I also used a redundancy analysis (RDA), based on a combination of multivariate linear regression

and principal components analysis (PCA), which can identify SNPs weakly associated with environmental covariates (Forester et al. 2015). RDA was accomplished with the *rda* function in the 'vegan' package in R (Oksanen et al. 2017). Formal significance tests for which constrained axes should be evaluated for candidate loci were performed with the *anova.cca* function and 999 permutations in the 'vegan' package. Significant (P-value < 0.05) constrained axes were retained for evaluation of candidate SNPs. Loci in the tails of the distribution of the SNP loadings on each axis were considered outliers. To keep false positives low, I used a two-tailed P-value of 0.0027 (based on 3 standard deviations) as a cut off for candidacy.

Linkage disequilibrium and gene ontology enrichment analyses

I estimated linkage disequilibrium (LD) decay to identify candidate loci that were physically linked to a known gene region in the reference genome. First, I phased the SNPs using BEAGLE 5.0, setting N_E to 1,000 to indicate my data were from a small and inbred population as recommended (Browning and Browning 2007). With the phased SNPs, I calculated LD in vcftools (-hap-r2 command) at multiple distances, from SNPs 10 bp to 1Mbp apart. I considered SNPs at the distance where LD as measured by r^2~0.10 to be physically linked.

I then further investigated the relationships between gene products using a gene ontology (GO) enrichment analysis. I used Gowinda v1.12 (Kofler and Schlötterer 2012) to evaluate overrepresentation of GO terms in candidate SNP lists, or lists of loci identified by core or auxiliary covariate models in BayPass and the RDA analysis. Gowinda input includes a list of all the SNPs considered in the outlier analysis, a list of identified candidate loci, a GO association file (FuncAssociate; Berriz et al. 2003), and a draft genome annotation file (Oh et al. in review).

The *P*-value (before FDR adjusted) is calculated as the proportion of simulations with more genes for a category with at least one candidate locus than the whole observed data set. I used the SNP mode (a gene region containing multiple SNPs was counted once for each SNP and assuming complete linkage equilibrium) to test against the GO categories, with 100,000 simulations to generate the null distribution. I also used gene lists derived from Gowinda for all analyses (core, auxiliary, RDA) to evaluate for significantly overrepresented functional annotation terms in DAVID (Database for Annotation, Visualization and Integrated Discovery; Huang et al. 2007) using default parameters. Lastly, I evaluated the potential effect of the candidate SNP variants identified by all tests in gene regions with SnpEff (Cingolani et al. 2012).

To visualize clustering of individuals into potentially adaptively divergent groups, I performed PCA on the candidate SNP loci and SNP loci in identified gene families with the *princomp* function in R and plotted the first three PCs using 'ggplot2' R package (Wickham 2009). For comparison, I also included plots of the first three PCs for analyses on all SNPs and putatively neutral SNPs. Allele frequencies for SNPs in genes of interest were calculated with 'gstudio' R package (Dyer 2014) and plotted with 'ggplot2' to visualize the clustering of similar populations.

Results

Population Genetic Structure Check

Pairwise multilocus F_{ST} as calculated from only putatively neutral SNPs correspond well by rank with previous microsatellite estimates, although the latter had much wider confidence intervals and appear to have consistently lower means (Figure 4.2A). The population covariance

matrix inferred from neutral SNPs also confirms our previous understanding of population structure. I included a heat-plot of the correlation matrix derived from the allele frequency covariance matrix estimated in the BayPass program to illustrate how populations are related (Figure 4.2B).

Genome Scans for Adaptive Divergence and Association with Environmental Variables

The BayPass core model identified 76 outlier loci located on 13 of the 35 pseudo-chromosomes that had SNPs (Table 4.2, Figure 4.3A). The auxiliary model identified significant associations for all covariates included except winter maximum vapor pressure deficit: 754 SNPs on 28 pseudo-chromosomes with spring precipitation, 467 SNPs on 23 pseudo-chromosomes with fall precipitation, 54 SNPs on 18 pseudo-chromosomes with spring maximum temperature, 919 SNPs on 28 pseudo-chromosomes with CTI, 5,544 SNPs on 30 pseudo-chromosomes with green-up rate, 515 SNPs on 24 pseudo-chromosomes with big sagebrush cover, and 1,016 SNPs on 26 pseudo-chromosomes with dryness index (Table 4.2, Figure 4.3B). Similarly, significant relationships were found with the principal components included as covariates: 135 for PC1 (highest loadings: maximum temperature (0.53), big sagebrush cover (0.54), green-up rate (-0.53)), 63 for PC2 (highest loadings: spring precipitation (0.53), winter vapor pressure deficit (0.54) and dryness index (-0.5)), and 284 for PC3 (highest loading: CTI (0.76)). See Appendix XVI Table S16.3 for all covariate loadings onto PCs. RDA identified a total of 615 SNPs as outliers with predictor covariates (highest loading) corresponding to spring precipitation, fall precipitation, and CTI. Overlap of loci identified with each analysis varied though no two analyses identified identical lists (Appendix XVII).

Table 4. 2- Summary of the number of SNPs (# Cand. SNPs) showing signatures of adaptive divergence in different models (Method), the number of chromosomes with candidate SNPs (# Chrome. W/Cand. SNPs) at *FDR* 0.01 and *FDR* 0.001. The number of GO terms associated with each candidate SNP list (# Sig. GO Terms) and number of unique genes associate with GO terms (# Genes Assoc. W/GO Terms) at *FDR* 0.05 and *FDR* 0.01 are included in the last four columns.

Method	# Cand. SNPs		# Chrome. W/Cand. SNPs		# Sig. GO Terms		# Genes Assoc. W/GO Terms	
Variable	*FDR* 0.01	*FDR* 0.001	*FDR* 0.01	*FDR* 0.001	*FDR* 0.05	*FDR* 0.01	*FDR* 0.05	*FDR* 0.01
BayPass								
--	76	3	13	2	51	33	8	2
PC1	135	8	19	5	24	5	5	3
PC2	63	10	12	4	13	1	2	1
PC3	284	26	24	12	29	11	21	7
Spring Precip.	754	141	28	21	38	5	27	14
Fall Precip.	467	30	23	9	5	0	12	0
Spring Max. Temp.	54	2	18	1	6	0	1	0
Winter Vapor PD	0	0	0	0	0	0	0	0
CTI	919	521	28	26	120	17	106	23
Green-up Rate	5544	521	30	26	0	0	0	0
Big Sagebrush	515	96	24	14	37	8	18	8
Dryness Index	1016	227	26	20	21	0	10	0
RDA	615	--	25	--	127	4	38	5

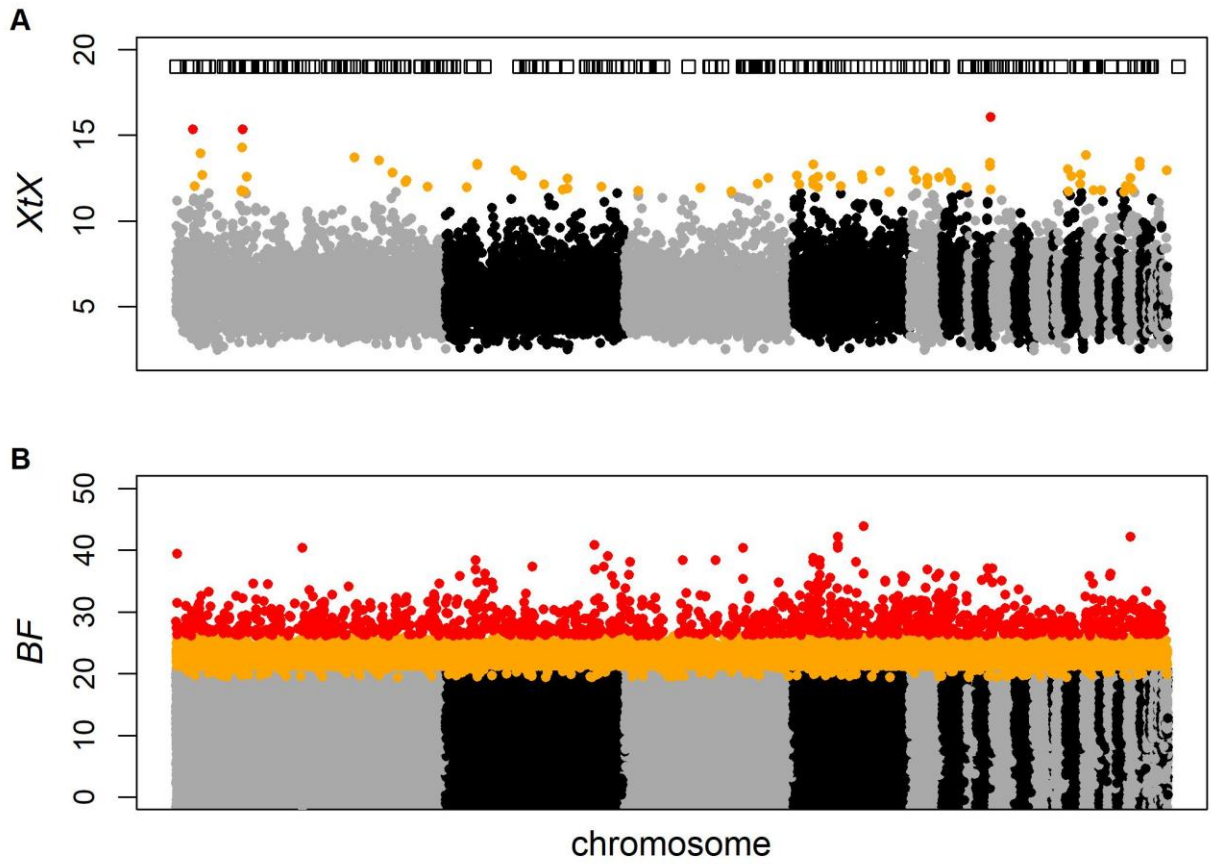

Figure 4. 3- (A) *XtX* and (B) Bayes Factor (*BF*) for each locus or each locus-covariate pair. X-axis corresponds to the SNP position along chromosomes, alternating gray and black indicate SNPs observed on different pseudo-chromosomes for Gunnison sage-grouse. SNPs with a *BF* (in the auxiliary model) or *XtX* (in the core model) > *FDR* 0.01 are orange; SNPs with *BF* or *XtX* > *FDR* 0.001 are red. Squares along the top of plot (A) indicate the locations of genes identified with Gowinda.

Table 4. 3- Summary of the outlier loci from Gunnison sage-grouse populations in gene regions with non-synonymous substitutions and enriched families or proteins. Findings from the core model ("Core"), the auxiliary model including principal component 3 ("PC3"), spring precipitation, fall precipitation, CTI, big sagebrush cover, dryness index, and RDA with associated predictor variable ("RDA: Spring Precip.", "RDA: Fall Precip.", "RDA: CTI". The gene code is listed in the left-hand column ("Gene Code"; see Appendix XVIII for a list of the corresponding full gene names and Appendix XIX for all putative adaptive genes) followed by the pseudo-chromosome number where it is located ("Chromosome"), the number of total number of SNPs identified as outliers in each gene region ("# SNPs"), indication of significance at *FDR* 0.05 (*) and *FDR* 0.01 (**) for BayPass in each model, and *FDR* 0.01 in Gowinda is shaded. Impact of each SNP as predicted by SnpEff is indicated in the by counts of SNPs in gene region in the corresponding effect column.

Gene Code	Chromosome	# SNPs	Model										Effect				
			Core	PC3	Spring Precip.	Fall Precip.	CTI	Big Sagebrush	Dryness Index	RDA: Spring Precip.	RDA: Fall Precip.	RDA: CTI	Moderate	Modifier	Downstream	Intron	Non-synonymous
Cytochrome P450																	
TBXAS1	1	1							*					1		1	
CYP2R1	5	3	*				**		**					3		3	
CYP2C23b	6	2									*			2		2	
CYP4B1	8	1								*				1		1	
Phosphatidylinositol 3-kinase Catalytic Subunit; Chain A, domain 5 & C2- domain Calcium/lipid binding domain																	
PIK3C2A	5	1		*			**							1		1	
PIK3C2G	1	1					*							1		1	
PIK3CA	9	1			*				*					1		1	
PRKCD	12	2		*	*		**							2		2	
SMURF1	14	1										*		1		1	
Non-synonymous SNP																	
CYB5R4	3	2							*				1	1		1	1
DDX60	4	6		*			**	**					1	4		4	1
INPP5E	17	1		*			**						1				1
SETX	17	2										*	2				2

Table 4. 4- Summary of the enriched GO terms ("GO Term") which were significant at FDR 0.05 or lower over all models. *P* = *P*-value, B = Benjamini-Hochberg correction. Category: OG = orthologous groups, P = proteins, BP = biological processes, CC = cellular component, MF = molecular function. For BP, CC, and MF only the top two terms are displayed here; see Appendix XX for complete list of GO terms. See Appendix XVIII for gene names corresponding to gene codes included in table below.

Category	Term	#	%	*P*	B	FDR	Genes
OG	Secondary metabolites biosynthesis, transport, and catabolism	4	2.21	0.07	0.60	38.97	CYP4B1, TBXAS1, CYP2C23b, CYP2R1
P	Cytochrome P450	4	2.21	0.01	0.93	13.49	CYP4B1, TBXAS1, CYP2C23b, CYP2R1
P	Phosphatidylinositol 3-kinase Catalytic Subunit; Chain A, domain 5	3	1.66	0.02	0.94	26.71	PIK3CA, PIK3C2A, PIK3C2G
P	C2- domain Calcium/lipid binding domain	5	2.76	0.07	1.00	58.94	PRKCD, SMURF1, PIK3CA, PIK3C2A, PIK3C2G
BP	single-organism organelle organization	33	18.23	0.00	0.15	0.10	DYNC1LI1, PRKCD, PHACTR1, SDCBP, DOCK2, MYO1B, NCAPD3, XRCC2, FAM101A, C5, ACTR2, MAP2, OMA1, RTTN, CHAF1B, PIK3CA, SIPA1L1, KIF2C, PDCD5, EHD3, SYNE3, TGFBRAP1, CRYAA, C16ORF45, TSC1, PKP2, RDX, NDUFS6, NCKAP1, SMURF1, SNAP47, PARVA, SSH2
BP	cytoskeleton organization	24	13.26	0.00	0.37	0.58	CRYAA, C16ORF45, PDZD8, PRKCD, PKP2, PHACTR1, TSC1, SDCBP, DOCK2, MYO1B, DMD, TGFB2, RDX, XRCC2, FAM101A, ACTR2, MAP2, NCKAP1, SIPA1L1, PIK3CA, KIF2C, PARVA, SSH2, SYNE3
CC	lamellipodium	6	3.31	0.02	1.00	18.87	TSC1, PIK3CA, ITGAV, DGKZ, RDX, PARVA
CC	cell junction	18	9.94	0.02	0.94	19.35	PRKCD, PKP2, PHACTR1, ITGAV, DMD, RDX, RPS13, DDB2, GABRA4, ACTR2, TJAP1, LCP2, SDK1, NCKAP1, VCL, EHD3, PARVA, GABRB3
MF	molecular function regulator	22	12.15	0.00	0.54	2.20	BIRC6, TBC1D9B, PRKCD, PHACTR1, TSC1, PSME4, MCF2L, CRB2, DOCK2, SERPINB12, TBC1D9, C5, ARGAHP20, RAPGEF1, CACNG4, DENND5A, PIK3CA, SIPA1L1, CPAMD8, OVSTL, PDCD5, STXBP5
MF	enzyme regulator activity	18	9.94	0.00	0.37	2.60	BIRC6, TBC1D9B, PRKCD, PHACTR1, TSC1, PSME4, CRB2, DOCK2, SERPINB12, C5, TBC1D9, ARGAHP20, SIPA1L1, CPAMD8, PIK3CA, OVSTL, PDCD5, STXBP5

Gene Ontology Enrichment Analyses

Global LD was estimated to be 0.02, dropping to r^2<0.10 at ~350 kbp. Of the 3,751 total candidate SNPs 307 were located within 350 kbp of one of 191 putative gene regions. Eight unique genes were identified in a gene ontology enrichment analysis of outliers identified by the core model (Table 4.2). At *FDR* 0.05, 51 GO terms were found to be enriched among these eight genes, 33 of which remained significant at *FDR* 0.01 (Table 4.2). Outlier lists for covariates identified variable numbers of enriched GO terms and associated genes, ranging from no GO terms and no genes at *FDR* 0.05 for green-up rate to 127 GO terms and 38 genes at *FDR* 0.05 (4 and 5 respectively at *FDR* 0.01) for RDA (see Table 4.2 for complete summarization of all tests).

The majority of outlier SNPs in gene regions were identified as potential modifiers (186) in introns (gene regions excised before translation into proteins) by SnpEff (Table 4.3 and Appendix XIX). Ten SNPs were identified as low (6) or moderate (4) impact variants (Appendix XIX). Additionally, 4 SNPs were indicated as non-synonymous variants, 6 as synonymous substitutions, 2 were down-stream of the gene regions, and 1 was up-stream (Appendix XIX). Genes with SNPs classified as a moderate impact include: cytochrome b5 reductase 4 (CYB5R4), DEAD (Asp-Glu-Ala-Asp) box polypeptide 60 (DDX60), inositol polyphosphate-5-phosphatase E (INPP5E), and senataxin (SETX).

DAVID identified several significant (P< 0.05) GO terms in each category though none with a significance that held up after adjustment for multiple testing, suggesting interesting though potentially spurious relationships. Top GO terms in each category included single-organism organelle and cytoskeleton organization for biological processes, molecular and enzyme function regulation for molecular function, and lamellipodium (a cytoskeleton protein

which plays a role in cell motility and migration) and cell junction for cellular components (Table 4.4; see Appendix XX for a complete list). Similarly, a cluster of orthologous genes had a low *P*-value (0.07), which corresponded to terms for secondary metabolites biosynthesis, transport, and catabolism and the following genes: cytochrome P450 family 2 subfamily R member 1 (CYP2R1), cytochrome P450, family 2, subfamily C, polypeptide 23b (CYP2C23b), cytochrome P450, family 4, subfamily B, polypeptide 1 (CYP4B1), and thromboxane A synthase 1 (TBXAS1; Figure 4.4A). These same four genes were also identified by enrichment of terms for protein domains belonging to the cytochrome P450 family of genes ($P<0.01$).

Population allele frequencies for candidate SNPs in putative gene regions illustrate patterns of diversifying selection. For the cytochrome P450 gene family genes Crawford and Dove Creek appear to be diversifying at TBXAS1, though allele frequency differences are slight, and San Miguel at CYP2R1 (Figure 4.4B). Allele frequencies at CYP2C23B more or less form two groups: Dove Creek, Gunnison Basin, and San Miguel in one, and Cimarron, Crawford, and Piñon Mesa in the other. The Piñon Mesa population is different at candidate loci in CYP4B1. Allele frequencies of non-synonymous SNPs indicate Crawford and Dove Creek group at SNPs in CYB5R4 and Cimarron at INPP5E (Figure 4.4C). No strong pattern is discernable at 6 candidate loic in DDX60. However, 2 SNP variants in DDX60 are in exons and predicted to be function modifiers (dark green circle and blue triangle in Figure 4.4D) and only a single SNP variant resulted in a non-synonymous amino acid substitution (red diamond in Figure 4.4D). Similarly, the two candidate SNPs in SETX are present in different frequencies in different populations indicating differing signals of diversifying selection in each population.

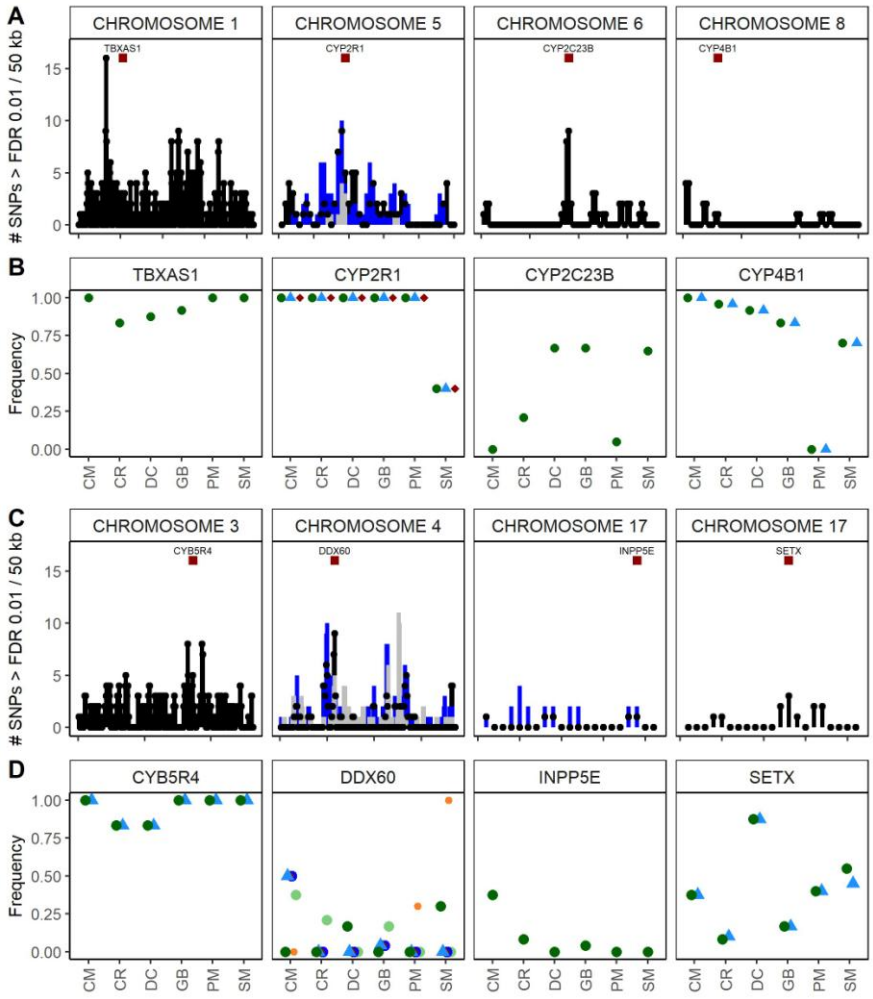

Figure 4. 4- (A) and (C) Sliding window counts of outlier loci (FDR 0.01) in 1 Mb windows with 500 kb overlap along pseudo-chromosomes corresponding to the the chicken genome Galgal4 numbering system (see Appendix XXI for R function). The x-axis indicates chromosome positions. Peaks indicate high densities of candidate loci for different models: TBXAS1 association with DRI in BayPass, CYP2R1 *XtX* (gray) and association with CTI (black) and DRI (blue) in BayPass, CYP2C23B RDA with fall precipitation as predictor, CYP4B1 RDA with spring precipitation as predictor, CYB5R4 association with DRI in BayPass, DDX60 association with PC3 (black), CTI (blue) and BS (gray) in BayPass, INPP5E association with PC3 (black) and CTI (blue) in BayPass, SETX in RDA with CTI as predictor. Red squares are indicating the x-axis location of each gene region. Reference allele frequency of outlier loci in the cytochrome P450 family of genes (B) and non-synonymous substitutions (D) for Gunnison sage-grouse populations. Different symbols indicate different loci located within each gene region (TBXAS1, CYP2R1, CYP2C23B,CYP4B1, CYPB5R4, DDX60, INPP5E,SETX). Five genes had more than one SNP in the gene region: CYP2R1 = 3, CYP4B1 = 2, CYB5R4 = 2, DDX60 = 6, SETX = 2. Populations are abbreviated along the x-axis: CM = Cimarron, CR = Crawford, DC = Dove Creek, GB = Gunnison Basin, PM = Piñon Mesa, SM = San Miguel .

Individuals generally cluster by population when candidate loci are used in a PCA (Figure 4.5C) which is somewhat similar to the clustering of individuals with all and putatively neutral SNP loci (Figure 4.5A & 4.5B), although Gunnison Basin, Crawford, and Cimarron cluster more tightly together while Dove Creek, Piñon Mesa, and San Miguel populations appear to separate from the other three populations and each other with candidate loci. A PCA plot of the SNPs in cytochrome P450 genes show that most individuals loosely cluster while some San Miguel individuals and nearly all Piñon Mesa individuals are clustering away from the remaining individuals (Figure 4.5D). PCA plots with SNPs from individual analyses showed similar clustering patterns to that of the overall outlier clustering (see Appendix XXII).

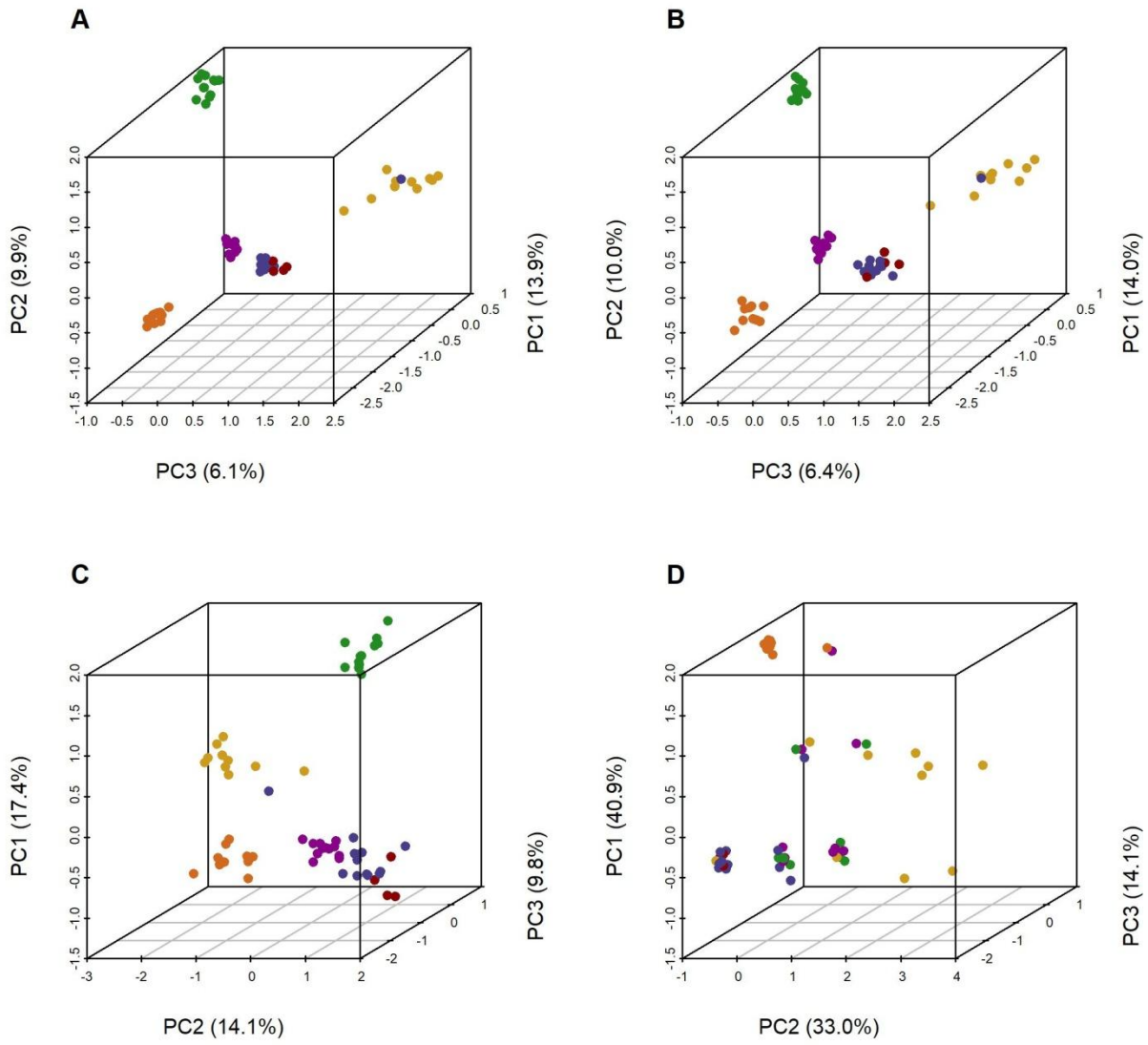

Figure 4. 5- Clustering of individual Gunnison sage-grouse using 3-D PCA plots with (A) all SNPs (15,033 loci; first 3 PCs account for 29.9% of the variation in the genotypes), (B) putatively neutral SNPs (11,282 loci; first 3 PCs account for 30.4% of the variation in the genotypes), (C) all candidate SNPs (3,751 loci; first 3 PCs account for 41.3% of the variation in the genotypes), (D) all cytochrome P450 candidate SNPs (7 loci; first 3 PCs account for 88.0% of the variation in the genotypes). Each point represents an individual color coded by the population where the sample was collected: Cimarron = red, Crawford = blue, Dove Creek = green, Gunnison Basin = purple, Piñon Mesa = orange, San Miguel = yellow.

Discussion

I found evidence of allelic differentiation at SNPs associated with potentially important gene families for local ecological adaptation between isolated populations of a single avian species. Four of the putatively adaptive genes identified contained SNPs that are expected to moderately impact putative gene function. An additional four genes are members of an ecologically significant gene family for sage-grouse: the cytochrome P450 gene family. The majority of the candidate SNPs were located in introns and may have no impact on the putative gene with which they are associated. Introns are most likely to be linked to coding or regulatory variation, yet intron variants can impact alternative splicing, gene expression, chromatin assembly, mRNA transport, and post transcriptional gene expression (Cooper 2010, Jo and Choi 2015). Future work could confirm F_{ST} of outliers in a larger sample, sequence haplotype blocks in the vicinity of outliers, measure expression of putatively adaptive genes as a function of SNP genotype, and/or evaluate the role of identified cytochrome P450 genes in chicken models of response to plant secondary compounds. My findings provide an initial look at adaptive divergence among populations for a species with a fragmented habitat, and variable conditions across the species' range.

Identification of signals of adaptive divergence in Gunnison sage-grouse populations also provides more evidence of natural selection occurring in unexpected situations. First, effective population size can influence the balance between selection and genetic drift. Large effective population sizes are less influenced by genetic drift and therefore natural selection is expected to be more efficient (Frankham 1996, Gossmann et al. 2012). The mating system of Gunnison sage-grouse indicates the species generally has a small effective population size, and so this work adds to the few documented examples where locally adapted variation persists despite small effective

population size (McKay et al. 2001, Phifer-Rixey et al. 2012). Second, geographic scale also plays a role in the likelihood of divergence. At large geographic scales gene flow is expected to be low among populations allowing divergence to occur even in the absence of strong selection (Rousset 1997, Slatkin 1993). At the microgeographic scale (when geographic distances between populations are within the known physical dispersal range of an organism) high gene flow is expected to impede local adaptation (Slatkin 1987), although some argue microgeographic local adaptation is more common than previously appreciated (Richardson et al. 2016). Though not a perfect system to evaluate microgeographic local adaptation, the populations of Gunnison sage-grouse are located within their known physical dispersal range. Few examples of microgeographic adaptation have been identified in birds, presumably because birds are considered vagile (Charmantier et al. 2016, Langin et al. 2017, Manthey and Moyle 2015, Termignoni-García et al. 2017). Identification of signals of adaptive divergence in Gunnison sage-grouse populations indicates distinct selective environments (Karlin and McGregor 1972, Levene 1953, Urban et al. 2017), a physical limit to dispersal (Fischer and Lindenmayer 2007, Slatkin 1987), mating signal divergence (e.g. Langin et al. 2015, Langin et al. 2017), or any type of assortative mating may be facilitating natural selection.

Population-level Divergence

Across all candidate loci, three of the Gunnison sage-grouse populations cluster together (Gunnison Basin, Crawford, and Cimarron) and three of the populations stand out as holding genetic variation with the signature of divergent selection (San Miguel, Piñon Mesa, and Dove Creek). The three populations with the most similar habitat conditions and in closest proximity

are those that cluster at putatively divergent loci. In general, the shrub composition in Gunnison Basin, Cimarron, and Crawford is dominated by big sagebrush cover with patches of oakbrush and juniper (Gunnison sage-grouse Rangewide Steering Committee 2005). San Miguel and Dove Creek are both characterized by patchy big sagebrush habitat, fragmented by agriculture in Dove Creek, whereas San Miguel lowlands dominated by low sagebrush cover. The shrub composition in Piñon Mesa varies along an elevation gradient; from low elevations dominated by sagebrush cover, saltbush, and greasewood, to piñon-juniper woodlands at mid elevations, and oakbrush with patchy sagebrush cover and snowberry at higher elevations. The majority of candidate loci were identified in environmental association analyses so the apparent clustering by differences in environment is not surprising, though it does suggest support for adaptation to local environmental conditions. In particular, the signal of diversifying selection is strongest in Dove Creek, San Miguel, and Piñon Mesa populations (Figure 4.5A). Previous population genetic studies show Crawford, Cimarron, and Gunnison Basin are the most genetically similar of the six populations (Oyler-McCance et al. 2005). However, neutral processes still separate these populations from each other, indicating the pattern I present in this chapter is not the same as that observed by putatively neutral loci, and includes signals of potential adaptive divergence.

Non-synonymous SNPs

The non-synonymous substitutions found in four putatively adaptive genes are indicative of potential impacts on gene functions. Previous experiments on chicken heat stress showed CYB5R4 was down-regulated (Sun et al. 2015). The two populations with two variants at the candidate SNPs associated with the dryness index in this putative gene, Dove Creek and

Crawford, are also the populations that experience the highest maximum temperature (26.49 °C) and the highest average temperature (12.40 °C), respectively (see Table 4.1). DDX60 is involved in antiviral responses (Schoggins et al. 2011, Zhang et al. 2016) and inflammation and immune response as an adaptation to high altitude in chickens (Zhang et al. 2016). DEAD Box helicases are a family of genes to which DDX60 belongs, and that play a role in detecting viral RNA in the cytoplasm. SETX has been implicated in response to viral pathogens, including West Nile Virus (WNV; Miller et al. 2015) as well as neurological degeneration in humans (Chen et al. 2004). All populations appear to be diversifying at one or more of the candidate SNPs in DDX60 and SETX which could indicate a response to variable levels of exposure and pressure from viral pathogens. Though it has yet to affect Gunnison sage-grouse specifically, WNV has impacted susceptible greater sage-grouse populations (Naugle et al. 2004) and incidence of the virus has been reported in other species within the range of Gunnison sage-grouse at variable levels (see Appendix XXIII for information on reported WNV incidence in populations). Adaptive divergence in genes that are involved in antiviral activity could result in variable abilities to respond to viral pathogens. INPP5E plays an essential role in characteristics of the cell surface through modification of the PI3K signaling pathway (Jacoby et al. 2009), a pathway containing proteins identified by DAVID as enriched with GO terms in our analyses (Appendix XX). Speculation on how adaptation in this gene could impact sage-grouse is difficult due to the open-ended possibilities such a fundamental molecular mechanism plays in cell modification, although mutations in genes belonging to this group have been implicated in multiple diseases of humans (Ooms et al. 2009).

Divergence in an Ecologically Relevant Gene Family

I identified four genes in the cytochrome P450 family as potentially divergent. My findings are consistent with the previously identified signals of divergence in this gene family in sage-grouse populations (Oh et al. in review). Different species of sagebrush have different compositions and quantities of PSMs (Frye et al. 2013, Kelsey et al. 1982) and divergence at genes involved in PSM metabolism may result in changes in ability to consume different species or subspecies of sagebrush. Sage-grouse are dietary specialists for sagebrush (Patterson 1952) and have been observed selectively consuming sagebrush leaves with lower levels of monoterpenes (Frye et al. 2013, Remington and Braun 1985). Because sage-grouse have mechanisms to neutralize inhibitory action of PSMs on digestive enzymes (Kohl et al. 2016), these genes could potentially be responsible for proteins or enzymes that aid in sagebrush digestion. Sagebrush species composition is known qualitatively to vary among populations, but quantitative cover data are currently available only at a coarse level, i.e., big sagebrush (typically *Artemisia tridentata* ssp.) versus low sagebrush (lower statured *Artemisia* sp.). The candidate SNPs in all cytochrome P450 gene regions were identified with one or more of the environmental association analyses: TBXAS1 and CYP2R1 with the dryness index, and CYP2C23B and CYP4B1 with fall and spring precipitation, respectively. CYP2R1 is the only putatively adaptive gene with SNPs associated with CTI and found in the *XtX* outliers.

Information on the documented functions for each cytochrome P450 gene is variable. CYP4B1 is up-regulated in response to hormones and indicated as a predictor for response to cancer treatments in humans (Harvell et al. 2008). It is also involved in metabolism of fatty acids, steroids, xenobiotics, and is important for chemical defense (Kirischian and Wilson 2012). TBXAS1 (aka CYP5A1) plays a role in antimicrobial responses in chickens, conferring resistance to fungicides (Wang et al. 2014). CYP2C23B is important to avian xenobiotic

metabolism (Watanabe et al. 2013). The most information about gene function is available for CYP2R1 which encodes an enzyme implicated in vitamin D metabolism in chickens (Cheng et al. 2004, Zhu et al. 2013, Thacher et al. 2015). The gene has also been implicated in reduced egg hatchability in chickens with some variants (Narbaitz et al. 1987). The San Miguel population has been documented to have an elevated hatch failure rate (~28% of eggs failed to hatch; Stiver et al. 2008). The identification of a gene involved in hatchability in a related species as divergent in a population with documented high hatch failure suggests there might be linkage between the gene impacting hatchability and a trait conferring higher local fitness that might actually be the gene selected for or perhaps this signal of divergence is actually a result of inbreeding or genetic drift.

Conservation Implications

Some of the potentially ecologically important identified genes or groups of genes for Gunnison sage-grouse could provide insight for conservation. Populations with different functional genetic variants could potentially impact management and conservation decisions (Savolainenet al. 2013). Theoretically, gene flow can have either a positive or negative impact on local adaptation of populations (Slatkin 1987, Wright 1931). If populations are locally adapted, increasing gene flow could risk outbreeding depression (Edmands 2007), especially if populations are small. This has been exemplified in populations of streamside salamanders with and without predators where gene flow constrained the evolution of effective anti-predator behaviors (Storfer and Sih, 1998). The finding that Gunnison sage-grouse populations have signals of adaptive divergence associated with the ability to digest different sagebrush species

(cytochrome P450 gene family) and respond to viral pathogens (DDX60 and SETX) could indicate that individuals from one population would be less fit in the environment of a differently adapted population. Given that translocation has been one of the conservation efforts employed for the species, these findings could provide insight into which populations could serve as source and recipient if future translocation efforts were to occur. The samples used for this manuscript were all collected prior to translocation efforts. In addition to informing any future translocation efforts, it would also be interesting to collect contemporary samples and use targeted resequencing of specific gene regions to evaluate whether the signals of selection in potentially ecologically important genes we have identified remain in populations despite translocation.

Similarly, if different populations are adapted to digest different species of sagebrush, habitat restoration efforts may require location specific sagebrush species as a seed source. Guidelines on seed and plant transfer zones for sagebrush species and subspecies have been based on moisture and elevation gradients in the past (Mahalovich and McArthur 2004), which may result in planting a species or subspecies which the local population is not adapted to digest. Although matching the local sagebrush type during restoration could be important, seed sources for different sagebrush species or subspecies are not always available and factors involved in establishment of seedlings is just starting to be understood (Brabec et al. 2016).

Captive reared populations of sage-grouse have been attempted in recent years (Apa and Wiechman 2015). Insight into adaptive differences could aid in making sure the captive population is similarly adapted to the intended release population. In the case of sagebrush digestion or disease response, releasing individuals without the appropriate genetic variants could result in wasted efforts at best and further population fitness declines at worst.

In conserving species with fragmented ranges and overall population declines, restoration of gene flow between isolated groups is a common objective. Our findings suggest increasing gene flow between Gunnison sage-grouse may require careful consideration of local adaptation. On the other hand, locally adapted variation can persist in the face of gene flow (Fitzpatrick et al. 2015) and the existence of adaptive environmental clines suggests gene flow via assisted migration can aid in range shifts in response to a changing climate (Kelly and Phillips 2016). We would be remiss to not acknowledge the potential for false positives in our analyses, however. Our outlier analysis methods generally control for demographic structure (i.e., incorporation of a kinship matrix or non-parametric approaches), though observed differentiation could still be a result of background selection, or linkage of neutrally evolving sites to sites under purifying selection (Shafer et al. 2015). However, LD decays to an $r^2 < 0.10$ at ~350 kb (see Appendix XXIV Figure S24.1), and we have restricted our inference to candidate adaptive loci that are within 350 kb of a known gene region to reduce the potential for random association. The reduced representation approach used here allowed us to break the entire genome down into more manageable pieces for investigation of putatively adaptive diversity, resulting in a low density of SNPs (~16 SNPs/Mb), and therefore many regions of the genome were not sampled (Tiffin and Ross-Ibarra 2014). Therefore, it is likely there are more regions of the genome under adaptive divergence and more processes involved. It is also possible that LD decays more slowly than we have assumed, or unevenly, and some of the putatively adaptive gene regions identified here are linked to a target of selection more distant than we have evaluated.

Additionally, the large proportion of SNPs correlated with green-up rate (5,544 of the total 15,033 SNPs) is potentially misleading. While most of the evaluated covariates vary among the populations, average green-up rate values appear to form two groups of similar populations:

Cimarron, Crawford, Dove Creek, Gunnison basin and San Miguel in one group (average values ranging between 80.34 and 104.33) and Piñon Mesa in another (average value = 298.44). Piñon Mesa is also the population with the highest mean F_{ST} (Figure 4.2A) and lowest correlation in all population comparisons (Figure 4.2B) suggesting these results might be confounded by demographic patterns and care should be taken when interpreting signals of selection from covariate correlation analyses when the covariates mimic demographic structure.

Conclusion

My results provide evidence of adaptive divergence among populations of Gunnison sage-grouse for potentially ecologically important genes and groups of genes. Through identification of molecular processes potentially involved in local adaptation, this study takes the first step in understanding and characterizing local adaptation within populations of Gunnison sage-grouse. My findings imply a fitness differential among populations, assuming high frequency alleles in a population within a gene also correspond to a higher fitness phenotype locally. This relationship could be confirmed or further probed through genomic methods which more directly evaluate fitness effects and function (Carneiro et al. 2014, Prasad et al. 2013). My study was done using historical samples and publicly available spatial variables. More insight from these historical samples could be obtained by using the lists of putatively adaptive genes under divergent selection as the subject of resequencing, or target enrichment, to identify functional variants supporting a putative role in adaptation and confirming signals of selection in a larger sample set (Jones and Good 2016). Many approaches used to draw more direct lines between the underlying genetic control and phenotype, such as quantitative trait analysis

(Kearsey 1998), gene expression and/or reciprocal transplant studies (Kawecki and Ebert 2004), may be attractive, especially given that many loci of varying effect size underlie adaptive divergence (Rockman 2012). However, these strategies are unlikely feasible due to difficulty in generating large segregating populations in captivity and given federal protection of the species under the Endangered Species Act. Genome wide association studies (GWAS), on the other hand, can also identify genetic regions underlying phenotypes and can be accomplished without the use of captive populations making it a much more reasonable approach. Nevertheless, my results have provided many avenues for future investigations of adaptation in an avian species of conservation concern.

LITERATURE CITED

Aldridge, C. L., and M. S. Boyce. 2008. Accounting for fitness: Combining survival and selection when assessing wildlife-habitat relationships. Israel Journal of Ecology & Evolution 54:389–419.

Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983–994.

Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for gunnison sage-grouse: A spatially explicit hierarchical approach. Journal of Wildlife Management 76:391–406.

Allendorf, F. W., P. A. Hohenlohe, and G. Luikart. 2010. Genomics and the future of conservation genetics. Nature Reviews 11:697–709.

Apa, A. D., and L. A. Wiechman. 2015. Captive-rearing of Gunnison sage-grouse from egg collection to adulthood to foster proactive conservation and recovery of a conservation-reliant species. Zoo Biology 15:1–15.

Baruch-Mordo, S., J. S. Evans, J. P. Severson, D. E. Naugle, J. D. Maestas, J. M. Kiesecker, M. J. Falkowski, C. A. Hagen, and K. P. Reese. 2013. Saving sage-grouse from the trees: A proactive solution to reducing a key threat to a candidate species. Biological Conservation 167:233–241.

Benedict, N. G., S. E. Oyler-McCance, C. E. Braun, and T. W. Quinn. 2003. Evaluation of the Eastern (*Centrocercus urophasianus urophasianus*) and Western (*Centrocercus*

urophasianus phaios) subspecies of sage-grouse using mitochondrial control-region sequence data. Conservation Genetics 4:301–310.

Berriz, G. F., O. D. King, B. Bryant, C. Sander, and F. P. Roth. 2003. Characterizing gene sets with FuncAssociate. Bioinformatics 19:2502–2504.

Blomberg, E. J., J. S. Sedinger, M. T. Atamian, and D. V. Nonne. 2012. Characteristics of climate and landscape disturbance influence the dynamics of greater sage-grouse populations. Ecosphere 3:1–20.

Brabec, M. M., M. J. Germino, and B. Richardson. 2016. Climate adaption and post-fire restoration of a foundational perennial in cold desert: Insights from intraspecific variation in response to weather. Journal of Applied Ecology.

Braun, C. E., T. Britt, and R. O. Wallestad. 1977. Guidelines for maintenance of sage-grouse habitats. Wildlife Society Bulletin 5:99–106.

Braun, C. E., J. W. Connelly, and M. A. Schroeder. 2005. Seasonal habitat requirements for sage-grouse : Spring , summer, fall, and winter. USDA Forest Service Proceedings RMRS-P-9-38 38–42.

Braun, C. E., S. J. Oyler-McCance, J. A. Nehring, M. L. Commons, J. R. Young, and K. M. Potter. 2014. The historical distribution of Gunnison sage-grouse in Colorado. The Wilson Journal of Ornithology 126:207–217.

Browning, B.L., and S.R. Browing. 2007. Rapid and accurate haplotype phasing and missing data inference for whole genome association studies by use of localized haplotype clustering. American Journal of Human Genetics 81:1084-97.

Carneiro, M., C. Rubin, F. Di Palma, F. W. Albert, A. M. Barrio, G. Pielberg, N. Rafati, and S. Sayyab. 2014. Rabbit genome analysis reveals a polygenic basis for phenotypic change during domestication. Science 345:1074–1079.

Charmantier, A., C. Doutrelant, G. Dubuc-Messier, A. Fargevieille, and M. Szulkin. 2016. Mediterranean blue tits as a case study of local adaptation. Evolutionary Applications 9:135–152.

Chen, Y. Z., C. L. Bennett, H. M. Huynh, I. P. Blair, I. Puls, J. Irobi, I. Dierick, A. Abel, M. L. Kennerson, B. A. Rabin, G. A. Nicholson, M. Auer-Grumbach, K. Wagner, P. De Jonghe, J. W. Griffin, K. H. Fischbeck, V. Timmerman, D. R. Cornblath, and P. F. Chance. 2004. DNA/RNA helicase gene mutations in a form of juvenile amyotrophic lateral sclerosis (ALS4). The American Journal of Human Genetics 74:1128–1135.

Cheng, J. B., M. A. Levine, N. H. Bell, D. J. Mangelsdorf, and D. W. Russell. 2004. Genetic evidence that the human CYP2R1 enzyme is a key vitamin D 25-hydroxylase. Proceedings of the National Academy of Sciences 101:7711–7715.

Cingolani, P., A. Platts, L. L. Wang, M. Coon, T. Nguyen, L. Wang, S. J. Land, X. Lu, and D. M. Ruden. 2012. A program for annotating and predicting the effects of single nucleotide polymorphisms, SnpEff. Fly 6:80–92.

Coop, G., D. Witonsky, A. Di Rienzo, and J. K. Pritchard. 2010. Using environmental correlations to identify loci underlying local adaptation. Genetics 185:1411–23.

Cooper, D. N. 2010. Functional intronic polymorphisms: Buried treasure awaiting discovery

within our genes. Human Genomics 4:284–288.

Cruickshank, T. E., and M. W. Hahn. 2014. Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow. Molecular Ecology 23:3133–3157.

Cross, T. B., D.E. Naugle, J.C. Carlson, and M.K. Schwartz. 2017. Genetic recapture identifies long-distance breeding dispersal in greater sage-grouse (*Centrocercus urophasianus*). The Condor 119:155–166.

De Wit, P., and S. R. Palumbi. 2013. Transcriptome-wide polymorphisms of red abalone (*Haliotis rufescens*) reveal patterns of gene flow and local adaptation. Molecular Ecology 22:2884–97.

Doherty, K. E., J. D. Hennig, J. B. Dinkins, K. A. Griffin, A. A. Cook, J. D. Maestas, D. E. Naugle, and J. L. Beck. 2018. Understanding biological effectiveness before scaling up range-wide restoration investments for Gunnison sage-grouse. Ecosphere 9:e02144.

Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat : The importance of managing at multiple scales. Journal of Wildlife Management 74:1544–1553.

Dyer, R. J. 2014. gstudio: Analyses and functions related to the spatial analysis of genetic marker data. R package version 1.3.

Edmands, S. 2007. Between a rock and a hard place: Evaluating the relative risks of inbreeding and outbreeding for conservation and management. Molecular Ecology 16:463–475.

Ellsworth, D. L., R. L. Honeycutt, and N. J. Silvy. 1995. Phylogenetic relationships among North American grouse inferred from restriction endonuclease analysis of mitochondrial DNA.

The Condor 97:492–502.

Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation : A synthesis. Global Ecology and Biogeography 16:265–280.

Fitzpatrick, S. W., J. C. Gerberich, J. A. Kronenberger, L. M. Angeloni, and W. C. Funk. 2015. Locally adapted traits maintained in the face of high gene flow. Ecology Letters 18:37–43.

Forester, B. R., J. R. Lasky, H. H. Wagner, and D. L. Urban. 2018. Comparing methods for detecting multilocus adaptation with multivariate genotype-environment associations. Molecular Ecology 2215–2233.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. Conservation Biology 10:1500–1508.

Fraser, D. J., and L. Bernatchez. 2001. Adaptive evolutionary conservation: Towards a unified concept for defining conservation units. Molecular Ecology 10:2741–2752.

Frye, G. G., J. W. Connelly, D. D. Musil, and J. S. Forbey. 2013. Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. Ecology 94:308–314.

Funk, W. C., J. K. McKay, P. A. Hohenlohe, and F. W. Allendorf. 2012. Harnessing genomics for delineating conservation units. Trends in ecology & evolution 27:489–96.

Gautier, M. 2015. Genome-wide scan for adaptive divergence and association with population-specific covariates. Genetics 201:1555–1579.

Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1992. Methods for trapping sage grouse in Colorado. Wildlife Society Bulletin 10:224–231.

Gossmann, T. I., P. D. Keightley, and A. Eyre-Walker. 2012. The effect of variation in the effective population size on the rate of adaptive molecular evolution in eukaryotes. Genome Biology and Evolution 4:658–667.

Gunnison sage-grouse Rangewide Steering Committee. 2005. Gunnison sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado USA.

Gunther, T., and G. Coop. 2013. Robust identificatin of local adaptation from allele frequencies. Genetics 195:205–220.

Harju, S. M., C. V Olson, M. R. Dzialak, J. P. Mudd, and J. B. Winstead. 2013. A flexible approach for assessing functional landscape connectivity, with application to greater sage-grouse (*Centrocercus urophasianus*). PloS one 8:e82271.

Harvell, D. M. E., J. K. Richer, M. Singh, N. Spoelstra, C. Finlayson, V. F. Borges, A. D. Elias, and K. B. Horwitz. 2008. Estrogen regulated gene expression in response to neoadjuvant endocrine therapy of breast cancers: Tamoxifen agonist effects dominate in the presence of an aromatase inhibitor. Breast Cancer Research and Treatment 112:489–501.

Huang, D. W., B. T. Sherman, Q. Tan, J. Kir, D. Liu, D. Bryant, Y. Guo, R. Stephens, M. W. Baseler, H. C. Lane, and R. A. Lempicki. 2007. DAVID Bioinformatics Resources: Expanded annotation database and novel algorithms to better extract biology from large gene lists. Nucleic Acids Research 35:169–175.

Jacoby, M., J. J. Cox, S. Gayral, D. J. Hampshire, M. Ayub, M. Blockmans, E. Pernot, M. V. Kisseleva, P. Compère, S. N. Schiffmann, F. Gergely, J. H. Riley, D. Pérez-Morga, C. G. Woods, and S. Schurmans. 2009. INPP5E mutations cause primary cilium signaling defects,

ciliary instability and ciliopathies in human and mouse. Nature Genetics 41:1027–1031.

Jo, B. S., and S. S. Choi. 2015. Introns: The functional benefits of introns in genomes. Genomics & Informatics 13:112.

Jones, M. R., and J. M. Good. 2016. Targeted capture in evolutionary and ecological genomics. Molecular Ecology 25:185–202.

Kahn, N. W., C. E. Braun, J. R. Young, S. Wood, D. R. Mata, and T. W. Quinn. 1999. Molecular analysis of genetic variation among large- and small-bodied sage grouse using mitochondrial control-region sequences. The Auk 116:819–824.

Karlin, S., and J. McGregor. 1972. Application of method of small parameters to multi-niche population genetic models. Theoretical Population Biology 3:186–209.

Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.

Kearsey, M. J. 1998. The principles of QTL analysis (a minmal mathematics approach). Animal Production 49:1619–1623.

Keenan, K., P. McGinnity, T. F. Cross, W. W. Crozier, and P. A. Prodohl. 2013. diveRsity: An R package for the estimation of population genetics parameters and their associated errors. Methods in Ecology and Evolution 4:782–788.

Kelly, E., and B. L. Phillips. 2016. Targeted gene flow for conservation. Conservation Biology 30:259–267.

Kelsey, R. G., J. R. Stephens, and F. Shafizadeh. 1982. The chemical constituents of sagebrush

foliage and their isolation. Journal of Range Management 35:617–622.

Kirischian, N. L., and J. Y. Wilson. 2012. Phylogenetic and functional analyses of the cytochrome P450 family 4. Molecular Phylogenetics and Evolution 62:458–471. Elsevier Inc.

Knick, S. T., S. E. Hanser, and K. L. Preston. 2013. Modeling ecological minimum requirements for distribution of greater sage-grouse leks: Implications for population connectivity across their western range, U.S.A. Ecology and Evolution 3:1539–51.

Kofler, R., and C. Schlötterer. 2012. Gowinda: Unbiased analysis of gene set enrichment for genome-wide association studies. Bioinformatics 28:2084–2085.

Kohl, K. D., J. W. Connelly, M. D. Dearing, and J. S. Forbey. 2016. Microbial detoxification in the gut of a specialist avian herbivore, the greater sage-grouse. FEMS Microbiology Letters 363:fnw144.

Kubota, A., J. J. Stegeman, J. V. Goldstone, D. R. Nelson, E. Kim, S. Tanabe, and H. Iwata. 2011. Cytochrome P450 CYP2 genes in the common cormorant: Evolutionary relationships with 130 diapsid CYP2 clan sequences and chemical effects on their expression. Comparative Biochemistry and Physiology part C: Toxicology and Pharmacology 153:280–289.

Langin, K. M., T. S. Sillett, W. C. Funk, S. a Morrison, M. A. Desrosiers, and C. K. Ghalambor. 2015. Islands within an island: Repeated adaptive divergence in a single population. Evolution 69:653–665.

Langin, K. M., T. S. Sillett, S. A. Morrison, and C. K. Ghalambor. 2017. Bill morphology and

neutral genetic structure both predict variation in acoustic signals within a bird population. Behavioral Ecology 28:866–873.

Langmead, B., and S. L. Salzberg. 2012. Fast gapped-read alignment with Bowtie 2. Nat Methods 9:357–359.

Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. The American Naturalist 87:331–333.

Li, H., B. Handsaker, A. Wysoker, T. Fennell, J. Ruan, N. Homer, G. Marth, G. Abecasis, and R. Durbin. 2009. The sequence alignment/map format and SAMtools. Bioinformatics 25:2078–2079.

Lynch, M., and K. Ritland. 1999. Estimation of pairwise relatedness with molecular markers. Genetics 152:1753–1766.

Mahalovich, M. F., and E. D. McArthur. 2004. Sagebrush (*Artemisia* spp.) seed and plant transfer guidelines. Native Plants Journal 5:141–148.

Manthey, J. D., and R. G. Moyle. 2015. Isolation by environment in white-breasted nuthatches (*Sitta carolinensis*) of the Madrean Archipelago sky islands: A landscape genomics approach. Molecular Ecology 24:3628–3638.

Mardis, E. R. 2008. Next-generation DNA sequencing methods. Annual Review of Genomics and Human Genetics 9:387–402.

McKay, J. K., J. G. Bishop, J. Z. Lin, J. H. Richards, A. Sala, and T. Mitchell-Olds. 2001. Local adaptation across a climatic gradient despite small effective population size in the rare sapphire rockcress. Proceedings of the Royal Society B: Biological Sciences 268:1715–

1721.

Meirmans, P. G. 2012. The trouble with isolation by distance. Molecular Ecology 21:2839–2846.

Metzker, M. L. 2010. Sequencing technologies the next generation. Nature Reviews Genetics 11:31–46. Nature Publishing Group.

Miller, M. R., J. P. Dunham, A. Amores, W. A. Cresko, and E. A. Johnson. 2007. Rapid and cost-effective polymorphism identification and genotyping using restriction site associated DNA (RAD) markers. Genome Research 17:240–248.

Miller, M. S., A. Rialdi, J. Sook, Y. Ho, M. Tilove, L. Martinez-Gil, N. P. Moshkina, Z. Peralta, J. Noel, C. Melegari, A. Maestre, P. Mitsopoulos, J. Madrenas, S. Heinz, C. Benner, J. A. . Young, A. R. Feagins, C. Basler, A. Fernandez-Sesma, O. J. Becherel, M. F. Lavin, H. van Bakel, and I. Marazzi. 2015. The helicase senataxin suppresses the antiviral transcriptional response and controls viral biogenesis. Nature Immunology 16:485–494.

Miyazawa, M., M. Shindo, and T. Shimada. 2001. Oxidation of 1, 8-cineole, the monoterpene cyclic ether originated from *Eucalyptus polybractea*, by cytochrome P450 3A enzymes in rat and human liver microsomes. Drug Metabolism and Disposition 29:200–205.

Narbaitz, R., C. Tsang, and A. Grunder. 1987. Effects of vitamin D deficiency in the chicken embryo. Calcified Tissue International 40:109–113.

Naugle, D. E., C. L. Aldridge, B. L. Walker, T. E. Cornish, B. J. Moynahan, M. J. Holloran, K. Brown, G. D. Johnson, E. T. Schmidtmann, R. T. Mayer, C. Y. Kato, M. R. Matchett, T. J. Christiansen, W. E. Cook, T. Creekmore, R. D. Falise, E. T. Rinkes, and M. S. Boyce. 2004. West Nile virus: Pending crisis for greater sage-grouse. Ecology Letters 7:704–713.

Nehring, J. A., and C. E. Braun. 2000. Gunnison sage-grouse investigations: Poncha Pass area, Colorado April- December 1999. Colorado Division of Wildlife, Fort Collins, CO, USA.

Newton, R. E., J.D. Tack, J.C. Carlson, M.R. Matchett, P.J. Fargey, and D.E. Naugle. 2017. Longest sage-grouse migratory behavior sustained by intact pathways. Journal of Wildlife Management 81:963–972.

Nielsen, R. 2005. Molecular signatures of natural selection. Annual Review of Genetics 39:197–218.

Oh, K. P., C. L. Aldridge, J. S. Forbey, C. Y. Dadabay, and S. J. Oyler-McCance. In Review. Conservation genomics in the sagebrush sea: Population divergence and adaptive metabolic variation in sage-grouse.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. M. Stevens, E. Szoecs, and H. Wagner. 2017. vegan: Community ecology package.

Ooms, L. M., K. A. Horan, P. Rahman, G. Seaton, R. Gurung, D. S. Kethesparan, and C. A. Mitchell. 2009. The role of the inositol polyphosphate 5-phosphatases in cellular function and human disease. Biochemical Journal 419:29–49.

Oyler-McCance, S. J., K. P. Burnham, and C. E. Braun. 2001. Influence of changes in sagebrush on Gunnison sage-grouse in southwestern Colorado. The Southwestern Naturalist 46:323–331.

Oyler-McCance, S. J., J. St. John, and T. W. Quinn. 2010. Rapid evolution in lekking grouse: Implications for taxonomic definitions. Ornithological Monographs 114–122. USA.

Oyler-McCance, S. J., J. St John, S. E. Taylor, A. D. Apa, and T. W. Quinn. 2005. Population genetics of Gunnison sage-grouse: Implications for management. Journal of Wildlife Management 69:630–637.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Wyoming Game and Fish Commission Sage Books, Inc., Denver, CO.

Phifer-Rixey, M., F. Bonhomme, P. Boursot, G. A. Churchill, J. Piálek, P. K. Tucker, and M. W. Nachman. 2012. Adaptive evolution and effective population size in wild house mice. Molecular Biology and Evolution 29:2949–2955.

Prasad, K. V. S. K., B. Song, C. Olson-Manning, J. T. Anderson, C. Lee, M. E. Schranz, A. J. Windsor, M. J. Clauss, A. J. Manzaneda, I. Naqvi, M. Reichelt, J. Gershenzon, S. G. Rupasinghe, M. A. Schuler, and T. Mitchell-Olds. 2013. A gain of function polymorphism controlling complex traits and fitness in nature. Science 337:1–10.

Rellstab, C., F. Gugerli, A. J. Eckert, A. M. Hancock, and R. Holderegger. 2015. A practical guide to environmental association analysis in landscape genomics. Molecular Ecology 24:4348–4370.

Remington, T. E., and C. E. Braun. 1985. Sage grouse food selection in winter , North Park , Colorado. The Journal of Wildlife Management 49:1055–1061.

Richardson, J. L., S. P. Brady, I. J. Wang, and S. F. Spear. 2016. Navigating the pitfalls and promise of landscape genetics. Molecular Ecology 25:849–863.

Rockman, M. V. 2012. The QTN program and the alleles that matter for evolution: All that's gold does not glitter. Evolution 66:1–17.

Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics 145:1219–1228.

Sampson, J. F., and M. Byrne. 2016. Assessing genetic structure in a rare clonal eucalypt as a basis for augmentation and introduction translocations. Conservation Genetics 17:293–304. Springer Netherlands.

Savolainen, O., M. Lascoux, and J. Merilä. 2013. Ecological genomics of local adaptation. Nature reviews. Genetics 14:807–20. Nature Publishing Group.

Schoggins, J. J. W., S. J. S. Wilson, M. Panis, M. M. Y. Murphy, C. C. T. Jones, P. Bieniasz, C. M. Rice, and R. CM. 2011. A diverse array of gene products are effectors of the type I interferon antiviral response. Nature 472:481–485.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. The Condor 106:363–376.

Schweizer, R. M., B. M. VonHoldt, R. Harrigan, J. C. Knowles, M. Musiani, D. Coltman, J. Novembre, and R. K. Wayne. 2016. Genetic subdivision and candidate genes under selection in North American grey wolves. Molecular Ecology 25:380–402.

Schweyen, H., A. Rozenberg, and F. Leese. 2014. Detection and removal of PCR duplicates in population genomic ddRAD studies by addition of a degenerate base region (DBR) in sequencing adapters. Biological Bulletin 227:146–160.

Shafer, A. B. A., J. B. W. Wolf, P. C. Alves, L. Bergström, M. W. Bruford, I. Brännström, G.

Colling, L. Dalèn, L. De Meester, R. Ekblom, K. D. Fawcett, S. Fior, M. Hajibabaei, J. A. Hill, A. R. Hoezel, J. Höglund, E. L. Jensen, J. Krause, T. N. Kristensen, M. Krützen, J. K. McKay, A. J. Norman, R. Ogden, E. M. Österling, N. J. Ouborg, J. Piccolo, D. Popović, C. R. Primmer, F. A. Reed, M. Roumet, J. Salmona, T. Schenekar, M. K. Schwartz, G. Segelbacher, H. Senn, J. Thaulow, M. Valtonen, A. Veale, P. Vergeer, N. Vijay, C. Vilá, M. Weissensteiner, L. Wennerström, C. W. Wheat, and P. Zielinski. 2015. Genomics and the challenging translation into conservation practice. Trends in Ecology and Evolution 30:78–87.

Shendure, J., and H. Ji. 2008. Next-generation DNA sequencing. Nature Biotechnology 26:1135–1145.

Skopec, M. M., J. R. Malenke, J. R. Halpert, and M. Denise Dearing. 2013. An in vivo assay for elucidating the importance of cytochromes P450 for the ability of a wild mammalian herbivore (*Neotoma lepida*) to consume toxic plants. Physiological and Biochemical Zoology 86:593–601.

Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. Science 236:787–792.

Slatkin, M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. Evolution 47:264–279.

Smith, T., A. Heger, and I. Sudbery. 2017. UMI-tools: Modeling sequencing errors in unique molecular identifiers to improve quantification accuracy. Genome Research 27:491–499.

Spaulding, A. 2007. Rapid courtship evolution in grouse (Tetraonidae): contrasting patterns of

acceleration between the Eurasian and North American polygynous clades. Proceedings. Biological sciences / The Royal Society 274:1079–1086.

Stiver, J. R., A. D. Apa, T. E. Remington, and R. M. Gibson. 2008. Polygyny and female breeding failure reduce effective population size in the lekking Gunnison sage-grouse. Biological Conservation 141:742–781.

Storfer, A., and A. Sih. 1998. Gene flow and ineffective antipredator behavior in a stream-breeding salamander. Evolution 52:558–565.

Sun, L., S. J. Lamont, A. M. Cooksey, F. McCarthy, C. O. Tudor, K. Vijay-Shanker, R. M. DeRita, M. Rothschild, C. Ashwell, M. E. Persia, and C. J. Schmidt. 2015. Transcriptome response to heat stress in a chicken hepatocellular carcinoma cell line. Cell Stress and Chaperones 20:939–950.

Tack, J. D., D.E. Naugle, J.C. Carlson, and P.J. Fargey. 2011. Greater sage-grouse *Centrocercus urophasianus* migration links the USA and Canada: A biological basis for international prairie conservation. Oryx 46:64–68.

Termignoni-García, F., J. P. Jaramillo-Correa, J. Chablé-Santos, M. Liu, A. J. Shultz, S. V. Edwards, and P. Escalante-Pliego. 2017. Genomic footprints of adaptation in a cooperatively breeding tropical bird across a vegetation gradient. Molecular Ecology 26:4483–4496.

Tiffin, P., and J. Ross-Ibarra. 2014. Advances and limits of using population genetics to understand local adaptation. Trends in Ecology and Evolution 29:673–680. Elsevier Ltd.

United States Fish and Wildlife Service. 2014. Endangered and Threatened Wildlife and

Plants;Threatened Status for Gunnison sage-grouse, 79 Fed. Reg. ss 224 (final rule Nov. 20, 2014) (to be codified at 50 C.F.R. part 17).

Urban, M. C., J. L. Richardson, N. A. Freidenfelds, D. L. Drake, J. F. Fischer, and P. P. Saunders. 2017. Microgeographic adaptation of wood frog tadpoles to an apex predator. Copeia 105:451–461.

Uy, J. A. C., and G. Borgia. 2000. Sexual selection drives rapid divergence in bowerbird display traits. Evolution 54:273–278.

Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighing technique for capturing sage grouse. Wildlife Society Bulletin 20:425–426.

Wallestad, R., and R. L. Eng. 1975. Foods of adult sage grouse in central Montana. Journal of Wildlife Management 39:628–630.

Wang, D. Y., M. Gricourt, P. Arné, S. Thierry, D. Seguin, R. Chermette, W. Y. Huang, E. Dannaoui, F. Botterel, and J. Guillot. 2014. Mutations in the Cyp51A gene and susceptibility to itraconazole in *Aspergillus fumigatus* isolated from avian farms in France and China. Poultry Science 93:12–15.

Watanabe, K. P., Y. K. Kawai, Y. Ikenaka, M. Kawata, S. I. Ikushiro, T. Sakaki, and M. Ishizuka. 2013. Avian cytochrome P450 (CYP) 1-3 family genes: Isoforms, evolutionary relationships, and mRNA expression in chicken liver. PLoS ONE 8:1–3.

Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370.

Wenzel, M. A., and S. B. Piertney. 2015. Digging for gold nuggets: Uncovering novel candidate

genes for variation in gastrointestinal nematode burden in a wild bird species. Journal of Evolutionary Biology 28:807–25.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer, New York.

Wiley, R. H. 1973. Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus*. Animal Behaviour Monographs 6:85–109.

Williams, S. E., and E. A. Hoffman. 2009. Minimizing genetic adaptation in captive breeding programs: A review. Biological Conservation 142:2388–2400. Elsevier Ltd.

Wright, S. 1931. Evolution in mendelian populations. Bulletin of Mathematical Biology 52:241–295.

Young, J. R. 1994. The influence of sexual selection on phenotypic and genetic divergence among sage grouse populations. PhD Dissertation. Purdue University.

Young, J. R., C. E. Braun, S. J. Oyler-McCance, J. W. Hupp, and T. W. Quinn. 2000. A new species of sage-grouse (Phasianidae: *Centrocercus*) from Southwestern Colorado. The Wilson Bulletin 112:445–453.

Zhang, Q., W. Gou, X. Wang, Y. Zhang, J. Ma, H. Zhang, Y. Zhang, and H. Zhang. 2016. Genome resequencing identifies unique adaptations of Tibetan chickens to hypoxia and high-dose ultraviolet radiation in high-altitude environments. Genome Biology and Evolution 8:765–776.

Zhu, J. G., J. T. Ochalek, M. Kaufmann, G. Jones, and H. F. DeLuca. 2013. CYP2R1 is a major, but not exclusive, contributor to 25-hydroxyvitamin D production in vivo. Proceedings of the National Academy of Sciences 110:15650–15655.

CHAPTER V. AN EMPIRICAL COMPARISON OF POPUALTION GENETIC ANALYSES USING SNP AND MICROSATELLITE DATA FOR A SPECIES OF CONSERVATION CONCERN

Summary

Use of genomic tools to characterize wildlife populations has increased in recent years. In the past, genetic characterization has been accomplished with more traditional genetic tools (e.g., microsatellites). The explosion of genomic methods and the subsequent creation of large SNP data sets has led to the promise of increased precision in population genetic parameters and identification of demographically and evolutionarily independent groups, as well as questions about the future usefulness of the more traditional genetic tools. At present, few empirical comparisons of population genetic parameters and clustering analyses performed with microsatellites and SNPs have been conducted. Here I used microsatellite and SNP data generated from Gunnison sage-grouse samples to evaluate concordance of the results obtained from SNPs and microsatellites for common metrics of genetic diversity (H_O, H_E, F_{IS}, A_R) and differentiation (F_{ST}, G_{ST}, D_{Jost}). Additionally, I evaluated clustering of individuals using putatively neutral (SNPs and microsatellites), putatively adaptive, and a combined data set of putatively neutral and adaptive loci. I found high concordance between microsatellites and SNPs for H_E, F_{IS}, A_R, and all differentiation estimates. Although there was strong correlation between metrics from SNPs and microsatellites, the magnitude of the diversity and differentiation metrics were quite different in some cases. My clustering analyses suggest strong demographic independence among the six distinct populations of Gunnison sage-grouse and some indication of evolutionary independence in two or three populations. This study adds to a growing body of work comparing the use of SNPs and microsatellites to evaluate genetic diversity and

differentiation for a species with relatively high population structure using the most common method of obtaining SNP genotypes for non-model organisms.

Introduction

Accurate estimation of population genetic parameters has become an important part of wildlife conservation (Desalle and Amato 2004). Genetic characterization can be used to identify populations and understand gene flow (Paetkau et al. 1995, Broders et al. 1999, Hauser et al. 2002, Noël et al. 2007). More recently, genetic data have been used to begin to understand local adaptation (De Wit and Palumbi 2013, Lawson and Petren 2017, Brousseau et al. 2018) and to identify groups with distinct evolutionary or demographic characteristics (Holycross and Douglas 2007, Quintela et al. 2010, Funk et al. 2016, Prince et al. 2017). Most past genetic studies of wildlife species have been accomplished with relatively few highly variable microsatellite loci. Microsatellites, also called simple sequence repeats, were discovered in the 1980s and were quickly adopted as one of the most commonly used genetic markers (Tautz 1980, Miesfeld et al. 1981) because they tend to be highly polymorphic, are evenly distributed throughout the genome (Baumung et al. 2004, Schlötterer 2004), and are located in non-coding regions allowing the general assumption that neutral processes were being meausured. Unlike many other types of markers, microsatellites have a high mutation rate (that is quite variable across different loci), which is the result of slippage during replication, a process that is not well understood (Hansson and Westerberg 2002). The high mutation rate of microsatellites that results in highly informative markers, may also lead to an underestimate of heterozygosity through homoplasy, when two individuals have the same allelic state through independent mutation and not from a common ancestor (Hansson and Westerberg 2002). Additionally,

repeatability of genotyping across laboratories can be challenging (LaHood et al. 2002, Davison and Chiba 2003, Amos et al. 2007, Morin et al. 2009) largely because allele size calls are somewhat subjective and size determination methods can impact inferred fragment size (Kim et al. 2008), even with use of automated software (Vignal et al. 2002).

A single nucleotide polymorphism (SNP) is a location in the DNA sequence where individuals vary at a single nucleotide. Technological advancements have allowed creation of much larger SNP genotype data sets, greatly increasing the number of loci sampled with less effort and lower cost in comparison to microsatellite development and genotyping (Schlötterer 2004). Because of their high prevalence in the genome and the potential to target functional regions, SNPs are predicted to replace microsatellites for genetic characterization (Landegren et al. 1998). SNPs are more abundant and uniformly distributed across the genome than microsatellites, and have a well-understood mutational mechanism with low levels of homoplasy (Morin et al. 2004), but have lower allelic diversity (Xing et al. 2005). Lower allelic diversity in comparison to microsatellites is expected, because a nucleotide base at a SNP can only be one of four possible states. In reality, the natural pairing of certain bases in DNA structure results in the majority of SNPs being biallelic. Because of the relatively low allelic diversity, equal distribution throughout the genome, ascertainment bias of highly polymorphic microsatellite regions, and constant mutation rate, some have argued that SNPs provide a more accurate representation of genome-wide variation (Brumfield et al. 2003, Väli et al. 2008). Until recently, SNP data sets were only available for species with reference genomes, such as model organisms or important agricultural species. The development of reduced representation methods to obtain SNP genotypes without a reference genome has broadened the application of SNP markers to numerous species (Baird et al. 2008, Davey et al. 2011). One of the main appeals of SNP loci is

the ease with which high throughput/automatic analyses can be used in comparison with development and genotyping of microsatellites (Landegren et al. 1998, Krawczak 1999, Nielsen 2000) resulting in the generation of large numbers of genotypes in a relatively short period of time and for minimal cost. Further, increasing the number of loci sampled is expected to increase precision of population genetic estimates (Allendorf et al. 2010).

In addition to the potential improvement in precision of population parameter estimates from the increased number of loci, the explosion of genomic techniques and their application to non-model organisms has also led to the ability to ask new questions about conservation (Allendorf et al. 2013, Oyler-McCance et al. 2016). SNPs are found in coding and non-coding regions of the genome and they can represent both demographic (i.e., drift) and functional (i.e., selection) processes. Many authors have suggested that conservation units identified below the species level should incorporate an evaluation of demographic and evolutionary distinctness (Crandall et al. 2000, Fraser and Bernatchez 2001, Palsbøll et al. 2007, Funk et al. 2012, Robertson et al. 2014). Defining genetically similar units for conservation can inform management actions (e.g., habitat restoration, translocation) or it could potentially impact legal protection status under the Endangered Species Act (ESA), which allows for the separate protection of geographically and ecologically distinct populations (Waples 1995). The predicted advantages to using SNP data as opposed to microsatellite data for conservation, lead me, and others, to question if microsatellites will be a useful tool in the future or will be completely replaced by SNP data.

Previous studies have compared the ability of SNPs and microsatellites to evaluate levels of inbreeding (Miller et al. 2014), characterize clonal patterns in a highly inbred population (Mesak et al. 2014), and detect low levels of differentiation (Coates et al. 2009, Morin et al.

2012). Some studies have even used genome-wide SNP data to identify distinct population units (Pante et al. 2014, Funk et al. 2016, Prince et al. 2017, Langin et al. 2018). Here I used SNP and microsatellite data sets from the same group of Gunnison sage-grouse samples to empirically evaluate agreement across marker types for population genetic analyses. The data I used are typical of the type of data often used in conservation: opportunistically collected, variable source, variable quality, and from multiple populations of variable size that are represented by variable numbers of samples. Additionally, I used previously identified candidate adaptive loci (Chapter 4) to evaluate identification of distinct units using data sets composed of genetic markers reflecting different evolutionary processes.

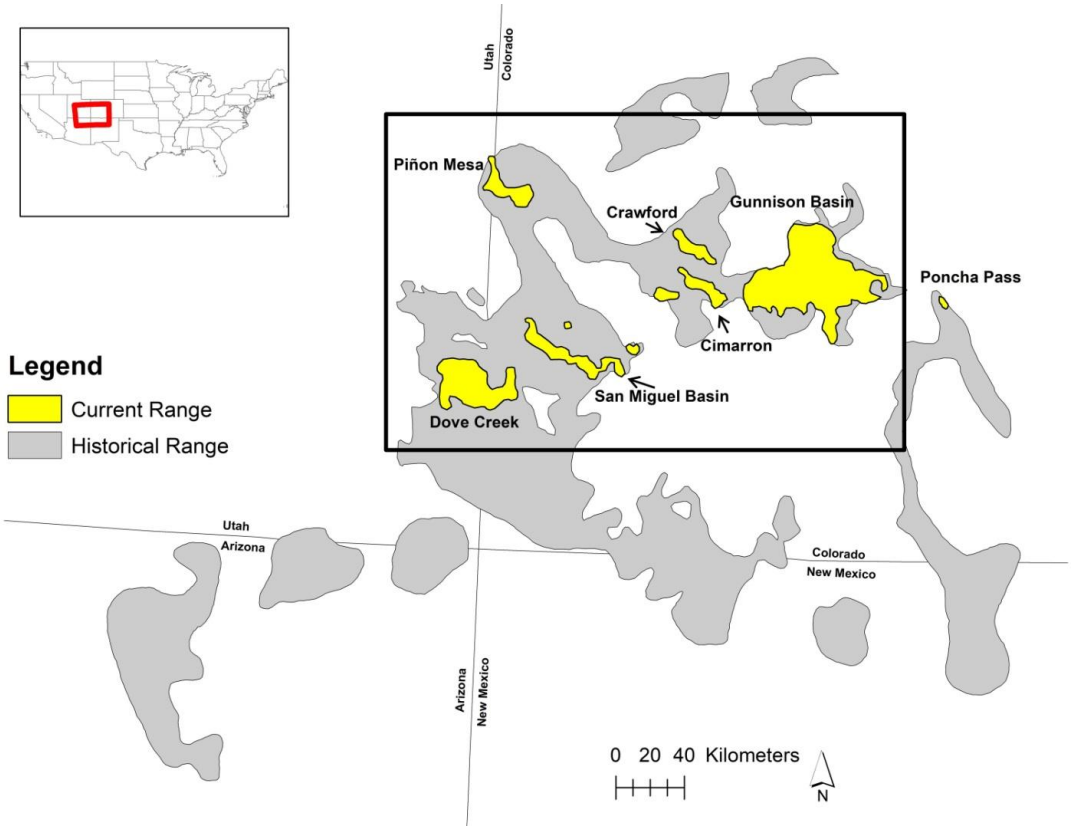

Figure 5. 1- Historical (gray) and current (yellow) distribution of Gunnison sage-grouse. Populations are labeled with respective names. Black rectangle designates the study area. The historical range map is as described by Braun et al. (2014); the two northernmost portions of the historical range correspond to an unknown species of sage-grouse and are not verified by Colorado Parks and Wildlife (Gunnison sage-grouse Rangewide Steering Committee 2005).

The Gunnison sage-grouse (*Centrocercus minimus*) is a sagebrush obligate avian species listed as threatened under the Endangered Species Act in 2014. The species exists as a network of seven populations predominantly occurring in Colorado, with a single population straddling the border between southwestern Colorado and southeastern Utah (Figure 5.1; Schroeder et al. 2004, Braun et al. 2014). The majority of individuals in the species (~85-90%) are located in the Gunnison Basin population, which is largest in land area and highest in genetic diversity (Oyler-McCance et al. 2005). The six remaining satellite populations support much smaller numbers of birds; in descending order San Miguel Basin, Piñon Mesa, Crawford, Dove Creek-Monticello (Dove Creek from here on), Cerro Summit-Cimarron-Sims Mesa (Cimarron from here on), and Poncha Pass (Table 5.1; United States Fish and Wildlife Service 2014). Genetic differentiation is high between all populations (Oyler-McCance et al. 2005), local environmental conditions are variable (Gunnison sage-grouse Range-wide Steering Committee 2005), and there is some evidence of adaptive divergence among populations (Chapter 4). The Poncha Pass population is thought to have been extirpated in the 1970s, re-established with individuals translocated from Gunnison Basin, and currently persists as the result of on-going translocations (Nehring and Apa 2000). Consequently, the Poncha Pass population was not included in these analyses.

Table 5. 1- Sample size for each population of Gunnison sage-grouse and each marker type: MSAT = microsatellites, SNP = single nucleotide polymorphisms. Population estimates of the 2004 population size = 2004 Pop. Est. (United States Fish and Wildlife Service 2014).

Population	# Samples		2004 Pop. Est.
	MSAT	SNP	
Cimarron	4	4	74
Crawford	21	12	157
Dove Creek	43	12	98
Gunnison Basin	116	12	3978
Pinon Mesa	19	10	182
Poncha Pass	0	0	10
San Miguel	51	10	206

I had three specific objectives in this study: (1) compare genetic diversity metrics across putatively neutral data sets, (2) compare genetic differentiation metrics across putatively neutral data sets and all SNPs, and (3) evaluate Gunnison sage-grouse for evidence of distinct evolutionary groups using putatively neutral, candidate adaptive loci, and a combination of both neutral and candidate adaptive loci.

Methods

Microsatellite Genotypes

I sampled 254 individuals across six of the populations. Sample size varied by population: Cimarron = 4, Crawford = 21, Dove Creek = 43, Gunnison Basin = 116, Piñon Mesa = 19, San Miguel = 51. I amplified 22 grouse-specific microsatellite loci using the Polymerase Chain Reaction (PCR) and with the components and concentrations described in Oyler-McCance and Fike (2011) with thermal profiles and annealing temperatures as originally published. The microsatellite primers used included: MSP11, MSP18, reSGCA5, reSGCA11, SG21, SG23, SG24, SG28, SG29, SG30, SG31, SG33, SG36, SG38, SG39, SGCTAT1, SGMS06.4, SGMS06.8, TTT3, TUT3, TUT4, and WYBG6 (Segelbacher et al. 2000, Piertney and Höglund

2001, Taylor et al. 2003, Caizergues et al. 2003, Oyler-McCance et al. 2010, Fike et al. 2015). See Chapter 2 for details on DNA extraction and genotyping.

Single Nucleotide Polymorphism (SNP) Genotypes

From the same 254 samples that were genotyped at microsatellite loci, a subset were chosen for RAD-Seq based on two criteria: population of origin and relatedness. The goal was to obtain an equal number of individuals from each population which were minimally related. The exception to these requirements was the Cimarron population, which only had four samples; consequently all Cimarron samples were included. These criteria for sample selection were necessary because of lmited funds and limited number of high quality samples. See Chapter 4 for details on RAD-Seq library preparation and bioinformatics. The SNP data set was composed of 15,033 loci across 35 "pseudo-chromosomes" (chromosome scaffolds inferred from synteny with chicken) for 60 individuals (Cimarron = 4, Crawford = 12, Dove Creek = 12, Gunnison Basin = 12, Pinon Mesa = 10, San Miguel = 10). A putatively adaptive SNP data set composed of all 3,751 loci identified as potentially under selection in outlier locus analyses and genotype-environment association analyses was also created. Environmental covariates used in the genotype-environment association included average spring precipitation, average fall precipitation, spring maximum temperature, winter maximum vapor pressure deficit, compound topographic index (a proxy for soil moisture), big sagebrush cover, and a dryness index (excluding the loci identified in the association with green-up rate; see Chapter 4 for details on loci under selection and a full explanation for excluding the loci associated with green-up rate). A putatively neutral SNP data set was created by excluding all putatively adaptive loci. The final putatively neutral SNP data set included 11,282 loci across 34 pseudo-chromosomes.

Analysis of genetic diversity

For each putatively neutral data set, I estimated observed heterozygosity (H_O), expected heterozygosity (H_E), allelic richness per locus (A_R), and inbreeding coefficient (F_{IS}) using the 'diveRsity' (Keenan et al. 2013) package in R (R Team 2016). Diversity metrics were calculated for each locus and reported as a mean and 95% confidence intervals constructed from the standard deviation across all loci. Mean allelic richness per locus (A_R) was estimate with 1,000 bootstraps. Diversity metrics were calculated for both data sets and used to compare estimates from microsatellite and putatively neutral SNPs. Pearson and Spearman rank correlation coefficients were estimated to evaluate congruence for all paired metrics. Wilcoxon paired signed-rank test in the R package 'MASS' (Venables and Ripley 2002) was used to evaluate ranking ability.

Analysis of Genetic Differentiation

For genetic differentiation I compared microsatellites, all SNPs, and putatively neutral SNPs. I used the 'diveRsity' package in R to calculate F_{ST} (Weir and Cockerham 1984) with confidence intervals based on 1,000 bootstraps. Because there is concern about comparing pair-wise F_{ST} values when using loci with variable levels of heterozygosity, I also calculated pair-wise G_{ST} (Hedrick 2005) and D_{Jost} (Jost 2008) with confidence intervals based on 1,000 bootstraps. D_{Jost} differs from both F_{ST} and G_{ST} in that it is a measure of the fraction of allelic variation among populations and is not constrained by the expected level of heterozygosity within the subpopulation (Jost 2008). Significance of relationships was evaluated with the Mantel *P*-value as calculated with the 'vegan' R package (Oksanen et al. 2017).

Analysis of Distinct Units

I compared the identification of distinct units using microsatellites, all SNPs, putatively neutral SNPs, and putatively adaptive SNPs. First, I performed discriminnant analysis of principal components (DAPC) with microstaellites, putatively neutral SNPs, all SNPs, and candidate adaptive loci with the 'adegenet' package in R (Jombart 2008). DAPC summarizes genotypes in principal components (PC) that are then used to construct linear functions that simulataneously maximize among-cluster variation and minimize within cluster variation.I used the K-means clustering algorithm and identified the number of genetic clusters based on the Bayesian Information Criterion (BIC). I retained all of the PCs, ran the algorithm for 100,000 iterations, and used 10 starting centroids per run. The number of genetic clusters (K) with the lowest BIC was selected, as recommended by Jombart et al. (2010). After I identified optimal K for each data set, I used the a-score method to identify the optimal number of PCs to retain in DAPC while constructing linear functions to describe genetic differentiation among K groups. Second, I created dendrograms for each data set using the hierarchical clustering algorithm *hclust* in R and using the "ward.D2" method (Ward 1963). The "ward.D2" method minimizes the total within cluster variance and minimizes information loss associated with each cluster. For comparison of hierarchical clustering methods I also included dendrograms created with a more conservative method tending to form loose groups, sometimes prematurely ("single" method; Appendix XXV) and a more relaxed method tending to form tighter and smaller groups ("complete" method; Appendix XXVI).

Results

Data

The putatively neutral data sets varied greatly in the number of loci and the number of individuals sampled. The microsatellite data set was composed of 22 sampled loci and 254

individuals in total, with variable representation by population (Cimarron = 4, Crawford = 21, Dove Creek = 43, Gunnison Basin = 116, Piñon Mesa = 19, San Miguel = 51). The putatively neutral SNP data set was composed of 11,282 sampled loci for 60 individuals (Cimarron = 4, Crawford = 12, Dove Creek = 12, Gunnison Basin = 12, Pinon Mesa = 10, San Miguel = 10). The putatively adaptive SNP data set was was compused of 3,751 sampled loci across the same 60 individuals. In contrast, the total SNP data set (composed of neutral and adaptive loci) was composed 15,033 SNPs for the same 60 individuals.

Genetic Diversity

For all diversity metrics 95% confidence intervals calculated from SNPs were narrower than confidence intervals from microsatellites (Figure 5.2, Appendix XXVII Table S27.1). Of the four metrics, H_O had the lowest correlation between values from microsatellites and SNPs (Spearman $\rho = 0.314$, Pearson $r = 0.324$). Microsatellite estimates had large confidence intervals, which resulted in no significant differences among population estimates of H_O. In contrast, SNPs produced much narrower confidence intervals resulting in significant differences between populations but also between most values from SNPs and microsatellites for all populations (Figure 5.2A). Values of H_O from microsatellites in all populations were ~0.500 (range: 0.464 – 0.548) while values from SNPs were lower, ~0.250 (range: 0.207 – 0.230; Figure 5.2B). However, both marker types were relatively consistent in ranking populations ($P = 0.031$, Wilcoxon paired signed-rank). High correlation between values from microsatellites and SNPs were observed for H_E (Spearman $\rho = 0.886$, Pearson $r = 0.938$), as well as relative consistency in ranking populations across marker types ($P = 0.031$, Wilcoxon paired signed-rank). The values for H_E were within similar ranges as H_O, microsatellite estimates at ~ 0.500 (range: 0.413 –

0.578) and SNP estimates at ~ 0.250 (range: 0.183 – 0.227; Figure 5.2C & 5.2D). Similarly, allelic richness showed high levels of correlation across marker types (Spearman $\rho = 1.000$, Pearson $r = 0.659$), consistent ranking of populations by levels of genetic diversity ($P = 0.031$, Wilcoxon paired signed-rank), although only the SNP data produced confidence intervals narrow enough to distinguish the populations (Figure 5.2E & 5.2F). Estimates of F_{IS} also showed relatively high correlation (Spearman $\rho = 0.829$, Pearson $r = 0.981$), however, ranking of populations was not consistent ($P = 0.438$, Wilcoxon paired signed-rank) and the magnitude of the values for each marker type resulted in different inferences (Figure 5.2G & 5.2H), where microsatellites indicated outbred (minimum value: -0.279) to slightly inbred (maximum value 0.071) populations while SNPs indicated slightly to moderately outbred populations (-0.193 – -0.006). In Cimarron, the excess of heterozygotes could be due to few parents contributing to successive generations in a small population.

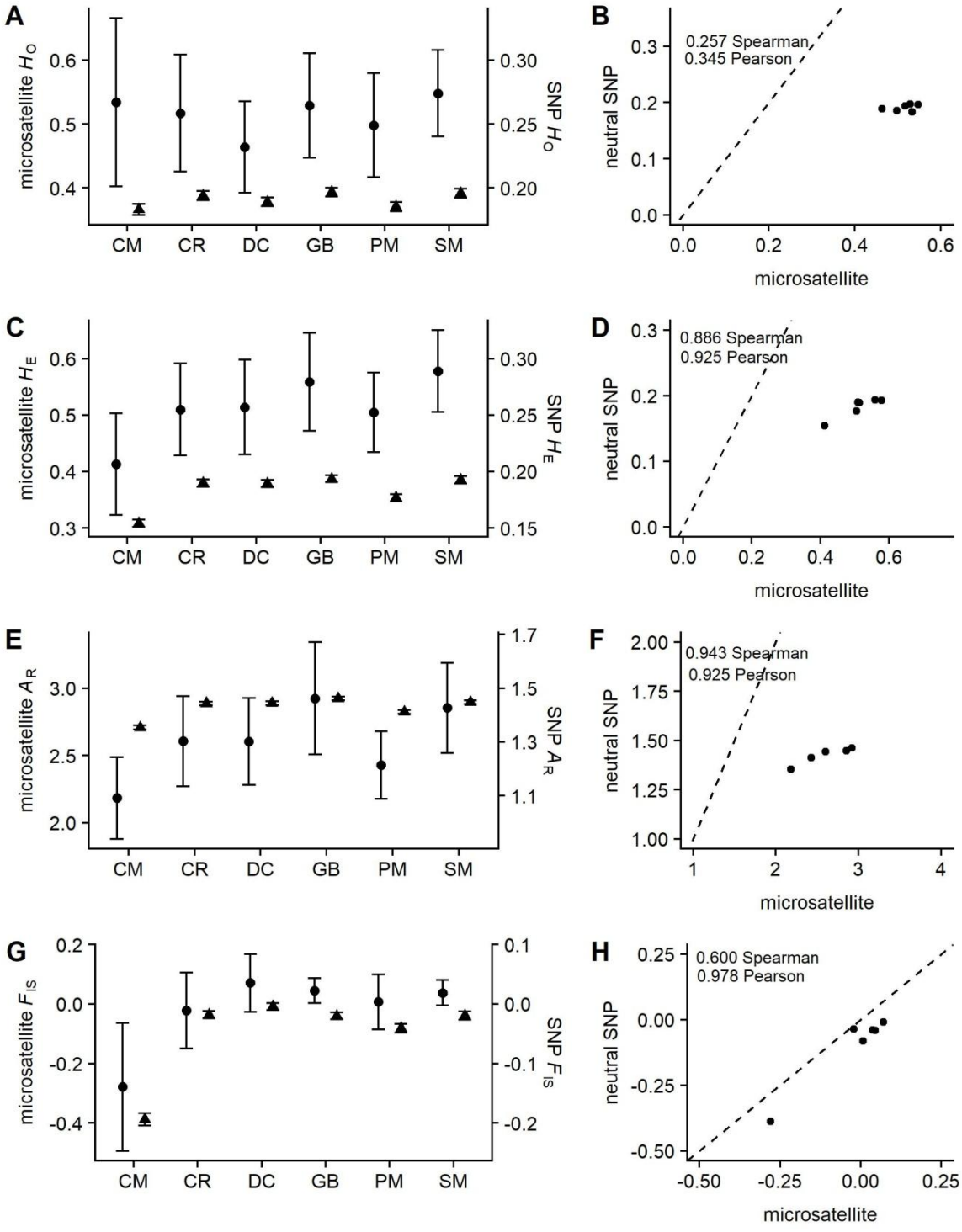

Figure 5. 2- Comparison of genetic diversity values for Gunnison sage-grouse populations with confidence intervals from microsatellite (●) and putatively neutral SNP (▲) loci. Estimates for observed heterozygosity (H_O; A), expected heterozygosity (H_E; C), allelic richness (A_R; E), and inbreeding coefficient (F_{IS}; G) are shown in the left-hand column. Populations are abbreviated along the x-axis: CM = Cimarron, CR = Crawford, DC = Dove Creek, GB = Gunnison Basin,

PM = Piñon Mesa, SM = San Miguel. Relationships between estimates from microsatellites and SNPs for H_O (B), H_E (D), A_R (F) and F_{IS} (H) are shown in the right-hand column. Spearman rank and Pearson's correlation coefficient are also included in the plots in the right-hand column. Dashed line corresponds to a 1:1 relationship.

Genetic Differentiation

Generally, genetic differentiation estimates from both SNP data sets had narrower confidence intervals in comparison to estimates from microsatellites (Figure 5.3, Appendix XXVIII Table S28.1) which were significantly correlated in all pair-wise comparisons (*Mantel r* = 0.9, $P = 0.001$). All differentiation metrics had a high correlation across data sets (Figure 5.4). Among data sets, estimates of F_{ST} had the lowest correlation between microsatellites and putatively neutral SNPs (Spearman $\rho = 0.911$, Pearson $r = 0.961$) and all SNPs (Spearman $\rho = 0.911$, Pearson $r = 0.940$) while G_{ST} and D_{Jost} had nearly equivalent levels of correlation between microsatellites and putatively neutral SNPs (G_{ST}: Spearman $\rho = 0.921$, Pearson $r = 0.967$; D_{Jost}: Spearman $\rho = 0.957$, Pearson $r = 0.966$) and all SNPs (G_{ST}: Spearman $\rho = 0.94$, Pearson $r = 0.95$; D_{Jost}: Spearman $\rho = 0.946$, Pearson $r = 0.951$). For F_{ST} and G_{ST}, confidence intervals for population estimates from microsatellites and both SNP data sets typically overlapped (Figure 5.3A & 5.3B). Estimates of D_{Jost} from microsatellites and both SNP data sets did not overlap and the magnitude of microsatellite estimates were consistently much higher in comparison to SNP estimates (Figure 5.3C), though the same general pattern remained (Figure 5.4C & 5.4I).

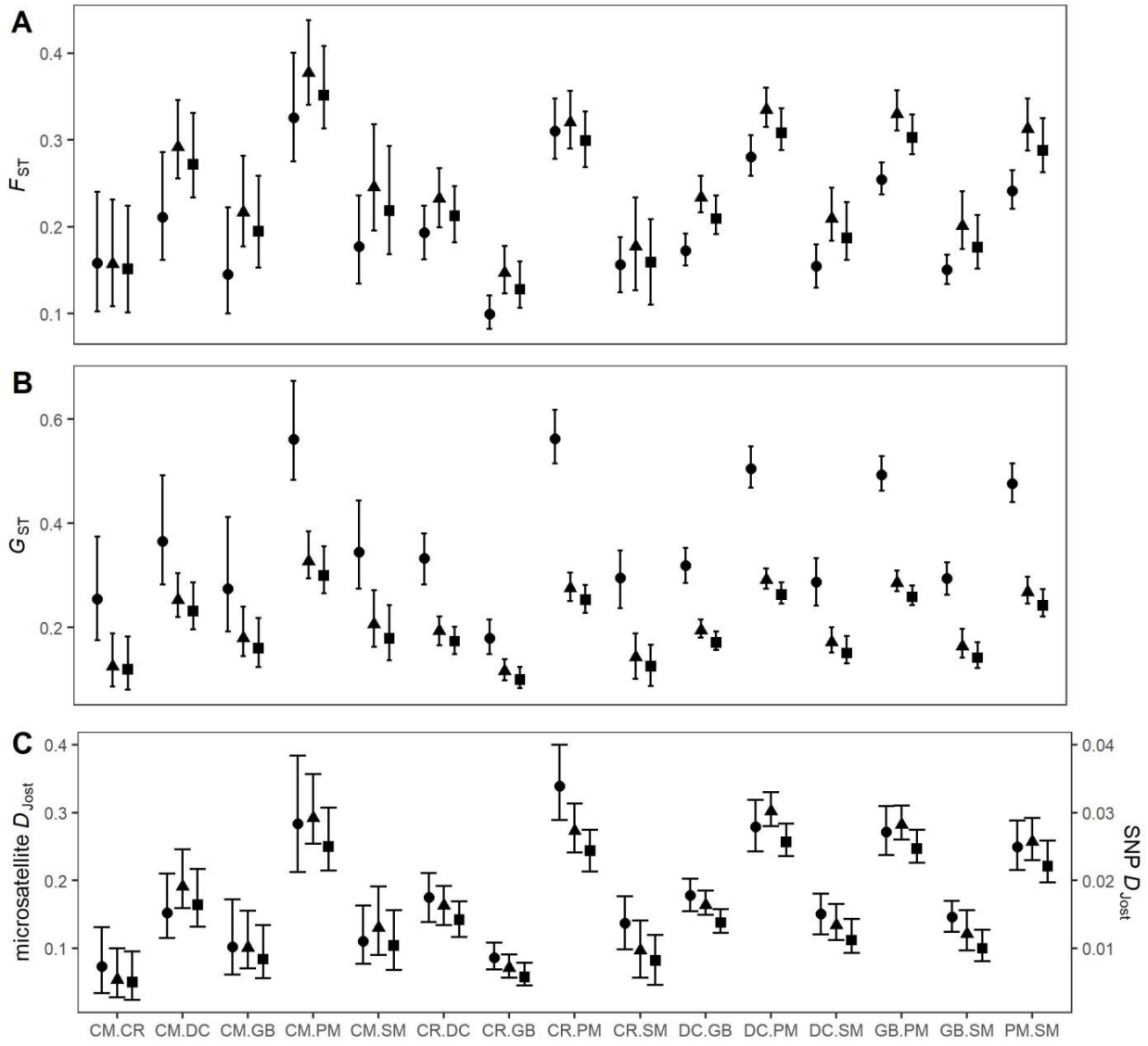

Figure 5. 3- Comparison of genetic differentiation values for pair-wise comparisons of Gunnison sage-grouse populations with confidence intervals from microsatellite (●), putatively neutral SNP (▲), and all SNP (■) loci. Pair-wise estimates are for F_{ST} (A), G_{ST} (B), and D_{Jost} (C). Populations in pair-wise comparisons are abbreviated along the x-axis: CM = Cimarron, CR = Crawford, DC = Dove Creek, GB = Gunnison Basin, PM = Piñon Mesa, SM = San Miguel; CM.CR = F_{ST} between Cimarron and Crawford.

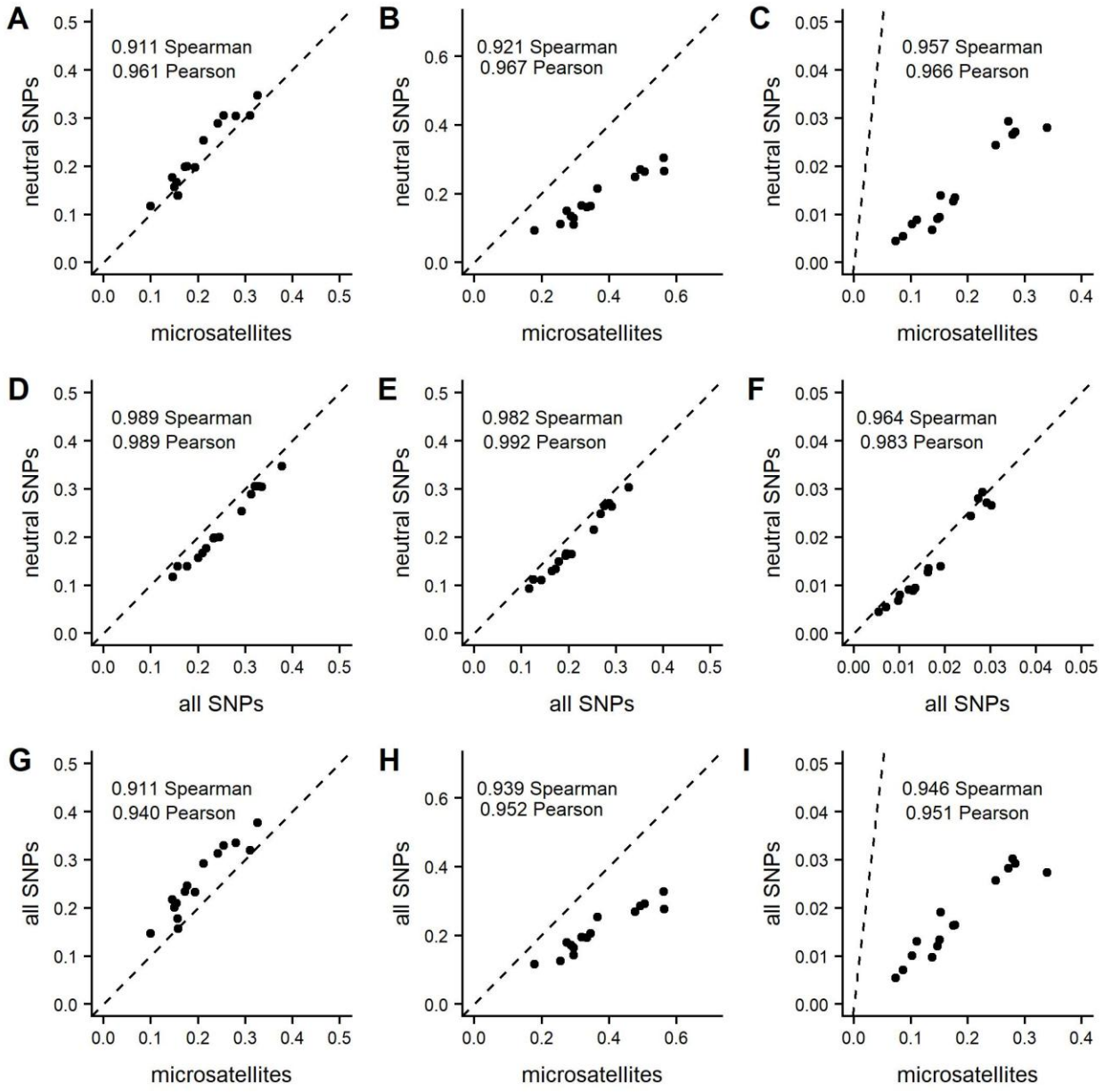

Figure 5. 4- Relationships between estimates from different data sets: microsatellites, putatively neutral SNPs, and all SNPs for F_{ST} (A,D,G), G_{ST} (B,E,H), and D_{Jost} (C,F,I) are shown in respective panels. Axes are labeled by data set. Spearman rank and Pearson's correlation coefficient are included in the upper left-hand corner of each panel. Dashed line corresponds to a 1:1 relationship.

Distinct Units

The lowest BIC for hypothetical genetic clusters in DAPC corresponded to 6 groups with microsatellites (BIC = 484.603) and 5 groups with all SNPs (BIC = 454.768), putatively neutral SNPs (BIC = 397.632), and putatively adaptive SNPs (BIC = 364.744). The optimal number of PCs as determined by the a-score method to include in the DAPC analysis was 22 for microsatellites, 6 for all SNPs, 5 for putatively neutral SNPs, and 1 for putatively adaptive SNPs. Clustering of individuals in DAPC with microsatellites identified Piñon Mesa as the only population that clearly separates from the other populations along discriminant function 1 (Figure 5.5A), while discriminant function 2 pulls populations into identifiable groups though still with overlap (Figure 5.6A). With all and putatively neutral SNPs, discriminant function 1 separates Gunnison Basin and Piñon Mesa from the other populations (Figures 5.5B & 5.5C), and discriminant function 2 separates Dove Creek (Figure 5.6B & 5.6C). The candidate adaptive loci data set shows Piñon Mesa and Dove Creek clearly separated along discriminant function 1, while San Miguel is beginning to separate from the overlapping peaks of Cimarron, Crawford, and Gunnison Basin (Figure 5.5D).

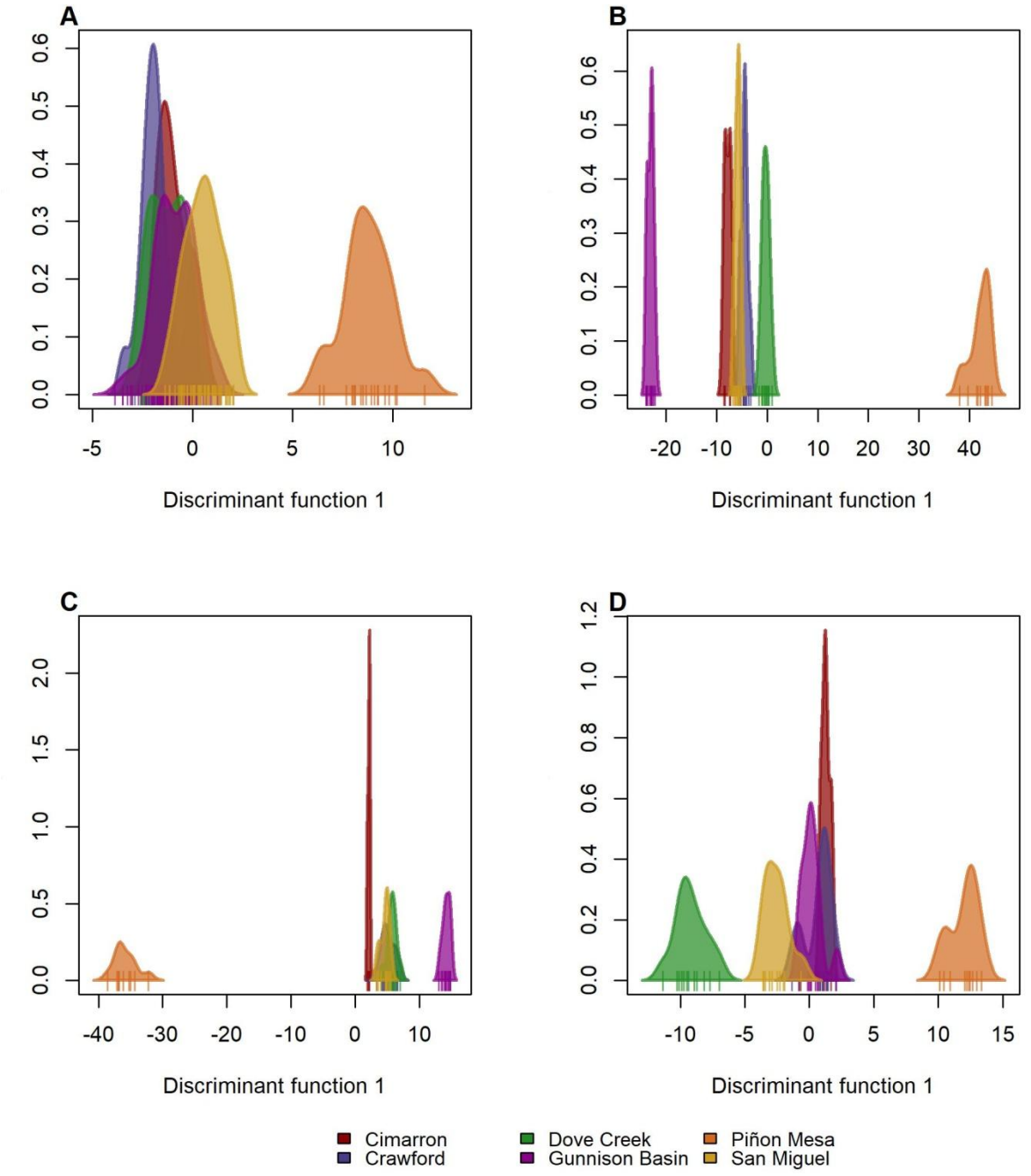

Figure 5. 5- Separation of Gunnison sage-grouse populations along discriminant function one. Individual density along the first axis from the discriminant analysis of principle components (DAPC) for microsatellite (A), all SNPs (B), putatively neutral SNPs (C), and candidate adaptive loci (D). Colors indicate sampling origin.

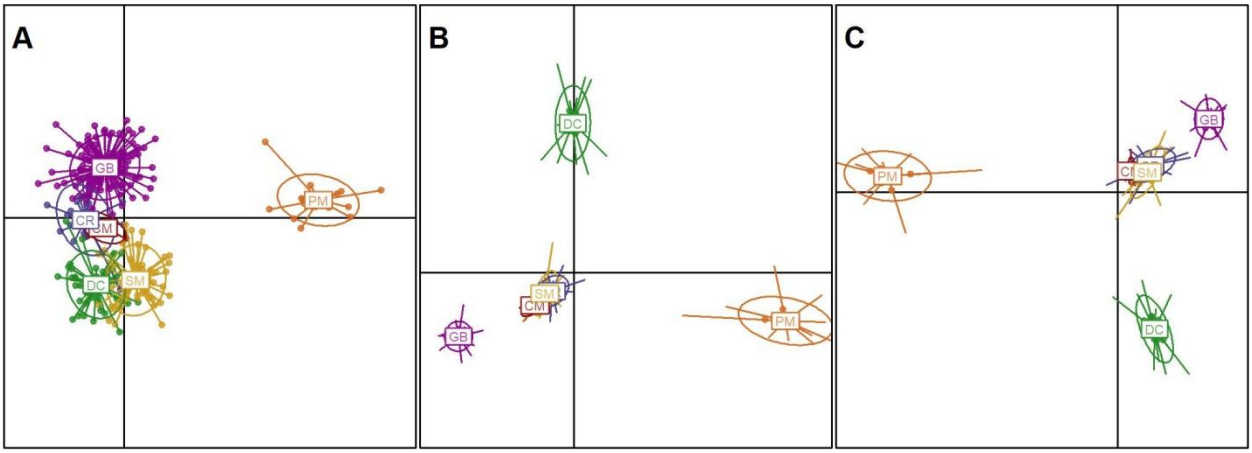

Figure 5. 6- Star plots of the first two axes from the discriminant analysis of principle components (DAPC) for Gunnison sage-grouse data sets composed of (A) microsatellite, (B) all SNPs, and (C) putatively neutral SNPs. Each point represents an individual color coded by sampling origin. The DAPC analysis with candidate adaptive loci only retained one PC so is excluded here.

The dendrogram created from microsatellite data generally grouped individuals into known populations where Cimarron, Crawford, and Gunnison Basin group closest together with Piñon Mesa, Dove Creek, and San Miguel grouping closer together but away from the Cimarron, Crawford, Gunnison Basin individuals (Figure 5.7A). Cimarron and Crawford individuals were grouped together on a single branch. Two individuals are inconsistent with the trend of clustering by geographic population, an individual from Gunnison Basin and an individual from San Miguel cluster with the Dove Creek individuals. Similar to the clustering pattern observed in DAPC, all SNPs and putatively neutral SNPs resulted in indistinguishable grouping patterns where all populations are identifiable on individual branches (Figure 5.7B & 5.78C). With both the all SNP and putatively neutral SNP data sets Cimarron, Crawford, and Gunnison Basin group most closely, Piñon Mesa is the most distant from the center, and a single individual sampled in Crawford groups with the San Miguel individuals. In addition to the Crawford individual

grouping with San Miguel, the putatively neutral SNPs show a San Miguel individual grouping with Cimarron (Figure 5.7C). Though similar to the other SNP dendrograms in that samples clustered into distinct populations, branch lengths appear somewhat longer in the candidate loci data set, in particular for Gunnison Basin, San Miguel, Piñon Mesa, and Dove Creek (Figure 5.7D). When considering hierarchical clustering using methods in addition to "ward.D2", the patterns are generally similar though some differences are notable, particularly when comparing the results of microsatellites to any of the SNP data sets. The "single" method, which bases distance between groups on the closest individual in each group, does not result in distinct populations using microsatellite data (Appendix XXV Figure S25.1A), but results in the same clustering pattern as the "ward.D2" method for all SNPs (Appendix XXV Figure S25.1B), putatively neutral SNPs (Appendix XXV Figure S25.1C), and candidate loci (Appendix XXV Figure S25.1D). The "complete" method, which bases distance between groups on the most distant individuals, shows Cimarron, Crawford, and San Miguel individuals nested between groups of Gunnison Basin individuals while Dove Creek and Piñon Mesa are distinct when using microsatellites (Appendix XXVI Figure S26.1A), but results in nearly the same clustering pattern as with "ward.D2" when using all SNPs (Appendix XXVI Figure S26.1B), putatively neutral SNPs (Appendix XXVI Figure S26.1C) and candidate adaptive loci (Appendix XXVI Figure S26.1D), though a single San Miguel individual clusters with Cimarron using all SNPs and putatively neutral SNPs (Appendix XXVI Figure S26.1B & S26.1C).

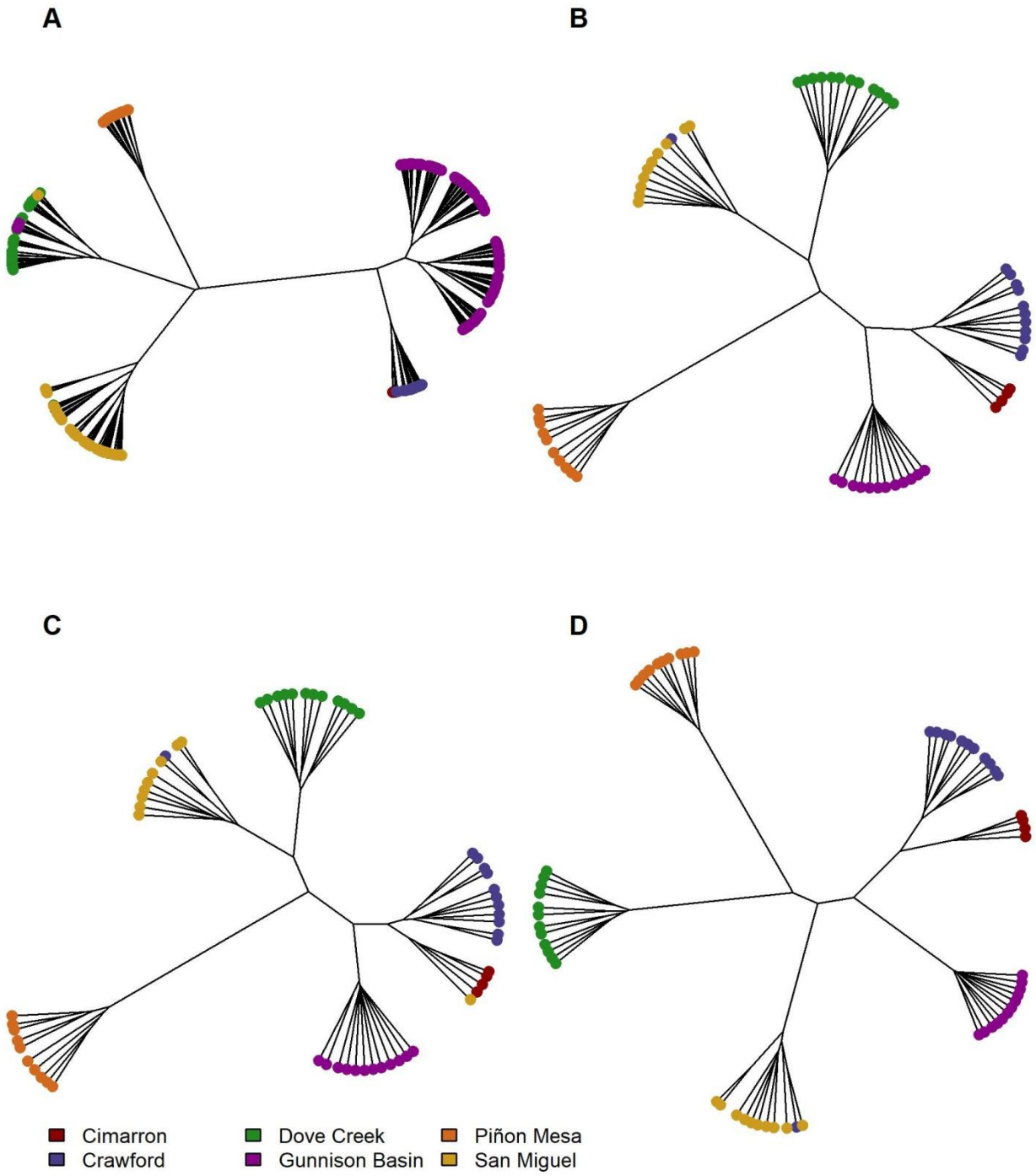

Figure 5. 7- Dendrograms created with the hierarchical clustering method ward.D2 for each data set: microsatellites (A), all SNPs (B), putatively neutral SNPs (C), and candidate adaptive loci (D). Colors indicate sampling origin.

Discussion

I found that measures of diversity and differentiation generated from microsatellite and SNP data were typically in agreement. However, metrics of differentiation had consistently higher correlation than most metrics of diversity. My results also confirmed that increased numbers of SNP loci can dramatically reduce the confidence intervals for mean estimates, increasing precision, although this was not true for F_{ST}. I also demonstrated that clustering of individuals for the purpose of identifying evolutionarily or demographically distinct units can be variable depending on clustering method used and marker type.

Genetic Diversity

Of the four diversity metrics evaluated here, H_E, F_{IS}, and A_R were the metrics with the highest correlation between microsatellites and SNPs (see Figure 5.2). H_O showed relatively low correlation across marker types. Additionally, the high variance in microsatellite data for all diversity metrics resulted in almost no significant difference between populations, which could be detected with SNPs, similar to findings by Fischer et al. (2017). Some previous work shows generally high correlation between estimates of heterozygosity from SNPs and microsatellites that became stronger as the number of SNPs used increased (Miller et al. 2014). However heterozygosity in this case was calculated as the standardized multilocus heterozygosity. The generally high correlation of H_E across marker types is consistent with previous studies by Fischer et al. (2017) and Langin et al. (2018). Neither of these studies report correlation of H_O, and so I could not compare my relatively low correlation across marker types for H_O to another study. However, the correlation between heterozygosity from different genetic marker types is

thought by some to be high only when the loci used represent a high proportion of the total polymorphism in a given genome (Chakraborty 1981, DeWoody and DeWoody 2005). It is possible that either my microsatellite or SNP genotype data sets do not reflect the true level of genome-wide polymorphism, and therefore H_O is not being accurately calculated. Despite my SNP data being composed of only biallelic loci, there was high correlation between estimates of allelic richness for microsatellites and SNPs (Figure 5.2E & 5.2F). There are diversity metrics developed specifically for SNP data such as nucleotide diversity (π) and the genomic inbreeding coefficient (F_{ROH}; Curik et al. 2017) that might be more appropriate for SNP data sets, especially if it is unknown whether the genome wide polymorphisms are sufficiently represented in the data. However, my results show generally high correlation between most diversity metrics calculated from microsatellites and SNPs, and the increased precision in estimates allow the distinction of populations when using SNP data.

Genetic Differentiation

All metrics of differentiation showed high correlation between microsatellites and all SNP data sets, with correlation coefficients greater than 0.900 in all tests (Figure 5.4) and significant Mantel correlations (*Mantel* $r > 0.9$, $P \leq 0.05$ for all comparisons). Although the case has been made that a single measure of differentiation can be constrained by within-population diversity or may be inadequate to capture the differentiation process (Meirmans and Hedrick 2011, Verity and Nichols 2014), my findings echo other empirical examples where different metrics result in the same inference (Coates et al. 2009, Funk et al. 2016), but only when ranking of populations is concerned (Wilcoxon paired signed-rank test $P \leq 0.05$ in all comparisons).

Different metrics of population differentiation showed a consistent pattern of which populations were most similar, though the magnitude of a metric was sometimes very different. If the magnitude of the differentiation metric is of relevance, then the marker types are not equivalent. Similar to some previous studies, I found D_{Jost} tended to produce values higher in magnitude with microsatellites than with SNPs (Langin et al. 2018). While I also found high G_{ST} estimates with microsatellites, the magnitude of difference between the values calculated from different marker types was not as dramatic as that with D_{Jost}. The consistently higher values for some differentiation metrics with microsatellites could result in different conclusions from a conservation perspective, simply due to the marker type that was used. The main difference between the three differentiation metrics evaluated here, is that one metric (F_{ST}) accounts for mutation rate of marker type while the other two (G_{ST} and D_{Jost}) do not (Whitlock 2011). Whitlock (2011) demonstrated that for low mutation rates, approximately that of SNPs (10E-9), relative to migration rates, and a small number of populations, D_{Jost} will be much smaller in magnitude, while this decline in magnitude was not as apparent in G_{ST} which may even be greater in magnitude than F_{ST}. Gunnison sage-grouse is composed of seven isolated populations, which previous genetic studies have indicated very low migration rates among populations, though not as low as SNP mutation rates. Nevertheless, the low migration rates are consistent with the impacts different population configurations can have on the suitability of different metrics for differentiation in different systems. My comparison of F_{ST} values across marker types demonstrates relatively consistent agreement between both magnitude and ranking of pair-wise comparisons (Figure 5.3A). In fact, in some population comparisons the F_{ST} values calculated from SNP data are significantly higher than the values calculated from microsatellites. In addition to performance differences across the metrics, the ecological question of interest can

also help when deciding which metric is most appropriate. D_{Jost} is an actual relative degree of differentiation of allele frequencies among populations (Jost 2009), while G_{ST} and F_{ST} are considered measures of the reduction in heterozygosity as a result of population structure or the variance in allele frequency among populations (Whitlock 2011). For example, if one was interested in locus specific effects, D_{Jost} would be more appropriate than G_{ST} or F_{ST}. Conversely, if population average effects are of interest, G_{ST} or F_{ST} would be more appropriate.

The number of alleles per locus can also impact the ability to detect reproductively isolated groups. If a locus only has two alleles, as is typical with SNP loci, the chances of populations differing in allele frequencies at high enough levels to detect isolation is lower. Conversely, if a locus has multiple alleles shared among populations, the differences in allele frequencies are more likely to be detected, therefore showing the level of reproductive isolation. The microsatellite loci used in this study had between three and 18 alleles per locus, while the SNP data only had two alleles per locus. However, the low number of microsatellite loci (22) compared to the greater number of SNP loci (11,282) used in my analyses might explain why metrics that are averaged over multiple loci were generally higher in magnitude for the data set with a greater number of alleles per locus. Some argue there is an ascertainment bias of highly polymorphic microsatellite loci as a result of the process of genetic marker development that can result in an upward bias in genome-wide diversity and a reduction in sensitivity to evaluate genome-wide levels of genetic differentiation (Brandström and Ellegren 2008, Väli et al. 2008). Additionally, Coates et al. (2009) found analogous patterns between F_{ST} estimates from SNPs and microsatellites, obtaining values with SNP data that were three times larger in magnitude than values from microsatellites, which they attributed to homoplasy at microsatellite loci resulting in an overestimate of gene flow. Contrary to my findings, Fischer et al. (2017) found

that whole-genome re-sequencing derived SNPs resulted in significantly lower F_{ST} values that they attribute to the detection of numerous rare variants that might otherwise be missed with a reduced representation sequencing approach like the one I used to generate SNP data.

In addition to the gain in precision in estimates of differentiation with SNPs, the clustering analyses showed a similar increase in precision. Individuals predominantly clustered into distinct populations with putatively neutral SNPs (Figure 5.5C and Figure 5.6C) versus the somewhat loose clusters of individuals with microsatellite loci (Figure 5.5A and Figure 5.6A). One of the differences in the microsatellite data was the number of individuals sampled (256 versus 60 in the SNP data sets), which might contribute to the lower resolution in clustering analyses when compared to the SNP data. However, when I looked at clustering of microsatellite data using only the 60 individuals included in the SNP data, the patterns of clustering remain the same (Appendix XXIX Figure S29.1 & Appendix XXX Figure S30.1).The observed neutral loci clustering pattern is consistent with previous studies on clustering analyses (Morin et al. 2012). We did not evaluate clustering with program STRUCTURE (Pritchard et al. 2000) although previous comparisons indicated variability across genetic marker types with this program (Morin et al. 2012). The patterns we observed with DAPC using microsatellite data mirror those we have observed in previous studies employing STRUCTURE on this data set (Chapter 2).

It has been suggested that two to 11 times more SNP loci would be required to obtain the resolution in differentiation comparable to that obtained with microsatellites (Kalinowski 2002; Morin et al. 2004, Inghelandt et al. 2010). However, more recent work has indicated fewer SNPs are sufficient (Ryynänen et al. 2007, Narum et al. 2008, Coates et al. 2009, Morin et al. 2009), even when identifying conservation units (Morin et al. 2009), and especially with a large population sample size (Morin et al. 2012). However, populations with low levels of

differentiation (e.g., demographic but not evolutionary independence) would be difficult to identify with fewer SNPs (Morin et al. 2009). I did not explicitly evaluate the number of SNP loci required to obtain estimates with the precision of microsatellites, though I do demonstrate that 11,282 SNPs results in comparable estimates as 15,033 SNPs. My study likely reflects a typical number of SNPs which would be obtained with a RAD-Seq protocol, the most commonly used approach for wildlife species. The high relatedness and polygynous mating system might result in low genetic diversity and therefore fewer polymorphic loci than would be expected from a random mating population with relatively high levels of genetic diversity. Nevertheless, my results indicate RAD-Seq generated SNP genotypes can produce comparable, and even more preceise, estimates to that obtained with microsatellites.

Distinct Units

My clustering analyses showed general agreement between the putatively neutral SNPs, all SNPs, and the candidate adaptive loci (Figure 5.5B, 5.5C, & 5.5D, Figure 5.6B, & 5.6C, Figure 5.7B, 5.7C, & 5.7D), where individuals generally cluster by population of origin. There is evidence that two or three of the populations are experiencing adaptive divergence when only candidate adaptive loci are considered: Piñon Mesa, Dove Creek, and potentially San Miguel (Figure 5.5D, Figure 5.7D). Cimarron, Crawford, and Gunnison Basin are clustering together suggesting they are adapting similarly. Though the small populations and small sample sizes could be causing fixation of alleles due to strong drift, the approaches used to identify candidate adaptive loci generally control for demography (e.g., BayPass; see Chapter 4 for details).

In the DAPC analysis of putatively neutral SNPs (Figure 5.5C), Gunnison Basin separates out and San Miguel clusters with Cimarron and Crawford. Previous work indicated San Miguel holds several candidate adaptive loci and/or genes (Chapter 4). When all SNP loci are considered it appears drift, or neutral processes, may be stronger than natural selection in San Miguel (Figure 5.5B). My findings suggest Piñon Mesa may be the most likely population to be evolving independently, and potentially Dove Creek. However, the ratio of neutral versus adaptive loci undoubtedly influences identification of evolutionarily distinct units. I previously identified 3,751 SNPs as potentially adaptive, which indicates ~25% of the SNPs in my all SNP data set are potentially under selection. When all SNPs were considered a subtle pattern of divergence in two populations, Gunnison Basin and Piñon Mesa, was observed (Figure 5.5B). Adaptive loci indicate three populations, Piñon Mesa, Dove Creek, and San Miguel, as distinct (Figure 5.5D). The total number of SNPs obtained is a function of the sampling method used and decisions made in the bioinformatics steps. When attempting to use both neutral and adaptive loci to characterize distinct evolutionarily significant units, in addition to considering themarker type, it could be important to identify a proportion of the genome which must hold the signal for adaptive divergence for formal designation. In other words, what proportion of the genome should be displaying adaptive divergence to designate a distinct group as evolutionarily significant? Tienderen et al. (2002) suggested considering divergence at ecologically important genes, referring to these as functionally significant units (FSUs). Perhaps clustering of individuals at both neutral loci and ecologically important coding regions could be investigated to identify FSUs. The idea of functional differences defining conservation units has recently been taken to an extreme, where a single gene of large effect marks the difference between populations of early and late migrating Pacific salmon (Prince et al. 2017). Most genes

underlying phenotypes are quantitative in nature, and so single gene definitions of conservation units will be rare at best (Kardos and Shafer 2018). The recent focus on defining conservation units has prompted some to urge the consideration of conserving or restoring habitat instead of using limited resources to identify functionally significant genes, unless the genes underlie demonstrably important traits and have acquired some degree of certainty in the significance of the important traits (Kardos and Shafer 2018). However, it should be remembered that the frequency of speciation through vicariance events indicates that over emphasizing adaptation when identifying variation important to evolution could result in missing essential units (Dimmick et al. 1999). It should also be stated that traits that are adaptive in a given environment presently may not be locally adapted in future environments, particularly if climate change is likely to result in alteration of the local environment. Importantly, questions of local adaptation and evolutionary independence cannot be addressed with microsatellite, or any neutral loci alone. Therefore, attempts to identify ESUs should focus on using SNP data, or a combination of neutral (microsatellite or SNP) and known ecologically important functional regions. It must also be acknowledged that conservation of specific genes is equivalent to artificial selection, which could ultimately result in reduced effective population size, increased inbreeding, and reduced adaptive capacity (Kardos and Shafer 2018).

Conclusion

This study is a comparison of the use of SNPs versus microsatellites to evaluate genetic diversity, genetic differentiation, and clustering for a species with relatively high population structure using the most common method of obtaining SNP genotypes for non-model organisms.

I have demonstrated that differentiation and diversity metrics generally have high concordance between genetic marker types. However, if values of any of the metrics evaluated here are to be used as conservation targets it should be remembered that different marker types may produce values that show similar patterns that differ substantially in magnitude. My results provide further support that the differentiation metric used and the expected magnitude of values will also depend on the migration rate between populations as well as the number of populations. Consequently, if thresholds for differentiation are of interest, consideration must be given to the marker type used for evaluation and the configuration of the species of interest. Given that values of differentiation can depend on marker type, use of thresholds for differentiation metrics to make decisions should be avoided if possible. If the magnitude of the value is not of importance, all metrics except H_O were able to consistently rank populations or population pairs across marker types in my study. However, SNPs may have an advantage over microsatellites with the increased precision of the estimates resulting in significant differences among populations, which were not detected with microsatellite data.

The clustering analyses generally showed the same patterns across marker types, although SNPs had more power to distinctly separate populations. Given that my results in the clustering analyses showed some variation based on clustering method and marker type, it might be important to evaluate clustering of individuals with multiple methods and multiple data sets when identifying demographically distinct units. If questions regarding non-neutral genetic processes are of interest, as is the case with the identification of ESUs, then SNP data sets are required. If only neutral genetic processes are of interest, then it may be useful to consider the precision required for the specific objective, as well as the resources required to obtain SNP data. Generating SNP data sets requires relatively large quantities of high quality DNA, which is often

difficult to obtain from species of conservation concern. However, it is possible to get SNP data from low quality DNA if a targeted capture approach can be used. Microsatellite analyses can be done using low quantities of relatively low quality DNA that can be non-invasively collected. Though development of microsatellite primers has been time consuming and costly in the past, recent approaches to develop microsatellites have made these data more accessible (e.g., Castoe et al. 2014). In cases where there are already microsatellite primers developed for a target of conservation, or where genetic data has been collected previously as a monitoring tool, it may not make sense to abandon the current work flow in favor of developing SNP loci. Although general usefulness of microsatellites in the future is uncertain, microsatellite loci will likely remain useful for parentage analysis due to their highly polymorphic nature. My evaluation of Gunnison sage-grouse for evidence of ESUs using neutral loci (microsatellites and SNPs), putatively neutral and adaptive loci, and candidate adaptive loci supported the hypothesis of independent evolution in two or three populations, though not overwhelmingly. Future investigation of ESUs using RAD-Seq generated SNP data should consider what proportion of the loci should be displaying signals of adaptive divergence, or which genes should hold these signals, to be categorized as an ESU, though great care should be taken when deciding which genes are ecologically significant.

LITERATURE CITED

Allendorf, F. W., P. A. Hohenlohe, and G. Luikart. 2010. Genomics and the future of conservation genetics. Nature Reviews 11:697–709.

Allendorf, F. W., G. Luikart, and S. N. Aitken. 2013. Conservation and the Genetics of Populations. 2nd edition. Volume 97. Wiley-Blackwell, New York.

Amos, W., J. I. Hoffman, A. Frodsham, L. Zhang, S. Best, and A. V. S. Hill. 2007. Automated binning of microsatellite alleles: Problems and solutions. Molecular Ecology Notes 7:10–14.

Baird, N. A., P. D. Etter, T. S. Atwood, M. C. Currey, A. L. Shiver, Z. a Lewis, E. U. Selker, W. a Cresko, and E. a Johnson. 2008. Rapid SNP discovery and genetic mapping using sequenced RAD markers. PloS one 3:e3376.

Baumung, B. R., H. Simianer, and I. Hoffmann. 2004. Genetic diversity studies in farm animals – a survey. Journal of Animal Breeding and Genetics 121:361–373.

Brandström, M., and H. Ellegren. 2008. Genome-wide analysis of microsatellite polymorphism in chicken circumventing the ascertainment bias. Genome Research 18:881–887.

Braun, C. E., S. J. Oyler-McCance, J. A. Nehring, M. L. Commons, J. R. Young, and K. M. Potter. 2014. The historical distribution of Gunnison sage-grouse in Colorado. The Wilson Journal of Ornithology 126:207–217.

Broders, H. G., S. P. Mahoney, W. A. Montevecchi, and W. S. Davidson. 1999. Population genetic structure and the effect of founder events on the genetic variability of moose, *Alces alces*, in Canada. Molecular Ecology 8:1309–1315.

Brousseau, L., P. V. A. Fine, E. Dreyer, G. G. Vendramin, and I. Scotti. 2018. Genomics of microgeographic adaptation in the hyperdominant Amazonian tree *Eperua falcata* Aubl. (Fabaceae). bioRxiv.

Brumfield, R. T., P. Beerli, D. A. Nickerson, and S. V. Edwards. 2003. The utility of single nucleotide polymorphisms in inferences of population history. Trends in Ecology and Evolution 18:249–256.

Caizergues, A., O. Rätti, P. Helle, L. Rotelli, L. Ellison, and J. Y. Rasplus. 2003. Population genetic structure of male black grouse (*Tetrao tetrix* L.) in fragmented vs. continuous landscapes. Molecular Ecology 12:2297–2305.

Castoe, T. A., A. W. Poole, A. P. J. de Koning, K. L. Jones, D. F. Tomback, S. J. Oyler-McCance, J. A. Fike, S. L. Lance, J. W. Streicher, E. N. Smith, and D. D. Pollock. 2012. Rapid microsatellite identification from Illumina paired-end genomic sequencing in two birds and a snake. PloS one 7:e30953.

Chakraborty, R. 1981. The distribution of the number of heterozygous loci in an individual in natural populations. Genetics 98:461–466.

Coates, B. S., D. V. Sumerford, N. J. Miller, K. S. Kim, T. W. Sappington, B. D. Siegfried, and L. C. Lewis. 2009. Comparative performance of single nucleotide polymorphism and microsatellite markers for population genetic analysis. Journal of Heredity 100:556–564.

Crandall, K. A., O. R. . Bininda-Emonds, G. M. Mace, and R. K. Wayne. 2000. Considering evolutionary processes in conservation biology. Trends in Ecology and Evolution 15:290–295.

Curik, I., M. Ferenčakovic, and J. Sölkner. 2017. Genomic dissection of inbreeding depression: A gate to new opportunities. Revista Brasileira de Zootecnia 46:773–782.

Davey, J. W., P. A. Hohenlohe, P. D. Etter, J. Q. Boone, J. M. Catchen, and M. L. Blaxter. 2011. Genome-wide genetic marker discovery and genotyping using next-generation sequencing. Nature Reviews Genetics 12:499–510. Nature Publishing Group.

Davison, A., and S. Chiba. 2003. Laboratory temperature variation is a previously unrecognized source of genotyping error during capillary electrophoresis. Molecular Ecology Notes 3:321–323.

De Wit, P., and S. R. Palumbi. 2013. Transcriptome-wide polymorphisms of red abalone (Haliotis rufescens) reveal patterns of gene flow and local adaptation. Molecular Ecology 22:2884–97.

Desalle, R., and G. Amato. 2004. The expansion of conservation genetics. Nature Reviews 5:702–712.

DeWoody, Y. D., and J. A. DeWoody. 2005. On the estimation of genome-wide heterozygosity using molecular markers. Journal of Heredity 96:85–88.

Dimmick, W. W., M. J. Ghedotti, M. J. Grose, A. M. Maglia, D. J. Meinhardt, and D. S. Pennock. 1999. The importance of systematic biology in defining units of conservation. Conservation Biology 13:653–660.

Fike, J. A., S. J. Oyler-McCance, S. J. Zimmerman, and T. A. Castoe. 2015. Development of 13 microsatellites for Gunnison sage-grouse (*Centrocercus minimus*) using next-generation shotgun sequencing and their utility in greater sage-grouse (*Centrocercus urophasianus*).

Conservation Genetics Resources 7:211–214.

Fischer, M. C., C. Rellstab, M. Leuzinger, M. Roumet, F. Gugerli, K. K. Shimizu, R. Holderegger, and A. Widmer. 2017. Estimating genomic diversity and population differentiation - an empirical comparison of microsatellite and SNP variation in Arabidopsis halleri. BMC Genomics 18:1–15.

Fraser, D. J., and L. Bernatchez. 2001. Adaptive evolutionary conservation: Towards a unified concept for defining conservation units. Molecular Ecology 10:2741–2752.

Funk, W. C., R. E. Lovich, P. A. Hohenlohe, C. A. Hofman, S. A. Morrison, T. S. Sillett, C. K. Ghalambor, J. E. Maldonado, T. C. Rick, M. D. Day, N. R. Polato, S. W. Fitzpatrick, T. J. Coonan, K. R. Crooks, A. Dillon, D. K. Garcelon, J. L. King, C. L. Boser, N. Gould, and W. F. Andelt. 2016. Adaptive divergence despite strong genetic drift: Genomic analysis of the evoutionary mechanisms causing genetic differentiation in the island fox (*Uryocyon littoralis*). Molecular Ecology 25:2176–2194.

Funk, W. C., J. K. McKay, P. A. Hohenlohe, and F. W. Allendorf. 2012. Harnessing genomics for delineating conservation units. Trends in Ecology & Evolution 27:489–96.

Gunnison sage-grouse Rangewide Steering Committee. 2005. Gunnison sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado USA.

Hansson, B., and L. Westerberg. 2002. On the correlation between heterozygosity and fitness in natural populations. Molecular Ecology 11:2467–2474.

Hauser, L., G. J. Adcock, P. J. Smith, J. H. Bernal Ramirez, and G. R. Carvalho. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of

New Zealand snapper (*Pagrus auratus*). Proceedings of the National Academy of Sciences 99:11742–11747.

Hedrick, P. 2005. A standardized genetic differentiation measure. Evolution 59:1633–1638.

Holycross, A. T., and M. E. Douglas. 2007. Geographic isolation, genetic divergence, and ecological non-exchangeability define ESUs in a threatened sky-island rattlesnake. Biological Conservation 134:142–154.

Inghelandt, D. Van, A. E. Melchinger, C. Lebreton, and B. Stich. 2010. Population structure and genetic diversity in a commercial maize breeding program assessed with SSR and SNP markers. Theoretical and Applied Genetics 120:1289–1299.

Jombart, T. 2008. adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405.

Jombart, T., S. Devillard, F. Balloux, D. Falush, M. Stephens, J. Pritchard, J. Pritchard, M. Stephens, P. Donnelly, J. Corander, P. Waldmann, M. Sillanpaa, J. Tang, W. Hanage, C. Fraser, J. Corander, C. Lee, A. Abdool, C. Huang, T. Jombart, T. Jombart, S. Devillard, A. Dufour, D. Pontier, T. Jombart, D. Pontier, A. Dufour, G. McVean, J. Novembre, M. Stephens, N. Patterson, A. Price, D. Reich, A. Price, N. Patterson, R. Plenge, M. Weinblatt, N. Shadick, D. Reich, H. Hotelling, H. Hotelling, K. Pearson, N. Liu, H. Zhao, R. Fisher, P. Lachenbruch, M. Goldstein, J. Aitchison, R. Reyment, A. Beharav, E. Nevo, C. Fraley, A. Raftery, H. Cann, C. de Toma, L. Cazes, M. Legrand, V. Morel, L. Piouffre, J. Bodmer, W. Bodmer, B. Bonne-Tamir, A. Cambon-Thomsen, S. Ramachandran, O. Deshpande, C. Roseman, N. Rosenberg, M. Feldman, L. Cavalli-Sforza, N. Rosenberg, J. Pritchard, J. Weber, H. Cann, K. Kidd, L. Zhivotovsky, M. Feldman, S. Wang, C. Lewis, M. Jakobsson,

S. Ramachandran, N. Ray, G. Bedoya, W. Rojas, M. Parra, J. Molina, C. Gallo, F. Balloux, N. Rosenberg, S. Mahajan, S. Ramachandran, C. Zhao, J. Pritchard, M. Feldman, A. Rambaut, O. Pybus, M. Nelson, C. Viboud, J. Taubenberger, E. Holmes, C. Russell, T. Jones, I. Barr, N. Cox, R. Garten, V. Gregory, I. Gust, A. Hampson, A. Hay, A. Hurt, D. Smith, A. Lapedes, J. de Jong, T. Bestebroer, G. Rimmelzwaan, A. Osterhaus, R. Fouchier, E. Holmes, E. Ghedin, N. Miller, J. Taylor, Y. Bao, K. S. George, B. Grenfell, S. Salzberg, C. Fraser, D. Lipman, J. Young, P. Palese, D. Benson, A. Karsch-Mizrachi, D. Lipman, J. Ostell, D. Wheeler, M. Larkin, G. Blackshields, N. Brown, R. Chenna, P. McGettigan, H. McWilliam, F. Valentin, I. Wallace, A. Wilm, R. Lopez, A. Waterhouse, J. Procter, D. Martin, M. Clamp, G. Barton, E. Paradis, J. Claude, K. Strimmer, L. Handley, A. Manica, J. Goudet, F. Balloux, D. Serre, S. Paabo, J. Corander, P. Marttinen, J. Siren, J. Tang, O. Francois, S. Ancelet, G. Guillot, K. Hunley, M. Healy, J. Long, R. Kittles, K. Weiss, A. Manica, F. Prugnolle, F. Balloux, F. Prugnolle, A. Manica, F. Balloux, I. Romero, A. Manica, L. Handley, F. Balloux, W. Amos, J. Hoffman, C. Fraley, A. Raftery, P. Peres-Neto, D. Jackson, K. Somers, G. Saporta, E. Paradis, S. Dray, A. Dufour, G. Schwarz, G. Evanno, S. Regnaut, J. Goudet, M. Jakobsson, N. Rosenberg, D. Chessel, A. Dufour, J. Thioulouse, S. Dray, A. Dufour, D. Chessel, W. Venables, B. Ripley, and M. Nei. 2010. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genetics 11:94.

Jost, L. 2009. D vs. G_{ST}: Response to Heller and Siegismund (2009) and Ryman and Leimar (2009). Molecular Ecology 18:2088–2091.

Jost, L. 2008. G_{ST} and its relatives do not measure differentiation. Molecular Ecology 17:4015–4026.

Kalinowski, S. 2002. How many alleles per locus should be used to estimate genetic distances? Heredity 88:62–65.

Kardos, M., and A. B. A. Shafer. 2018. The Peril of Gene-Targeted Conservation. Trends in Ecology & Evolution in press:1–12.

Keenan, K., P. McGinnity, T. F. Cross, W. W. Crozier, and P. A. Prodohl. 2013. diveRsity: An R package for the estimation of population genetics parameters and their associated errors. Methods in Ecology and Evolution 4:782–788.

Kim, K. S., S. T. Ratcliffe, B. W. French, L. Liu, and T. W. Sappington. 2008. Utility of EST-derived SSRs as population genetics markers in a beetle. Journal of Heredity 99:112–124.

Krawczak, M. 1999. Informativity assessment for biallelic single nucleotide polymorphisms. Electrophoresis 20:1676–1681.

LaHood, E. S., P. Moran, J. Olsen, W. Stewart Grant, and L. K. Park. 2002. Microsatellite allele ladders in two species of Pacific salmon: Preparation and field-test results. Molecular Ecology Notes 2:187–190.

Landegren, U., M. Nilsson, and P. Kwok. 1998. Reading bits of genetic information : Methods for single-nucleotide polymorphism analysis. Genome research 8:769–776.

Lawson, L. P., and K. Petren. 2017. The adaptive genomic landscape of beak morphology in Darwin's finches. Molecular Ecology 4978–4989.

Meirmans, P. G., and P. W. Hedrick. 2011. Assessing population structure: FST and related measures. Molecular Ecology Resources 11:5–18.

Mesak, F., A. Tatarenkov, R. L. Earley, and J. C. Avise. 2014. Hundreds of SNPs vs. dozens of SSRs: Which data set better characterizes natural clonal lineages in a self-fertilizing fish? Frontiers in Ecology and Evolution 2:1–8.

Miesfeld, R., M. Krystal, and N. Amheim. 1981. A member of a new repeated sequence family which is conserved throughout eucaryotic evolution is found between the human δ and β globin genes. Nucleic Acids Research 9:5931–5948.

Miller, J. M., R. M. Malenfant, P. David, C. S. Davis, J. Poissant, J. T. Hogg, M. Festa-Bianchet, and D. W. Coltman. 2014. Estimating genome-wide heterozygosity: Effects of demographic history and marker type. Heredity 112:240–247. Nature Publishing Group.

Morin, P. A., F. I. Archer, V. L. Pease, B. L. Hancock-hanser, M. Kelly, R. M. Huebinger, K. K. Martien, J. W. Bickham, J. C. George, D. Lianne, and B. L. Taylor. 2012. An empirical comparison of SNPs and microsatellites for population structure, assignment, and demographic analyses of bowhead whale populations. Endangered Species Research 19:1–27.

Morin, P. A., G. Luikart, and R. K. Wayne. 2004. SNPs in ecology , evolution and conservation. Trends in Ecology and Evolution 19:208–219.

Morin, P. A., C. Manaster, S. L. Mesnick, and R. Holland. 2009. Normalization and binning of historical and multi-source microsatellite data: Overcoming the problems of allele size shift with allelogram. Molecular Ecology Resources 9:1451–1455.

Narum, S. R., M. Banks, T. D. Beacham, M. R. Bellinger, M. R. Campbell, J. Dekoning, A. Elz, C. M. Guthrie, C. Kozfkay, K. M. Miller, P. Moran, R. Phillips, L. W. Seeb, C. T. Smith, K.

Warheit, S. F. Young, and J. C. Garza. 2008. Differentiating salmon populations at broad and fine geographical scales with microsatellites and single nucleotide polymorphisms. Molecular Ecology 17:3464–3477.

Nehring, J. A., and A. D. Apa. 2000. Gunnison sage-grouse population augmentation to Poncha Pass , Saguache County & Sims Mesa , Montrose County. Colorado Division of Wildlife, Fort Collins, CO, USA.

Nielsen, R. 2000. Estimation of population parameters and recombination rates from single nucleotide polymorphisms. Genetics 154:931–942.

Noël, S., M. Ouellet, P. Galois, and F. J. Lapointe. 2007. Impact of urban fragmentation on the genetic structure of the eastern red-backed salamander. Conservation Genetics 8:599–606.

Oh, K. P., C. L. Aldridge, J. S. Forbey, C. Y. Dadabay, and S. J. Oyler-McCance. In review. Conservation genomics in the sagebrush sea: Population divergence and adaptive metabolic variation in sage-grouse.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. M. Stevens, E. Szoecs, and H. Wagner. 2017. vegan: Community ecology package.

Oyler-McCance, S.J., K.P. Oh, K.M. Langin, and C.L. Aldridge. 2016. A field ornithologists's guide to genomics: Practical considerations for ecology and conservation. Auk 133:626-648.

Oyler-McCance, S. J., and J. A. Fike. 2011. Characterization of small microsatellite loci isolated in endangered Indiana bat (*Myotis sodalis*) for use in non-invasive sampling. Conservation

Genetics Resources 3:243–245.

Oyler-McCance, S. J., J. St. John, and T. W. Quinn. 2010. Rapid evolution in lekking grouse: Implications for taxonomic definitions. Ornithological Monographs 114–122. USA.

Oyler-McCance, S. J., J. St John, S. E. Taylor, A. D. Apa, and T. W. Quinn. 2005. Population genetics of Gunnison sage-grouse: Implications for management. Journal of Wildlife Management 69:630–637.

Paetkau, D., W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4:347–354.

Palsbøll, P. J., M. Bérubé, and F. W. Allendorf. 2007. Identification of management units using population genetic data. Trends in Ecology & Evolution 22:11–16.

Pante, E., J. Abdelkrim, A. Viricel, D. Gey, S. C. France, M. C. Boisselier, and S. Samadi. 2014. Use of RAD sequencing for delimiting species. Heredity 114:450–459.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Peakall, R., and P. E. Smouse. 2012. GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research - an update. Bioinformatics 28:2537–2539.

Piertney, S. B., and J. Höglund. 2001. Polymorphic microsatellite DNA markers in black grouse (*Tetrao tetrix*). Molecular Ecology Resources 1:303–304.

Prince, D. J., S. M. O'Rourke, T. Q. Thompson, O. A. Ali, M. Arciniega, H. S. Lyman, I. K. Saglam, A. J. Clementon, T. J. Hotaling, A. P. Kinziger, A. P. Spidle, J. C. Garza, D. E.

Pearse, and M. R. Miller. 2017. The evolutionary basis of premature migration in Pacific salmon highlights the utility of genomics for informing conservation. Science Advances 3:e1603198.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–59.

Quintela, M., S. Berlin, B. Wang, and J. HÖglund. 2010. Genetic diversity and differentiation among *Lagopus lagopus* populations in Scandinavia and Scotland: Evolutionary significant units confirmed by SNP markers. Molecular Ecology 19:2380–2393.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Robertson, J. M., K. M. Langin, T. S. Sillett, S. A. Morrison, C. K. Ghalambor, and W. C. Funk. 2014. Identifying evolutionarily significant units and prioritizing populations for management on islands. Monographs of the Western North American Naturalist 397–411.

Ryynänen, H. J., A. Tonteri, A. Vasemägi, and C. R. Primmer. 2007. A comparison of biallelic markers and microsatellites for the estimation of population and conservation genetic parameters in Atlantic salmon (*Salmo salar*). Journal of Heredity 98:692–704.

Schlötterer, C. 2004. Opinion: The evolution of molecular markers — just a matter of fashion? Nature Reviews Genetics 5:63–69.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004.

Distribution of sage-grouse in North America. The Condor 106:363–376.

Segelbacher, G., R. J. Paxton, G. Steinbruck, P. Tronteljs, and I. Storch. 2000. Characterization of microsatellites in capercaillie *Tetrao urogallus* (AVES). Molecular Ecology 9:1934–1935.

Tautz, D. 1980. Hypervariability of simple sequences as a general source for polymorphic DNA markers. Nucleic Acids Research 8:4321–4326.

Taylor, S. E., S. J. Oyler-McCance, and T. W. Quinn. 2003. Isolation and characterization of microsatellite loci in greater sage-grouse (*Centrocercus urophasianus*). Molecular Ecology Notes 3:262–264.

United States Fish and Wildlife Service. 2014. Endangered and Threatened Wildlife and Plants;Threatened Status for Gunnison sage-grouse, 79 Fed. Reg. ss 224 (final rule Nov. 20, 2014) (to be codified at 50 C.F.R. part 17).

Väli, Ü., A. Einarsson, L. Waits, and H. Ellegren. 2008. To what extent do microsatellite markers reflect genome-wide genetic diversity in natural populations? Molecular Ecology 17:3808–3817.

van Tienderen, P. H., A. A. de Haan, C. G. van der Linden, and B. Vosman. 2002. Biodiversity assessment using markers for ecologically important traits. Trends in Ecology and Evolution 17:577–582.

Venables, W.N. and B.D. Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

Verity, R., and R. A. Nichols. 2014. What is genetic differentiation, and how should we measure

it - G_{ST}, D, neither or both? Molecular Ecology 23:4216–4225.

Vignal, A., D. Milan, M. SanCristobal, and A. Eggen. 2002. Exploring the assumptions underlying genetic variation in host. Genetics Selection Evolution 40:241–264.

Waples, R. S. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. American Fisheries Society Symposium 17:8–27.

Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association 58:236–244.

Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370.

Whitlock, M. C. 2011. G_{ST} and D do not replace F_{ST}. Molecular Ecology 20:1083–1091.

Xing, C., F. R. Schumacher, G. Xing, Q. Lu, T. Wang, and R. C. Elston. 2005. Comparison of microsatellites, single-nucleotide polymorphisms (SNPs) and composite markers derived from SNPs in linkage analysis. BMC Genetics 6:1–5.

CHAPTER VI. CONCLUSION

The dramatic population declines and loss of genetic diversity in Gunnison sage-grouse (Oyler-McCance et al. 2005) has resulted in much concern over long-term persistence and ultimately in a federal designation of threatened under the Endangered Species Act (United States Fish and Wildlife Service 2014). Many conservation and management actions have been employed, including habitat restoration and translocation of individuals, however, some of these actions have unknown impacts, and potentially unforeseen consequences, on the species stability (Gunnison sage-grouse Rangewide Steering Committee 2005). Additionally, much of our understanding of habitat requirements and how sage-grouse use the landscape are derived from greater sage-grouse literature, which has a more naturally contiguous habitat distribution and differs somewhat in habitat composition from that of Gunnison sage-grouse. Although information from greater sage-grouse can provide a starting point, the naturally fragmented habitat and unique elements present within the range of Gunnison sage-grouse suggest there may be important differences in how the species uses and responds to landscape conditions. Genetic data can provide unique insight into the way the Gunnison sage-grouse interacts with the landscape. The findings I present in this dissertation add to our understanding of the impact of conservation and management actions, further characterizes populations, and provides insight into how the species interacts with different landscape features.

In my second chapter, I evaluated the genetic impact of translocation efforts on satellite populations. I used genetic samples collected before and after individuals were translocated between populations to evaluate change which could be attributed to translocation efforts. Though the impact varied by population, I found some degree of change in all metrics evaluated suggesting that translocated individuals were surviving, integrating into the recipient

populations, and reproducing. This approach addresses several of the metrics for evaluation of translocation success suggested by Baxter et al. (2008) because detection of reproducing individuals indicates that translocated individuals are surviving, integrating into the resident population, attending leks, nesting, and recruiting offspring as evidenced by transmission of genetic information into the next generation. Together, my findings indicate this approach could be used to evaluate future translocation efforts should they occur. Additionally, my study provides a baseline for comparison of future change. Prior to my study, a 12 month survival rate for some of the translocated individuals was the only proxy available for evaluating the impacts of translocation.

In my third chapter, I used a landscape genetics approach to understand the connectivity as measured by gene flow of Gunnison sage-grouse across the landscape both among populations and among leks within the Gunnison Basin. I found that habitat is important for gene flow at both scales, however, the quality and structure of the habitat is important for facilitation of gene flow among leks while presence of habitat and timing of resource availability is important for gene flow among populations. These findings are consistent with other studies of habitat use in that wildlife often make hierarchical decisions (Wiens and Milne 1989, Aldridge et al. 2012). The results I present support the idea that the formation of isolated populations of Gunnison sage-grouse is largely a result of conversion of habitat for anthropogenic use. In addition to providing insight into how the landscape impacts effective dispersal, my characterization of how different landscape components affect gene flow, could be used in conservation planning to identify specific impediments or facilitators of movement, to identify areas that might be conserved for habitat, restored as a potential dispersal route, or when making land-use change decisions.

In my fourth chapter, I evaluated the populations of Gunnison sage-grouse for evidence of adaptive divergence. I used a reduced representation sequencing approach to sample the genome, followed by a search for loci displaying signatures of selection (outlier locus analysis and genotype-environment associations), and identification of the putative function of associated gene regions holding strong signals of selection (GO term enrichment analyses). I identified a total of 191 genes holding strong signals of selection. Of particular interest were genes which were predicted to have non-synonymous amino acid substitutions implicated in heat stress response (CYB5R4; Sun et al. 2015), response to viral pathogens (DDX60 & SETX; Schoggins et al. 2011, Miller et al. 2015, Zhang et al. 2016), and four genes with signals of selection in the cytochrome P450 family (TBXAS1, CYP2R1, CYP2C23B, CYP4B1). Genes in the cytochrome P450 family have been previously implicated in the ability of chicken and sage-grouse to digest plant secondary metabolites like those found in sagebrush species (Kelsey et al. 1982, Miyazawa et al. 2001), a critical challenge for sagebrush obligates. The results I present here are a first look at the potential adaptive divergence of populations, and future work could be done to confirm these signals. However, the potentially ecologically important genes identified could have some conservation consequences. If translocations were to be implemented in the future, it might be important to move individuals between similarly adapted populations. For sagebrush habitat restoration, it might be important to consider the composition of plant secondary metabolites in the species of sagebrush being planted. Similarly, it may be important to ensure that captive reared populations are appropriately adapted for their intended release site.

In my fifth chapter, I provide a comparison of the use of marker types for population genetic analyses from a conservation perspective. The recent explosion of genomic techniques has resulted in the ability to create much larger multilocus genotype data sets than previous

genetic approaches, which sample coding in addition to non-coding regions of the genome (Landegren et al. 1998). While these large genotype data sets allow us to ask new questions about coding regions, it is also thought that they can be used in population genetic analyses. I compared the estimates of common metrics of genetic diversity (H_O, H_E, F_{IS}, A_R) and differentiation (F_{ST}, D_{Jost}, G_{ST}) using a genetic (microsatellite) and genomic (SNP) data set. In general, I found high concordance between microsatellites and SNPs for H_E, F_{IS}, A_R, and all differentiation estimates. Though there was strong correlation among SNPs and microsatellites, the magnitude of the diversity and differentiation metrics were significantly different in some cases, consistent with previous comparisons of marker types (e.g., Langin et al. 2018, Whitlock 2011). The two marker types are the result of very different mutation rates (microsatellites mutate much faster than SNPs) that are accounted for differently in different metrics of differentiation (Whitlock 2011), F_{ST} appearing more robust to the variability. If values of any of the metrics evaluated here are to be used as conservation targets, consideration must be given to the marker type used and the configuration of the species of interest, since migration rate and number of populations can also impact the magnitude of differentiation metrics (Whitlock 2011). If the magnitude of the value is not of importance, all metrics except H_O were able to consistently rank populations or population pairs across marker types. However, SNPs may have an advantage over microsatellites with the increased precision of the estimates resulting in significant differences among populations that were not detected with microsatellite data. More specifically for Gunnison sage-grouse, we evaluated clustering of individuals using putatively neutral (SNPs and microsatellites), putatively adaptive, and a combined data set of putatively neutral and adaptive loci. Our clustering analyses suggest strong demographic independence between the six distinct populations of Gunnison sage-grouse and some indication of

evolutionary independence in at least two populations. The clustering analyses generally showed similar patterns across marker types, though SNPs had more power to separate populations. This work contributes an additional comparison of marker types being used in population genetic analyses and also provides further evidence of evolutionary independence in some populations, highlighting the complexity involved in making conservation decisions for Gunnison sage-grouse.

Though each chapter provides some insight into conservation, the direct and immediate application of each piece of information presented here in conservation or management actions will be variable. Using genetic data to evaluate translocation is an application that can be used immediately. The results I present here could serve as a baseline for comparison of future changes. More work is needed to gain a complete understanding of why the measured response in genetic change varied in each population. The limited resources often available for conservation also mandate a need for optimization of efforts. For translocation, studies of the individual contribution of different translocated individuals (i.e., male vs. female, age class, number of individuals) to the recipient population would be useful to minimize effort and maximize impact. Increased genetic diversity in satellite populations will eventually diminish with continued genetic drift if individuals are not periodically translocated or natural connectivity is not restored. Characterization of the impact different landscape features have on gene flow can provide some insight into restoring the natural connectivity. The results I present here, indicate likely drivers of gene flow at two scales, though the uncertainty regarding the magnitude of the impact remains great. This may pose problems for immediate implementation into conservation action. However, the landscape genetics approach I used is an improvement over previous methods in that it allows for the estimation of uncertainty, which could still be

used to make decisions. The identification of potentially adaptive genes in populations of Gunnison sage-grouse points to important considerations for conservation though the actual impact of the detected differences in these genes remains uncertain. Developing conservation targets solely on the genes I identified as potentially adaptive could be misleading until the actual functional ecological importance has been determined. However, if adaptive alleles are confirmed impacts of future translocation efforts could be monitored to determine if the frequency of any adaptive alleles change with the introduction of alternate or maladaptive alleles from a different population.The comparison of marker types in conservation applications can be immediately useful if genetic data were going to be used to set conservation targets. However, the comparison of marker types to identify evolutionarily significant units brings up more questions. Much like the use of potentially adaptive variation for conservation targets, more thought must be given to what a meaningful level of evolutionary independence is for the Gunnison sage-grouse before actions are taken based on this information alone, especially since much of this genetic independence is the result of isolation through anthropogenic fragmentation and should be minimized.

Future work could expand on each of these topics by addressing one or more of the unknown aspects which might prevent full implementation. The individual contribution of translocated individuals could be evaluated with simulation techniques. In the connectivity analyses, the biggest hindrance is the amount of variation in the impact of each landscape feature on gene flow. Future analyses could explore longer algorithm runs, or try to reduce variability by attempting to account for impacts of lag effects in genetic signal from landscape change (Epps and Keyghobadi 2015), relaxing the assumption of symmetric gene flow (Hanks and Hooten 2013), or allowing the coefficient to vary across the landscape using splines (Hanks and Hooten

2013). Characterization of adaptive divergence in populations would benefit from direct evaluation of fitness effects and function (Prasad et al. 2013, Carneiro et al. 2014), target enrichment (Jones and Good 2016), genome-wide association studies (GWAS), gene expression studies and/or reciprocal transplant (Kawecki and Ebert 2004). However, some of these strategies are unlikely feasible due to lethal means required for sampling birds, and given federal protection of the species under the Endangered Species Act. Similarly, the identification of evolutionarily significant units based on genetic data would be supported by further investigation of the genes potentially under selection and confirmation of their ecological importance (Kardos and Shafer 2018). In total, the work I present in this dissertation provides an example of using genetic and genomic data for conservation questions, identifies some further areas of investigation, and contributes to our knowledge of the Gunnison sage-grouse.

LITERATURE CITED

Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for Gunnison sage-grouse: A spatially explicit hierarchical approach. Journal of Wildlife Management 76:391–406.

Baxter, R. J., J. T. Flinders, and D. L. Mitchell. 2008. Survival, movements, and reproduction of translocated greater sage-grouse in Strawberry Valley, Utah. Journal of Wildlife Management 72:179–186.

Carneiro, M., C. Rubin, F. Di Palma, F. W. Albert, A. M. Barrio, G. Pielberg, N. Rafati, and S. Sayyab. 2014. Rabbit genome analysis reveals a polygenic basis for phenotypic change during domestication. Science 345:1074–1079.

Epps, C. W., and N. Keyghobadi. 2015. Landscape genetics in a changing world: disentangling historical and contemporary influences and inferring change. Molecular Ecology 24:6021–6040.

Gunnison sage-grouse Rangewide Steering Committee. 2005. Gunnison sage-grouse rangewide conservation plan. Colorado Division of Wildlife, Denver, Colorado USA.

Hanks, E. M., and M. B. Hooten. 2013. Circuit theory and model-based inference for landscape connectivity. Journal of the American Statistical Association 108:22–33.

Jones, M. R., and J. M. Good. 2016. Targeted capture in evolutionary and ecological genomics. Molecular Ecology 25:185–202.

Kardos, M., and A. B. A. Shafer. 2018. The peril of gene-targeted conservation. Trends in Ecology and Evolution 1–12.

Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.

Kelsey, R. G., J. R. Stephens, and F. Shafizadeh. 1982. The chemical constituents of sagebrush foliage and their isolation. Journal of Range Management 35:617–622.

Landegren, U., M. Nilsson, and P. Kwok. 1998. Reading bits of genetic information : Methods for single-nucleotide polymorphism analysis. Genome Research 8:769–776.

Langin, K. M., C. L. Aldridge, J. A. Fike, R. S. Cornman, K. Marint, G. T. Wann, A. E. Seglund, M. A. Schroeder, C. E. Braun, D. P. Benson, B. C. Fedy, J. R. Young, J. R. Wilson, D. H. Wolfe, and S. J. Oyler-McCance. 2018. Characterizing range-wide divergencein an alpine-endemic bird: A comparison of genetic and genomic approaches. Conservation Genetics.

Miller, M. S., A. Rialdi, J. Sook, Y. Ho, M. Tilove, L. Martinez-Gil, N. P. Moshkina, Z. Peralta, J. Noel, C. Melegari, A. Maestre, P. Mitsopoulos, J. Madrenas, S. Heinz, C. Benner, J. A. . Young, A. R. Feagins, C. Basler, A. Fernandez-Sesma, O. J. Becherel, M. F. Lavin, H. van Bakel, and I. Marazzi. 2015. The helicase senataxin suppresses the antiviral transcriptional response and controls viral biogenesis. Nature Immunology 16:485–494.

Miyazawa, M., M. Shindo, and T. Shimada. 2001. Oxidation of 1, 8-cineole, the monoterpene cyclic ether originated from *Eucalyptus polybractea*, by cytochrome P450 3A enzymes in rat and human liver microsomes. Drug Metabolism and Disposition 29:200–205.

Oyler-McCance, S. J., J. St John, S. E. Taylor, A. D. Apa, and T. W. Quinn. 2005. Population genetics of Gunnison sage-grouse: Implications for management. Journal of Wildlife Management 69:630–637.

Prasad, K. V. S. K., B. Song, C. Olson-Manning, J. T. Anderson, C. Lee, M. E. Schranz, A. J. Windsor, M. J. Clauss, A. J. Manzaneda, I. Naqvi, M. Reichelt, J. Gershenzon, S. G. Rupasinghe, M. A. Schuler, and T. Mitchell-Olds. 2013. A gain of function polymorphism controlling complex traits and fitness in nature. Science 337:1–10.

Schoggins, J. J. W., S. J. S. Wilson, M. Panis, M. M. Y. Murphy, C. C. T. Jones, P. Bieniasz, C. M. Rice, and R. CM. 2011. A diverse array of gene products are effectors of the type I interferon antiviral response. Nature 472:481–485.

Sun, L., S. J. Lamont, A. M. Cooksey, F. McCarthy, C. O. Tudor, K. Vijay-Shanker, R. M. DeRita, M. Rothschild, C. Ashwell, M. E. Persia, and C. J. Schmidt. 2015. Transcriptome response to heat stress in a chicken hepatocellular carcinoma cell line. Cell Stress and Chaperones 20:939–950.

United States Fish and Wildlife Service. 2014. Endangered and Threatened Wildlife and Plants;Threatened Status for Gunnison sage-grouse, 79 Fed. Reg. ss 224 (final rule Nov. 20, 2014) (to be codified at 50 C.F.R. part 17).

Whitlock, M. C. 2011. G_{ST} and D do not replace F_{ST}. Molecular Ecology 20:1083–1091.

Wiens, J. A., and B. T. Milne. 1989. Scaling of “landscapes” in landscape ecology, or, landscape ecology from a beetle’s perspective. Landscape Ecology 3:87–96.

Zhang, Q., W. Gou, X. Wang, Y. Zhang, J. Ma, H. Zhang, Y. Zhang, and H. Zhang. 2016. Genome resequencing identifies unique adaptations of Tibetan chickens to hypoxia and high-dose ultraviolet radiation in high-altitude environments. Genome Biology and Evolution 8:765–776.

APPENDIX I

I simulated the amount of genetic diversity I would expect to have lost in the time period between collection of the two data sets using Bottlesim (Kuo and Janzen 2003). Bottlesim has limited options for matching the demographic history of different species. For instance, sage-grouse are a male dominant polygynous species where few males participate in the majority of matings, and Bottlesim allows me to specify only whether there is complete random mating or a single male mating per generation. Though only ~10-15% of males on a Gunnison sage-grouse lek have been observed breeding per year, and one to two of those males accounting for ~90% of the copulations (Young 1994), it is not correct to assume a single male is mating in all populations per generation. A more likely assumption is that a single male per lek is mating per generation. There is genetic evidence of higher levels of extra pair copulation than previously assumed within greater sage-grouse populations (Bird et al. 2013, Bush et al. 2010, Semple et al. 2001). However, these findings are in particularly small, and isolated populations of Greater sage-grouse where females may be compensating for low genetic diversity, as has been observed in other polygynous lek mating systems (Lank et al. 2002) and when female sage-grouse select males with lower parasite or disease load (Boyce 1990). Levels of reproduction in males might approach that of random mating if there is female overcompensation (Bird et al. 2013). My assumption of one male per lek per generation is likely also an overestimate of reproduction since all leks are not equal in the number of individuals which attend and reproduce. I therefore believe that one male per lek per generation is a reasonable estimate given what we know about the species biology.

To accomplish the simulations with one mating male per lek per generation I divided the population estimate for each year by the number of active leks with an estimated population size

greater than 1 as of 2005 (GSRSC 2005). For each year the number of replicates that were simulated was equal to the number of active leks, and the individuals simulated were equally spread across those leks (replicates; see Table S1.1). After each year, simulated genotypes were then combined across leks (replicates) and used as input to generate the allele frequencies to simulate the next year. This process of simulating a single year of reproduction across several leks, combining all leks into a single input file, then simulating the next year was repeated until 9 years had been simulated. The final genotype output file from the ninth year of simulated data was then used to estimate diversity metrics. The entire 9 year simulation process was repeated in 10 replicates for each population. The diversity metric values used in the main manuscript are averages across the replicates.

Table S1.1. The number of active leks per Gunnison sage-grouse population and two sub-populations (Monticello and Iron Springs), and the number of individuals that were simulated per lek (Lek Size) based on dividing the population size (Pop Size) by the number of active leks for each year of simulation. Dove Creek and Monticello and San Miguel and Iron Springs are geographically separated, and so were simulated separately then combined for analysis as they are considered the same population.

		Cimarron	Crawford	Dove Creek	Monticello	Gunnison Basin	Piñon Mesa	San Miguel	Iron Springs
	# Active Leks	1	4	1	3	74	9	4	1
Year 0	Pop Size	25	191	14	182	5720	167	317	17
	Lek Size	25	48	14	61	77	19	79	17
Year 1	Pop Size	49	201	13	178	6220	152	359	19
	Lek Size	49	4	1	3	80	8	5	1
Year 2	Pop Size	34	113	17	228	5480	123	308	16
	Lek Size	34	27	18	78	68	15	68	14
Year 3	Pop Size	10	98	17	228	4371	108	205	11
	Lek Size	10	4	1	3	64	7	3	1
Year 4	Pop Size	39	78	13	178	4386	78	154	8
	Lek Size	39	21	14	61	68	11	51	11
Year 5	Pop Size	5	20	9	123	4023	74	117	6
	Lek Size	5	1	1	2	59	7	2	1
Year 6	Pop Size	29	44	11	151	4150	64	88	5
	Lek Size	29	47	17	75	70	9	39	8

		Cimarron	Crawford	Dove Creek	Monticello	Gunnison Basin	Piñon Mesa	San Miguel	Iron Springs
	# Active Leks	1	4	1	3	74	9	4	1
Year 7	Pop Size	54	98	10	137	4621	54	163	9
	Lek Size	54	2	1	2	66	6	4	1
Year 8	Pop Size	44	108	9	114	4773	152	177	9
	Lek Size	44	52	14	62	73	26	42	9
Year 9	Pop Size	74	157	7	91	4705	182	196	10
	Lek Size	74	3	0	1	65	7	5	1

It was unclear whether this workaround affected the results in other ways than the intended addition of mating males per generation. In order to test this, I simulated diversity loss for the Gunnison Basin population using a single mating male but with the manual steps described above where one year was simulated and the output was used in a second simulation for the next year, and so on. We found no difference in the estimates obtained from the continuously simulated data vs. the data that was simulated a single year a time in a *t*-test (Table S1.2).

Table S1.2. *T*-test results for a difference of mean heterozygosity (H_O) in the continuously simulated diversity loss ('Continuous') vs. the single year at a time simulated diversity loss ('One Year at a Time'). The mean H_O shows no significant difference in both one- and two-tailed *t*-tests.

	Continuous	One Year at a Time
Mean (H_O)	0.447	0.448
Variance	0.002	0.001
Observations	10	5
Pooled Variance	0.001	
Hypothesized Mean Difference	0	
df	13	
t Stat	-0.074	
P($T \leq t$) one-tail	0.471	
t Critical one-tail	1.771	
P($T \leq t$) two-tail	0.942	
t Critical two-tail	2.160	

I also compared values obtained for the inbreeding coefficient (F_{IS}) and heterozygosity (H_O) from simulation models assuming one male mating per generation, one male per lek mating per generation, and random mating for all populations. All simulation scenarios fit my expectation that the one male mating per lek per generation would give an intermediate estimate of H_O when compared to the two extreme scenarios (Figure S1.1). This pattern was largely met with F_{IS} as well, though the changes are smaller and there is considerable overlap in error bars for all the satellite populations. Unsurprisingly, the effects of estimated diversity loss had the largest impact on the Gunnison Basin population. Because this population has the most leks and presumably the most reproductive events per generation, a single mating male per generation is likely a large underestimate of reproduction.

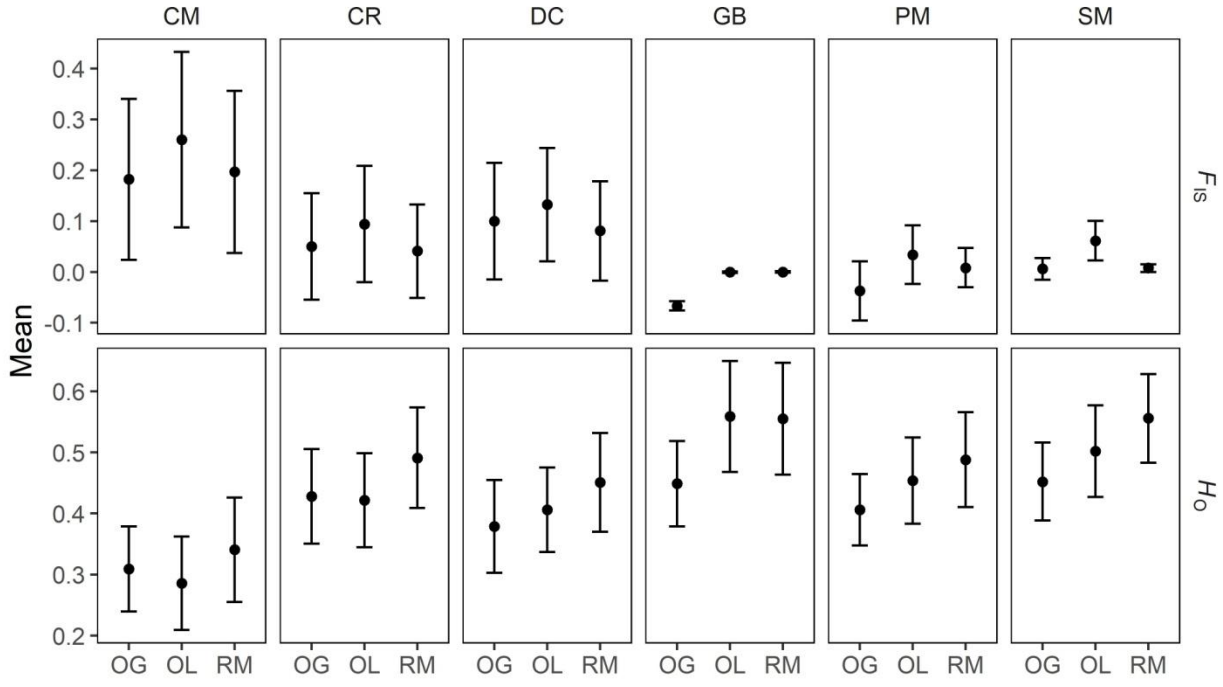

Figure S1.1. A comparison of the simulated values for heterozygosity (H_O) and the inbreeding coefficient (F_{IS}) in the satellite population under three different scenarios: assuming one male mating per generation (OG), one male mating per lek per generation (OL), and completely random mating (RM). Error bar construction: Mean value +/- 1.96**SE*. Gunnison Basin = GB, Dove Creek = DC, Piñon Mesa = PM, Cimarron = CM, Crawford = CR, San Miguel = SM.

I further investigated the deviation from our expectation of observed F_{IS} values from simulated data with the one-male-per lek assumption modification. I simulated diversity loss with Bottlesim for a large and a small population under stable and fluctuating population sizes with one mating male per generation and with complete random mating for 100 generations. The input genetic data used for the large population and the small population were pre-translocation Gunnison Basin and Crawford genetic data, respectively. I generated the hypothetical population trends for 100 years by calculating the mean and standard deviation of the population trends for each population over the 9 year period examined in this manuscript, then drew random numbers from a normal distribution centered on the estimated mean and standard deviation. For the stable population trend, I used the estimated standard deviation. I wanted to also evaluate how F_{IS} might change with varying degrees of fluctuation in population size, which I accomplished by increasing the value used for the standard deviation when drawing random numbers from a normal distribution. For Crawford, I multiplied the standard deviation by 0.25. For the fluctuating population trend in Gunnison Basin, I multiplied the estimated standard deviation by 1.50 and for Crawford I multiplied by 0.5. The different standard deviations were used to account for the fluctuations present in the real populations. If the estimated standard deviation was used as a stable variance for Crawford, the population occasionally goes extinct and prevented simulations from proceeding. All other parameters in the simulation were the same: completely overlapping generations, mean longevity of 3 years, reproductive maturity reached at 1 year, and 10 iterations. The results are shown in Figure S1.2. Declines in heterozygosity fit my expectations over all scenarios; the large populations with random mating (BFRM and BSRM) maintained heterozygosity and the small population with random mating (SFRM and SSRM) slowly declined over time, while simulations with one male mating per generation declined more

rapidly. Over the long term, the change in the inbreeding coefficient followed expectations with random mating, stable population sizes, and the large population, increasing more slowly than simulations with one mating male per generation, fluctuating population sizes, and smaller mean population size. In the first twenty generations, however, the inbreeding coefficient appears to decrease or remain constant for all scenarios. The lag in the expected effect indicates F_{IS} is not a reliable metric to use for genetic diversity change in a relatively short time frame.

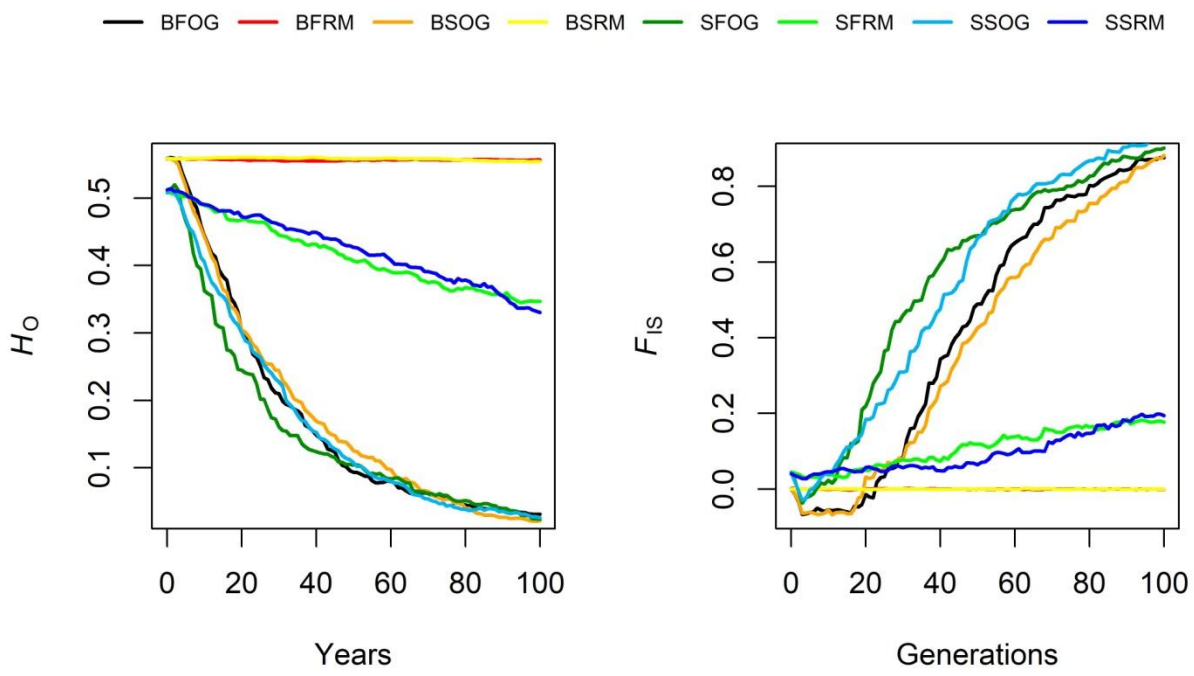

Figure S1.2. Simulated heterozygosity (H_O) and inbreeding coefficient (F_{IS}) under different scenarios for 100 generations. Simulation scenarios: BFOG = big fluctuating population with one male mating per generation, BFRM = big fluctuating population with random mating, BSOG = big stable population with one male mating per generation, BSRM = big stable population with random mating, SFOG = small fluctuating population with one male mating per generation, SFRM = small fluctuation population with random mating, SSOG = small stable population with one mating male per generation, SSRM = small stable population with random mating. We used the real genetic data for Gunnison Basin (big) and Crawford (small) as input.

All scenarios (one male per generation, one male per lek per generation, random mating) and values from collected data are shown in Figure S1.3. As mentioned above, observation of

mating behavior has led to the assertion that a single male dominates a lek and participates in the vast majority of copulations (Young 1994), however, genetic analyses within small and/or declining greater sage-grouse populations indicate extra pair copulations may be more frequent than previously assumed (Bird 2013). While it seems the Gunnison Basin might be robust to the assumption of a single male mating per lek per generation because it meets my expectations of diversity loss based on population trend, this might not be true for the small and/or declining satellite populations, one of which has shown indications of inbreeding depression (Stiver et al. 2008). While I recognize the potential for extra pair copulation to significantly impact the small satellite populations, given the small size and likely uneven reproduction at each lek, the assumption of a single mating male per lek is most appropriate for the satellite populations.

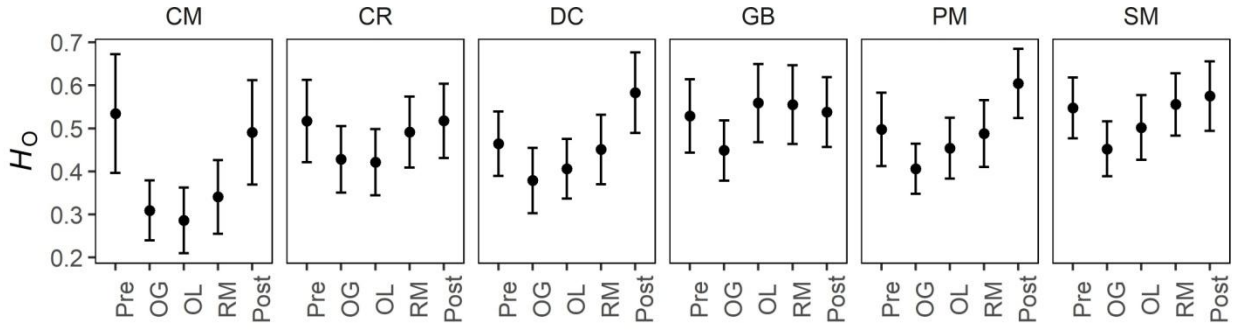

Figure S1.3. Heterozygosity (H_O) values obtained before (Pre) and after (Post) translocation of Gunnison sage-grouse and values form simulated data under three different scenarios: assuming one male mating per generation (OG), one male mating per lek per generation (OL), and completely random mating (RM). Error bar construction: Mean value +/- 1.96**SE*. Gunnison Basin = GB, Dove Creek = DC, Piñon Mesa = PM, Cimarron = CM, Crawford = CR, San Miguel = SM.

I assumed a sex ratio of two females to every male as reported by Stiver et al. (2008). However, the sex ratio will vary depending on the age structure of the population. Adult males have a higher mortality rate than juveniles, which would push the sex ratio to be dominated by females in years of low recruitment. Conversely, in years of high recruitment the sex ratio will be

closer to 1:1 because juvenile males and females have similar mortality rates. The long term (1977-1993) average sex ratio for Gunnison sage-grouse is 1.6: 1 females to males (GSRSC 2005). I simulated diversity loss with Bottlesim assuming a sex ratio of 2:1 and 1.6:1 in ten replicates for two populations (Crawford and Gunnison Basin) to test the impact of sex ratio estimates. I also simulated diversity loss for both populations, and both sex ratios to compare random mating and a single mating male per generation. The heterozygosity values obtained for both sex ratios within populations and mating scenarios showed no difference (Figure S1.4).

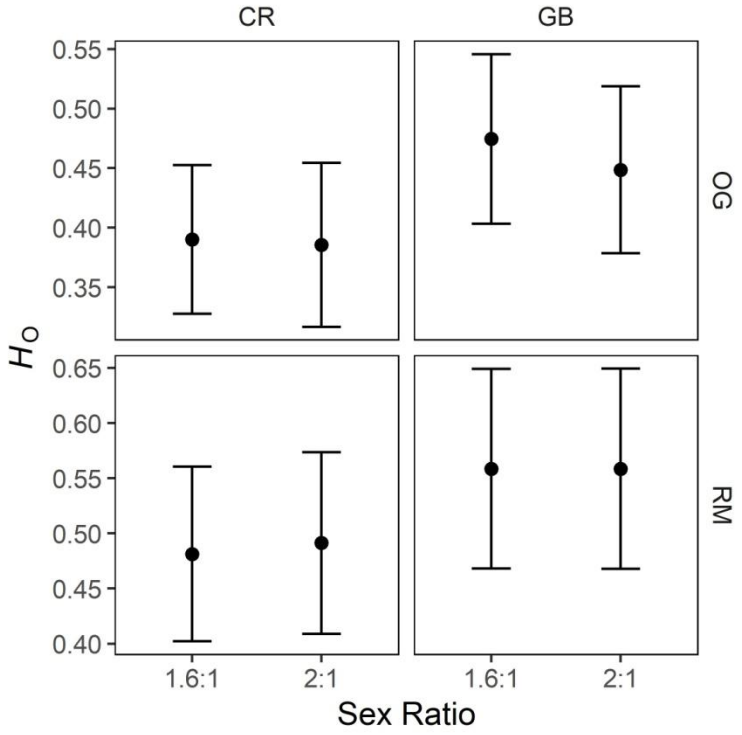

Figure S1.4. Comparison of heterozygosity (H_O) values for diversity loss simulated with Bottlesim for two Gunnison sage-grouse populations (CR = Crawford, GB = Gunnison Basin) assuming a sex ratio of 1.6:1 and 2:1 females to males. Error bar construction: Mean value +/- 1.96**SE*.

APPENDIX II

Table S2.1. *Q*-value 5th and 95^{h} percentile thresholds used to identify reproduction categories (F1 = first generation offspring of Gunnison Basin x satellite population cross, BC1 to SP = offspring of an F1 individual x satellite population individual, BC1 to GB = offspring of an F1 individual x Gunnison Basin individual, SP = individuals identified as satellite population ancestry, GB = individuals identified as Gunnison Basin ancestry). Values represent the proportion of ancestry from the satellite population in all categories except GB where values represent the proportion of ancestry from the Gunnison Basin population.

	CR		DC		PM		SM	
Cross	5th	95th	5th	95th	5th	95th	5th	95th
SP	0.86	0.96	0.86	0.97	0.89	0.97	0.77	0.96
F1	0.15	0.77	0.23	0.67	0.23	0.67	0.25	0.76
BC1SP	0.48	0.93	0.52	0.95	0.52	0.95	0.54	0.91
BC1GB	0.07	0.46	0.07	0.44	0.07	0.44	0.09	0.42
GB	0.89	0.97	0.84	0.97	0.84	0.97	0.77	0.96

Table S2.2. Estimates of the percentage of full-siblings ("FS"), half-siblings ("HS"), and the combination of both ("Relatives") Pre- and Post-translocation for each Gunnison sage-grouse population. Estimates were obtained from COLONY. Cimarron, Gunnison Basin and San Miguel have increases in the percentage of relatives, while Crawford, Dove Creek, and Piñon Mesa have a decrease in the percentage of relatives.

	Pre			Post		
Population	FS	HS	Relatives	FS	HS	Relatives
Cimarron	25.0	25.0	50.0	25.0	50.0	75.0
Crawford	23.8	42.9	66.7	19.4	38.7	58.1
Dove Creek	18.6	60.5	79.1	0.0	37.5	37.5
Gunnison Basin	57.8	0.0	57.8	5.1	62.8	67.9
Piñon Mesa	68.4	26.3	94.7	18.9	48.6	67.6
San Miguel	15.7	60.8	76.5	10.0	77.5	87.5

Table S2.3. Alleles private to Gunnison Basin prior to translocation and where they were detected after translocations. Locus = the name of the microsatellite primer, Allele = fragment size, Freq = frequency of the allele prior to translocation, Still? = Y indicates the allele is still unique to the Gunnison Basin post translocation and N indicates the allele is no longer unique to the Gunnison Basin post translocation. Each cell in a population column holds a "*" if the formerly private Gunnison Basin allele is now present in that population. The total numbers of alleles previously private to Gunnison Basin now found in each population are along the bottom. Five alleles remained private to Gunnison Basin. Notably, only a single low frequency allele (SG28, fragment size 141) showed up in Cimarron post-translocation.

Locus	Allele	Freq	Still?	Cimarron	Crawford	Dove Creek	Piñon Mesa	San Miguel
SG29	130	0.04	N				*	*
SG29	154	0.013	N		*		*	
SG29	168	0.007	Y					
SG38	154	0.009	Y					
SG38	158	0.005	Y					
SG38	164	0.147	N				*	*
SG38	166	0.023	N				*	
SG38	188	0.037	N				*	
SG38	194	0.005	Y					
SG38	196	0.014	N					*
WYBG6	285	0.018	N			*		
WYBG6	289	0.055	N		*	*	*	*
WYBG6	297	0.087	N		*		*	*
WYBG6	301	0.032	N				*	
SG21	158	0.004	Y					
SG28	139	0.066	N				*	
SG28	141	0.009	N	*		*	*	
SG28	147	0.102	N		*		*	
SGMS06.8	115	0.009	N			*	*	
TTT3	194	0.004	N		*	*	*	
TTT3	224	0.022	N		*		*	*
SG33	142	0.004	N		*			
SG36	223	0.035	N		*			
SGMS06.4	130	0.005	Y					
SGMS06.4	146	0.083	N				*	
SGMS06.4	158	0.05	N		*	*	*	
SG23	335	0.063	N				*	
SG23	339	0.032	N		*			
SG23	343	0.005	Y					
TUT3	148	0.035	N		*		*	*
SG31	129	0.009	N				*	

Table S2.4. Individuals within each population of Gunnison sage-grouse identified as having mixed ancestry between the satellite population and Gunnison Basin 9 years post-translocation. N = the number of individuals with mixed ancestry in the population, F1 = first generation offspring of Gunnison Basin x satellite population cross (count and percentage), BC1 to SP = offspring of an F1 individual x satellite population individual (count and percentage), BC1 to GB = offspring of an F1 individual x Gunnison Basin individual (count and percentage), SP = individuals identified as satellite population ancestry (count and percentage), GB = individuals identified as Gunnison Basin ancestry (count and percentage). Values are displayed for both pre- and post- translocation data sets.

		F1		BC1 to SP		BC1 to GB		SP		GB		?		Total Repro.
	N	#	%	#	%	#	%	#	%	#	%	#	%	%
Crawford	31	1	3.2	4	12.9	0	0.0	19	61.3	4	12.9	3	9.7	16.1
Dove Creek	8	1	12.5	0	0.0	2	25.0	2	25.0	0	0.0	3	37.5	37.5
Piñon Mesa	74	15	20.3	11	14.9	2	2.7	19	25.7	9	12.2	18	24.3	37.8
San Miguel	40	2	5.0	2	5.0	0	0.0	33	82.5	0	0.0	3	7.5	10.0

Table S2.5. Summary of Gunnison sage-grouse individuals with private alleles from the Gunnison Basin and from a satellite population post-translocation. Hybrid? = Y indicates the individual was identified in the STRUCTURE hybrid analysis N indicates it was not, Pop = satellite population abbreviation (PM= Piñon Mesa, CR = Crawford, DC = Dove Creek, SM = San Miguel), Locus = the microsatellite primer, Allele = the fragment size, *P* = the probability the private allele was present in the satellite population or the Gunnison Basin but was not sampled assuming the allele was as frequent in the population it was not detected in as in the population it was detected in.

			Gunnison Basin			Satellite Population		
Sample	Hybrid?	Pop	Locus	Allele	*P*	Locus	Allele	*P*
LL04	Y	PM	SG28	147	0.16	SG28	133	0.00
LL41	Y	PM	TTT3	194	0.92	MSP11	242	0.01
PMS02	Y	PM	TUT3	148	0.51	SG30	137	0.01
						SGCTAT1	112	0.01
PMS04	N	PM	SG38	188	0.51	TTT3	226	0.01
TR09	Y	PM	SG29	154	0.85	MSP11	203	0.01
TR27	Y	PM	TUT3	148	0.51	SG30	182	0.01
DL22	Y	CR	SG33	142	0.91	SGCTAT1	108	0.00
SEC21	Y	CR	WYBG6	297	0.15	SG21	178	0.00
			TTT3	194	0.91	SG30	169	0.00
HF02	Y	DC	SGMS06.8	115	0.69	SG21	218	0.00
			SGMS06.4	158	0.12	SG30	172	0.00
WF02	N	DC	WYBG6	285	0.45	SG28	113	0.00
			TTT3	194	0.93	SG28	157	0.00
SMM52	Y	SM	SG29	130	0.23	reSGCA11	174	0.00

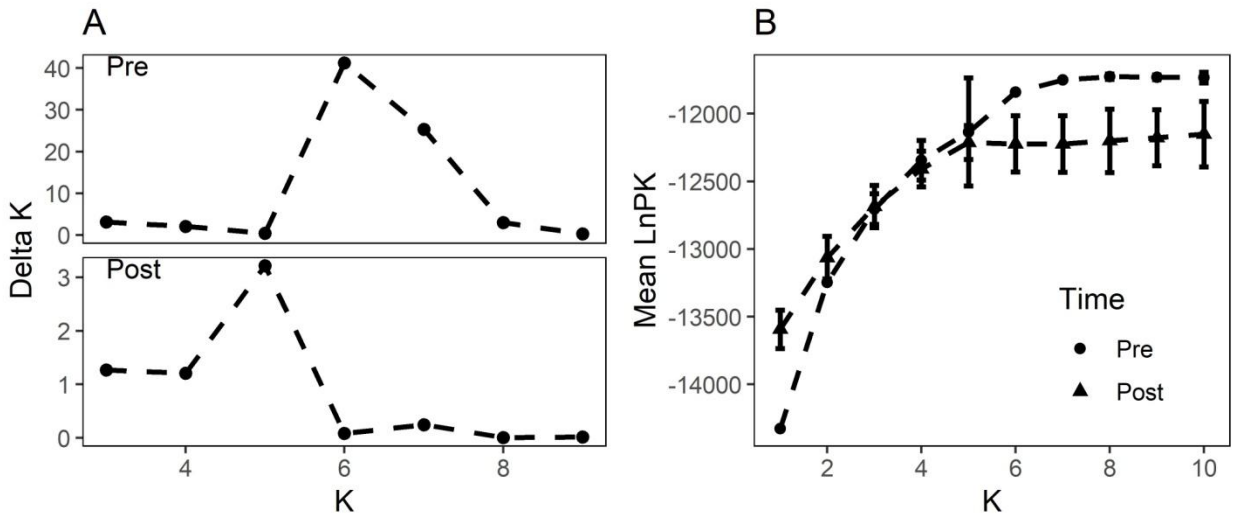

Figure S2.1. Identifying the number of optimal genetic groups in Gunnison sage-grouse with STRUCTURE output for the Evanno method (A) and the mean likelihood of K method (B) for the pre- (●) and post- (▲) data sets. Error bar construction: Mean value +/- 1.96*SD).

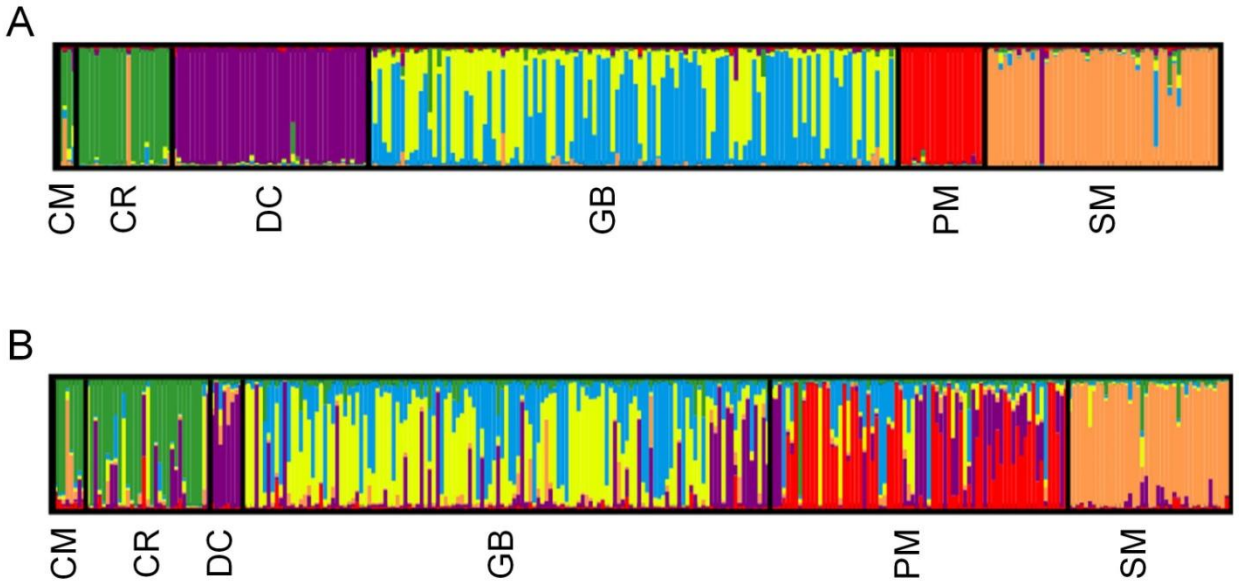

Figure S2.2. Estimated population genetic structure of Gunnison sage-grouse based on allele frequencies from 22 microsatellite loci for both the pre- (A) and post- (B) translocation data sets as calculated in STRUCTURE. Each vertical bar represents an individual Gunnison sage-grouse that is color coded by the proportion of genetic inheritance each individual has from one of the 6 distinct clusters (K = 6 was the optimal number of distinct genetic groups in pre-translocation data set and K = 5 was optimal for the post-translocation data set though K = 6 is shown for both data sets to illustrate change, see Figure S3 for K = 5 barplot for the post-translocation data). Pre-translocation N =254, post-translocation N = 785. Gunnison Basin = GB, Dove Creek = DC, Piñon Mesa = PM, Cimarron = CM, Crawford = CR, San Miguel = SM.

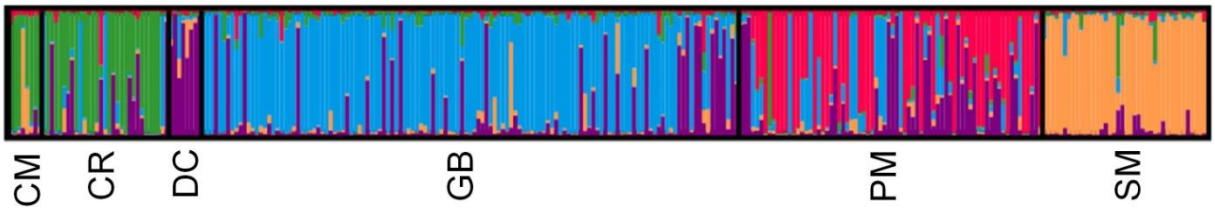

Figure S2.3. Estimated population genetic structure of Gunnison sage-grouse based on allele frequencies from 22 microsatellite loci for both the post-translocation data sets as calculated in STRUCTURE. Each vertical bar represents an individual Gunnison sage-grouse that is color coded by the proportion of genetic inheritance each individual has from one of the 5 distinct clusters.

APPENDIX III

Cimarron power

The low sample size of Cimarron pre- and post-translocation and the unexpected results of more change in the diversity metrics than expected (based on simulations), led me to investigate whether I actually had enough power to detect the predicted changes or if significance was random. I used the power.t.test function in R, a significance level of $P<0.05$, the predicted effect size, and a sample size of 8 corresponding to the post-translocation sample size in a one-sided test of power for both F_{IS} and H_O. The test yielded power values of 0.99 for both tests, indicating 8 samples was adequate to detect the predicted change.

I also noted that increased population estimates in the time frame being evaluated may have led to an unexpected result in the diversity and differentiation metrics. I have included the population trend below (Figure S3.1) for reference.

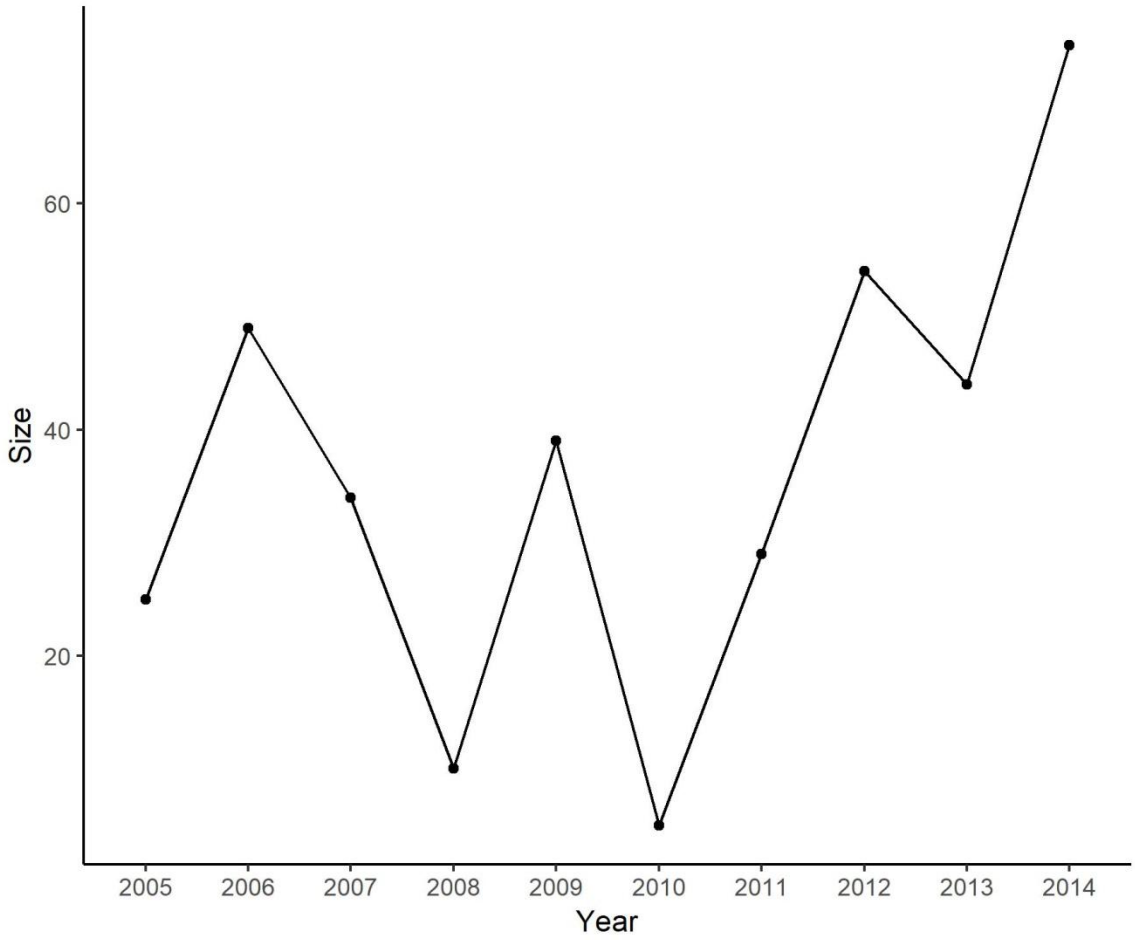

Figure S3.1. Population trend for the Cimarron satellite population of Gunnison sage-grouse. Values shown were obtained from the federal register (United States Fish and Wildlife Service 2014).

Population trends

For Crawford and Piñon Mesa, the number of translocated individuals corresponded to a comparable increase in population size (Figure S3.2A). Cimarron, as discussed in the main manuscript, received 6 translocations into the southwestern area of the population which were never relocated and assumed to have died or tried to return to Gunnison Basin. The population increase may be due to movements from Crawford. Dove Creek and San Miguel had a decline in population trend overall, despite receiving similar numbers of transplants. Twenty-three of the transplants to San Miguel arrived in the fall of 2013. Since sample collection was completed in

spring of 2014, the reproductive impacts of these 23 individuals would not have been realized in the data. Both Dove Creek and San Miguel have subdivision within the populations which might complicate or diminish contribution of transplants to the overall population dynamics.

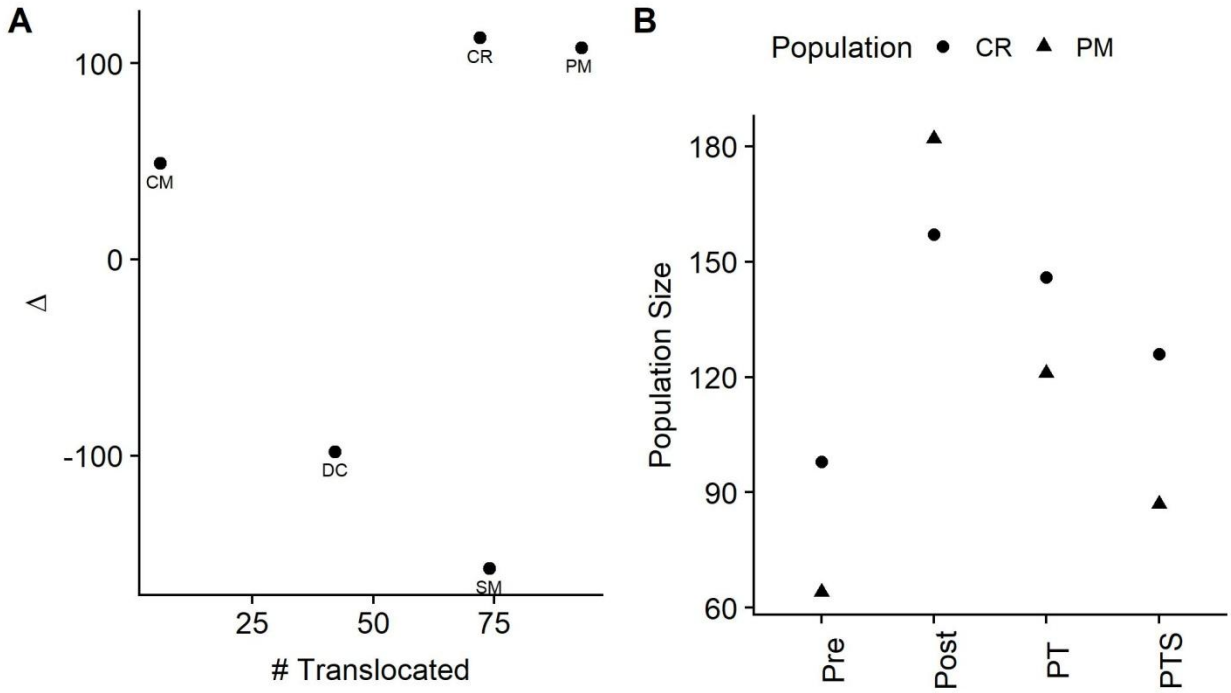

Figure S2. (A) Gunnison sage-grouse population response (Δ) as a function of the number of individuals translocated into each population. Points are labeled by population: CM = Cimarron, CR = Crawford, DC = Dove Creek, PM = Piñon Mesa, SM = San Miguel. Change in population size was estimate from population estimates in the Federal Register (TSGSG 2014). (B) Population sizes for two Gunnison sage-grouse populations (CR = Crawford, PM = Piñon Mesa) over the period in which the majority of individuals were translocated. Pre = population size in 2011 for PM and 2012 for CR. Post = population size in 2014. PT = Pre population size + number of individuals translocated. PTS = Pre population size + number of individuals translocated * 12 month survival rate. All information was obtained from the Federal Register (TSGSG 2014).

Two populations, Crawford and Piñon Mesa, experienced population growth greater than the increase from the addition of individuals from Gunnison Basin, supporting potential genetic rescue (Figure S3.2B). For example, 48 birds were moved to Crawford between 2012 and 2014. Overall, the population grew from 98 to 157 individuals in this same period, for an increase of 59 birds. If we applied the 12 month survival rates from 2013 (TSGSG 2014) to the number

translocated from 2012 to 2014, we would expect there to be an increase of aproximately 28 birds due to translocation. When considering the expected survival rate, the increase in population size is now approximately twice what is expected from the addition of birds from Gunnison Basin. Similarly, Piñon Mesa received 57 birds from the Gunnison Basin between 2011 and 2014. An increase of 118 individuals (from 64 to 182) was observed in this same time period. Accounting for population specific survival rates estimated for 2013 (TSGSG 2014), the expected increase in pouplation size would have been ~23 if the increase was due to translocation alone. Although radio collars may negatively impact survival (Gibson et al. 2013), survival rates of translocated birds in the satellite populations are comparable to sex specific Gunnison Basin estimates (0.39 male, 0.61 female) (Davis et al. 2015) indicating translocation is unlikely to significantly impact the survival rates.

APPENDIX IV

Table S4.1. Lek name and number of samples included in connectivity analyses for the Gunnison Basin extent. HMC = highest count of males observed on a lek during counting efforts in a year; values are included for both 2012 and 2013 to give an idea of the proportion of individuals using the lek sampled and yearly variability in number of individuals at a sampled lek (HMC values obtained from Jackson and Seward (2013)).

Lek	Name	# Sample	HMC 2012	HMC 2013
AL	Almont	3	8	6
ALL	Allen Lane	1	16	14
AN	Antelope North Blinberry Gulch	8	14	11
BM	Big Mesa	6	8	5
CB	Campbell	4	6	7
CG	Chance Gulch	20	18	17
CGE	Chance Gulch E	12	15	14
FTS	Flat Top Section 31	7	15	27
HG	Hartman Gulch	34	45	43
HR	Henkel Road	13	8	4
KBN	Kezar Basin North	40	20	30
KBS	Kezar Basin South	1	0	0
LC	Lost Canyon 2	2	0	0
MB	7MB Lek	9	7	7
MBE	7MB Eagle	3	70	50
MBH	7MB Hupp	3	11	4
MCL	McCabe's Lane	2	3	2
MR	Miller Ranch	19	39	31
MY	Meyers	1	8	10
NM	Ninemile	1	0	0
RC	Razor Creek	5	17	12
RCD	Razor Creek Divide	2	35	37
RD	Razor Dome 1 & 2	36	0	12
RL	Ridgeline	2	4	3
SAC	Sapinero Corral	3	0	0
SBC	South Beaver Creek	16	18	15
SC	Sugar Creek	21	43	62
SG	Sewell Gulch	2	6	13
SGP	Signal Peak	3	0	0
SMH	South 6 Mile Hupp	1	0	0
SML	South 6 Mile Meadow	5	0	4
SMP	Sapinero 10 Mile Spring	20	0	3
SMR	South 6 Mile Ridge	14	24	17

Lek	Name	# Sample	HMC 2012	HMC 2013
SP1	South Parlin 1	33	0	0
SP3	South Parlin 3	12	32	25
SPOW	Sapinero Powerline	12	12	15
SPU	South Parlin Upper	25	32	38
SPW	Signal Peak West	6	10	10
SR	Sapinero Ridge	16	6	7
SS	Sapinero South	57	58	50
ST	Scout	17	15	25
STC	Steven's Creek East	2	6	9
TL	Taila's Lek	12	11	11
TO	Teachout 1 & 2	17	26	0
TT	Teachout 3,5,6	31	49	74
VT	Vito	21	6	20
WG	Wood's Gulch	26	6	7
WN	Waunita	11	22	11
WNW	Waunita NW	7	5	23

APPENDIX V

Spatial Data Processing

All spatial analyses were performed in ArcGIS10.1 unless stated otherwise.

Daymet

We obtained individual tiles of Daymet data corresponding to the range-wide study area (tiles 11376, 11377, 11556, 11557, 11558) for the time period 1997 to 2005 and basin wide (tile 11557) for the time period 2006 to 2014 in the form of a NETcdf file. Different time frames were used for the different extents to match the sampling period of the genetic data. The NETcdfs required conversion to raster format and all tiles for the range-wide analysis required joining into a single raster. This was accomplished with python scripts available at https://daymet.ornl.gov/tools.html. Once each year at both extents were processed into the correct raster format I calculated the average growing degree days (GDD) and a dryness index (DRI) for the respective nine year periods. GDD was calculated by finding the average temperature, and counting the number of days in each year between 1 March and 31 August with temperatures greater than 5°C. The final GDD raster layer is an average of 9 years. DRI was calculated by dividing GDD by the cumulative precipitation between 1 March and 31 August for each year. The final DRI raster layer is an average of 9 years. The resolution of Daymet data is 1000 m. Mean moving window analyses were performed at the following radii: 3 km, 6.4 km, 10 km, 15 km, and 20 km.

DEM Derived

Compound topographic index (CTI) is a function of slope and the area upstream potentially contributing run-off and is used as a proxy for soil moisture (Gessler et al. 1995). Two data sets were available for CTI and slope with differing extents and resolution through the USGS GIS library. The higher resolution data (10-m) was available only for the Gunnison Basin, and was clipped to the study area extent and a circular moving window analysis for the mean was performed for each of the following radii: 564 m, 1 km, 3 km, 6.4 km, 10 km, 15 km, and 20 km. For the range-wide study area, CTI and slope were available at a 30-m resolution. The range-wide CTI and slope data were extracted using the corresponding landscape extent as a mask and circular moving window analyses for the mean were performed for the following radii: 564 m, 1 km, 3 km, 6.4 km, 10 km, 15 km, and 20 km. The terrain ruggedness index (TRI) was only available for the Gunnison Basin at a resolution of 10 m. TRI was clipped to the Gunnison Basin extent and the following circular moving window radii applied to find the mean at different scales: 564 m, 1000 m, 3000 m, 6400 m, 10000 m, 15000 m, and 20000 m. Low values of TRI indicate low slope, moderate values indicate steep but even, high values indicate steep and uneven.

Landfire

Spatial data for dominant existing vegetation were obtained from 30-m resolution Landfire data. I broke the cover types up into all sagebrush cover, low sagebrush cover, big sagebrush cover, and conifer cover, reclassifying a raster for each variable with the target variable given a 1 and everything else a 0. At the original 30-m resolution, cover type is presence-absence based. Moving window analyses were applied at radii of 564 m, 1 km, 3 km, 6.4 km, 10 km, 15 km, and 20 km to estimate the proportion of each cover type at several scales/extents. I was also interested in the configuration of conifer cover, or how the conifer is arranged on the landscape (clumped or dispersed). To assess configuration, I first had to convert the 30-m conifer cover raster to point data. Next I applied a nearest neighbor analysis using the "near" tool in the analysis tools of arcMap. The output was then converted back to a raster and the nearest neighbor index was calculated by dividing the raster output by the mean distance (0.5*sqrt(total area/# of points in the distribution). Values less than 1 are considered clustered, while values greater than one are considered dispersed as in Baruch-Mordo et al. (2013).

LandScan

I obtained population density spatial data with a 1-km resolution from Oak Ridge National Laboratory for 2004 and 2014 (High Resolution global Population Data Set copyrighted by UT-Battelle, LLC, operator of Oak Ridge National Laboratory under Contract No. DE-AC05-00OR22725 with the United States Department of Energy). Data from each year was clipped to the corresponding study area extent. Moving window analyses to calculate the mean population density were performed with radii of 3 km, 6.4 km, 10 km, 15 km, and 20 km.

NLCD

The National Land Cover Data allowed me to evaluate the proportion of agricultural land cover, the proportion of developed land, and the distance to developed land. The data was downloaded in separate tiles which were then aligned together into a single raster, and then projected into NAD 1983 UTM zone 12N spatial coordinate system. The new raster was clipped to the target spatial extents for both range-wide and the Gunnison Basin. I created an agriculture and development layer by reclassifying cover types into presence-absence. For agriculture, pixels corresponding to cultivated crops (NLCD code 81) or pasture/hay (NLCD code 82) were assigned a 1 and everything else a 0. For development, pixels corresponding to low intensity development (NLCD code 22) and medium intensity development (NLCD code 23) were assigned a 1 and everything else a 0. There were no instances of high intensity development in either study area extent. The resolution of the data is 30-m and the mean was calculated at the following circular moving window radii: 564 m, 1 km, 3 km, 6.4 km, 10 km, 15 km, and 20 km. The distance to development variable was calculated by first reclassifying all 0 values to No Data, and calculating the Euclidean distance to the nearest development pixel, and clipping the resulting raster to both spatial extents.

Oil and Gas

Oil and gas well locations were obtained as a shapefile for Utah (oilgas.ogm.utah.gov) and Colorado (cogcc.state.co.us). The individual shapefiles were merged into one and clipped to the study area extent. I was interested in two metrics: well density and distance to wells. I calculated the point density with moving window extents of 564 m, 1 km, 3 km, 6.4 km, 10 km, 15 km, and 20 km. Distance to wells was estimated with the Euclidean distance to wells.

Phenology Layers

The phenology tool (Talbert et al. 2013) derives several variables which are proxies for timing and duration of a growing season, from normalized difference vegetation index (NDVI) data. The values I used correspond to the NDVI value for the variables green-up (beginning of growing season), brown-down (end of growing season), green-up rate (left derivative of the phenology curve), brown-down rate (right derivative of the phenology curve), and season length as proxies for potential resources available to sage-grouse in a spatial context. Values for the years 2000 to 2010 were averaged for season 1 (the onset of growth). The landscape extent was projected into the same spatial reference system as the phenology layers, and subsequently used to clip each phenology layer to the target spatial extent. The clipped phenology layers were then projected back into NAD 1983 UTM zone 12N spatial coordinate system. The phenology data resolution is 1000 m, limiting the moving window analysis radii to 1 km, 3 km, 6.4 km, 10 km, 15 km, and 20 km. A circular moving window analysis for the mean was then applied to the clipped and re-projected phenology layers for each of the previously listed radii.

PRISM

I obtained 30-year normals for annual rainfall and maximum annual temperature at a resolution of 800 m from PRISM Climate Group. Raster layers were projected to the spatial reference UTM NAD 1983 zone 13 and clipped to the study area extent. Moving window analyses were performed at the following radii: 1 km, 3 km, 6.4 km, 10 km, 15 km, and 20 km.

Roads

Different road spatial data sets were available for our different spatial extents. I relied primarily on TIGER data for the range-wide analysis, subsetting the types of roads into primary, secondary, neighborhoods, and vehicular trails. Each road type was treated as a unique variable, but road types were also combined for additional variables: primary and secondary roads; primary, secondary, and neighborhoods; primary, secondary, neighborhoods, and vehicular trails. I also obtained a more recent road layer which more accurately covers vehicular trails and light duty roads developed by USGS Fort Collins Science Center from TIGER (accessed 15 December 2017), BLM (USGS Fort Collins Science Center), USFS (accessed 17 November 2017), road data and digitized aerial imagery, which I also included in my analyses. For the Gunnison Basin I was able to use a more recent spatial data set developed from 2005 NAIP based on Bureau of Land Management classification system which was collaboratively developed by BLM, U.S. Forest Service, NPS, Gunnison County, and USGS across the

Gunnison sage-grouse range within the Gunnison Basin. These data were previously used for the development of seasonal resource selection models (Aldridge et al. 2012). I focused on the following variables: roads classified 1 to 4, primary and secondary roads, roads classified 4 to 7, two tracks or vehicular trails, and all roads. All spatial data was projected into NAD 83 zone 13. I was interested in the density of roads and the distance to roads. The linear density (km/km^2) was calculated in Arcmap for each study area and each variable for the following moving window radii: 564 m, 1 km, 3 km, 6.4 km, 10 km, 15 km, and 20 km. Distance to roads was estimated with the Euclidean distance.

Sagebrush Product

In addition to the Landfire data which provided an indication of the proportion of cover type on the landscape I used spatial products which estimate the percent cover of different vegetation types. The product for this region was not publicly available at the time of this work, though was provided by C. Homer and D. Meyer and developed using the methods outlined by Xian et al. (2015). I was interested in sagebrush cover (*Artemisia* spp.), all big sagebrush (all subspecies combined), and shrub height. I extracted the data using the range-wide extent and the Gunnison Basin extent as a mask in ArcMap 10.1. I created multiple variants of each variable using a moving window average with the following radii: 564 m, 1 km, 3 km, 6.4 km, 10 km, 15 km, and 20 km.

Table S5.1. Average value for each spatial variable (1 km moving window average) within each study area extent (Range-wide, Gunnison Basin) and each discrete population.

Covariate	Range-wide	Gunnison Basin	Crawford	Cimarron	Dove Creek	Piñon Mesa	San Miguel
Density of class 2 roads	0.05	0.07	0.00	0.07	0.08	0.00	0.02
Distance to class 2 roads	9503.92	4976.11	8494.02	3639.14	4367.94	14446.07	8935.55
Density of class 4 roads	0.74	1.04	0.62	0.58	1.12	0.46	1.08
Distance to class 4 roads	1099.68	505.56	849.98	744.37	434.48	943.77	564.20
Density of class 5 roads	0.04	0.02	0.00	0.01	0.01	0.04	0.01
Distance to class 5 roads	6165.24	7800.05	7587.34	5533.74	7252.42	4465.77	5730.49
Density of class 1 & 2 roads	0.06	0.07	0.00	0.08	0.08	0.00	0.03
Distance to class 1 & 2 roads	9075.69	4852.23	8231.43	3479.74	4323.29	7886.59	8887.45
Density of class 1,2, & 4 roads	0.81	1.12	0.62	0.65	1.20	0.47	1.10
Distance to class 1,2, & 4 roads	1075.52	483.61	849.98	706.59	419.37	943.03	562.33
Density of development	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Proportion of agriculture	0.04	0.05	0.00	0.08	0.01	0.00	0.01
Density of all roads	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Distance to all roads	978.50	458.89	849.98	700.28	412.61	831.78	557.40
Proportion of all sagebrush cover	0.11	0.22	0.23	0.27	0.30	0.20	0.29
Brown-down	337.36	301.18	346.74	311.40	334.84	336.37	338.71
Brown-down rate	124.04	100.43	104.86	142.58	57.46	146.50	93.03

Covariate	Range-wide	Gunnison Basin	Crawford	Cimarron	Dove Creek	Piñon Mesa	San Miguel
Proportion of big sagebrush cover	0.11	0.22	0.22	0.27	0.30	0.19	0.29
Proportion of conifer cover	0.39	0.12	0.31	0.17	0.16	0.29	0.30
Compound topographic index	10.54	10.80	10.45	10.62	11.95	10.54	11.55
Distance to development	7957.88	10744.09	12027.65	6671.21	1526.27	5936.52	7166.49
Distance to light duty roads	614.83	443.01	300.48	287.13	350.50	378.01	304.29
Distance to population density	0.23	0.20	0.12	0.17	0.11	0.34	0.19
Distance to oil and gas wells	11648.78	15484.07	7053.73	7222.29	2757.12	21984.29	3521.99
Dryness index	154.86	152.77	160.35	148.45	190.33	161.21	129.88
Growing degree days	128.59	119.63	132.39	130.81	139.16	134.21	133.89
Green-up	133.37	112.46	136.49	116.00	130.32	132.62	132.81
Green-up rate	148.35	123.87	134.50	188.34	75.53	213.41	104.08
Density of light duty roads	1.79	1.24	2.44	2.31	1.79	1.50	2.01
Proportion of low sagebrush cover	0.00	0.00	0.01	0.00	0.00	0.01	0.00
Population density	3.01	2.61	1.03	2.37	1.03	0.12	0.76
Mean annual rainfall	521.43	375.66	513.20	482.55	397.82	486.41	479.68
Mean maximum temperature	13.87	12.23	14.65	14.39	15.94	14.59	15.48
Conifer configuration	1.86	3.18	1.72	1.66	1.84	1.81	2.29
Presence of sagebrush cover	0.11	0.21	0.20	0.25	0.29	0.22	0.30
Oil and gas well density	0.09	0.00	0.00	0.01	0.06	0.00	0.25
Percentage of big sagebrush cover	2.51	8.21	5.84	3.95	4.36	2.96	4.87
Percentage of all sagebrush cover	3.24	10.30	8.25	4.91	6.11	4.07	6.14
Shrub height	8.00	20.26	22.45	12.54	14.93	10.16	17.03
Season length	203.62	188.49	208.56	195.09	204.04	203.26	205.90
Slope	12.16	9.76	10.05	9.12	2.75	10.76	5.38

APPENDIX VI

Evaluation of DIC to identify univariable form.

I used DIC to rank multiple univariable models representing a single covariate at different average moving window extents in order to optimize the variable for the scale at which Gunnison sage-grouse is most likely to respond. I used the proportion of all sagebrush cover to evaluate the ability of DIC to identify the best scale. Moving window extents considered here included 564 m, 1km, 3 km, 6.4 km, 10 km, 15 km, and 20 km. I simulated a genetic distance matrix from the generalized Wishart distribution defining the intercept as 2, the coefficient for all sagebrush cover as -3, the τ parameter as 0.1, and using the 6.4km moving window radius. Each model was fit with 50,000 MCMC iterations, discarding the first 20,000 iterations as a burn-in period in a Metropolis-Hastings sampler. Convergence was visually inspected with trace and density plots of the posterior distributions for each parameter (plots not included).

Evaluation of DIC ranking shows that the moving window extent used to simulate data was identified as the second best model in all replicates (Table S1). However, the posterior means and credible intervals for the top two models overlapped, indicating they are not significantly different and inference would be approximately the same. Additionally, all moving window averages were highly correlated.

Table S6.1. Means and 95% credible intervals of the posterior distribution and DIC values obtained for each moving window radius. align decimals and use long dash.

MW (m)	Rep	Intercept	β	τ	DIC	Δ DIC	Dbar	Dhat
3000	1	1.00 [0.75 – 1.23]	-2.79 [-3.26 – -2.29]	0.20 [0.19 – 0.20]	-598058.7	0.0	5005.9	603064.6
6400	1	1.43 [1.13 – 1.72]	-3.32 [-3.88 – -2.79]	0.20 [0.20 – 0.21]	-591684.0	6374.7	4977.3	596661.4
10000	1	1.35 [1.07 – 1.63]	-2.88 [-3.36 – -2.41]	0.20 [0.19 – 0.20]	-586107.7	11951.0	4984.0	591091.7
15000	1	1.30 [0.99 – 1.59]	-2.56 [-2.98 – -2.11]	0.20 [0.20 – 0.20]	-583764.4	14294.3	5002.3	588766.7
1000	1	0.61 [0.41 – 0.81]	-3.84 [-3.23 – -2.64]	0.20 [0.20 – 0.21]	-574248.1	23810.6	5020.0	579268.2
20000	1	1.37 [1.07 – 1.67]	-2.45 [-2.88 – -2.02]	0.20 [0.20 – 0.20]	-571597.6	26461.1	5008.5	576606.2
564	1	0.57 [0.37 – 0.76]	-3.35 [-4.00 – -2.68]	0.20 [0.19 – 0.20]	-567828.6	30230.1	5022.5	572851.1
3000	2	0.99 [0.74 – 1.22]	-2.77 [-3.26 – -2.29]	0.20 [0.20 – 0.20]	-597562.3	0.0	5006.1	602568.4
6400	2	1.44 [1.12 – 1.72]	-3.32 [-3.86 – -2.78]	0.20 [0.20 – 0.21]	-590868.3	6694.0	4977.5	595845.8
10000	2	1.36 [1.06 – 1.63]	-2.88 [-3.32 – -2.43]	0.20 [0.20 – 0.20]	-584575.7	12986.6	4983.9	589559.6
15000	2	1.26 [0.98 – 1.54]	-2.53 [-2.95 – -2.08]	0.20 [0.19 – 0.20]	-583166.2	14396.0	5002.2	588168.4
1000	2	0.61 [0.42 – 0.80]	-3.25 [-3.82 – -2.68]	0.20 [0.20 – 0.21]	-571382.5	26179.8	5020.0	576402.5
20000	2	1.39 [1.08 – 1.68]	-2.46 [-2.90 – --2.04]	0.20 [0.20 – 0.21]	-571099.7	26462.5	5008.3	576108.0
564	2	0.57 [0.37 – 0.76]	-3.98 [-3.98 – -2.70]	0.20 [0.19 – 0.21]	-566341.1	31221.2	5022.3	571363.4
3000	3	1.00 [0.76 – 1.24]	-2.79 [-3.26 – -2.32]	0.20 [0.20 – 0.20]	-598851.3	0.0	5006.2	603857.5
6400	3	1.41 [1.13 – 1.71]	-3.28 [-3.83 – -2.76]	0.20 [0.20 – 0.21]	-586573.8	12277.5	4977.6	591551.3
15000	3	1.29 [1.02 – 1.56]	-2.54 [-2.97 – -2.12]	0.20 [0.20 – 0.20]	-583929.9	14921.3	5002.3	588932.2
10000	3	1.36 [1.10 – 1.64]	-2.90 [-3.33 – -2.46]	0.20 [0.20 – 0.20]	-583382.0	15469.3	4983.8	588365.8

1000	3	0.61 [0.42 – 0.81]	-3.24 [-3.85 – -2.62]	0.20 [0.20 – 0.20]	-572671.3	26180.0	5020.0	577691.3
20000	3	1.39 [1.06 – 1.70]	-2.47 [-2.90 – -2.04]	0.20 [0.19 – 0.21]	-568561.9	30289.4	5008.7	573570.6
564	3	0.58 [0.38 -0.76]	-3.35 [-3.98 – -2.69]	0.20 [0.20 – 0.21]	-563581.8	35269.5	5022.4	568604.2

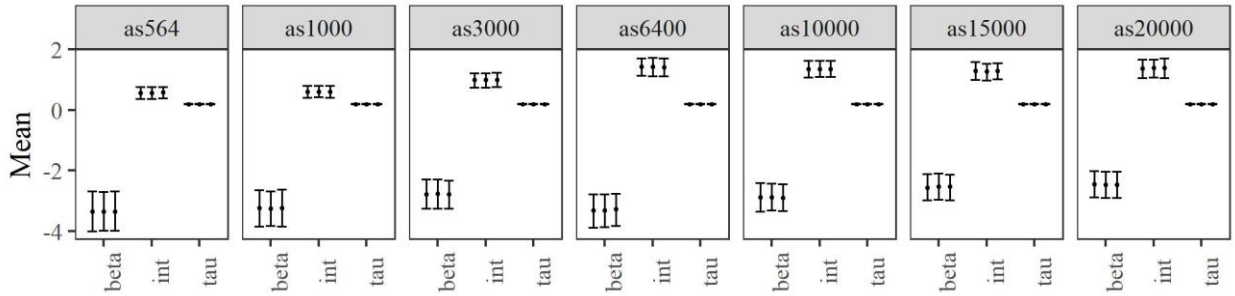

Figure S6.1. Posterior means and credible intervals of parameters for each moving window radius.

Additionally, the posterior means and CIs across replicates return nearly completely overlapping estimates (Figure S6.1).

Evaluation of DIC to identify multivariable model.

I used DIC to rank multivariable models representing different hypotheses of landscape drivers of gene flow for Gunnison sage-grouse. I fit connectivity models to a genetic distance matrix simulated from the generalized wishart distribution using covariates representing a hypothesis of habitat components predominantly driving connectivity (all sagebrush cover at 564 m scale and conifer configuration at the 20,000 m scale) and defining the intercept as 2, the coefficient for all sagebrush cover as 1, the coefficient for conifer configuration as -4, and the τ parameter as 0.1. The hypotheses of connectivity fit to the simulated data in the connectivity model include the following: anthropogenic (proportion of agriculture at the 6,400 m scale, density of BLM roads at the 10,000 m scale, proportion of development at the 15,000 m scale), habitat (truth), climate (mean annual rainfall at the 10,000 m scale and mean maximum temperature at the 3,000 scale), phenology (green-up rate at the 3,000 m scale, brown-down at the 1,000 m scale, and green-up at the 15,000 m scale), topography (CTI at the 564 m scale and terrain ruggedness index at the 10,000 scale), and RSF (nesting habitat selection model). Each model was fit with 50,000 MCMC iteration, discarding the first 20,000 iterations as a burn-in period in a Metropolis-Hastings sampler. Convergence was visually inspected with trace and density plots of the posterior distributions for each parameter.

Evaluation of DIC ranking shows that the multivariable model used to simulate data was identified as the best model in all replicates (Table S6.2).

Table S2. Means and 95 % credible intervals of the posterior distributions for all parameters and DIC values obtained for each multivariable hypothesis.

Model	Rep	Intercept	$\beta 1$	$\beta 2$	$\beta 3$	τ	DIC	Δ DIC
Habitat	1	1.22 [0.97 – 1.42]	0.99 [0.27 – 1.79]	-3.98 [-4.54 – -3.39]		0.21 [0.20 – 0.21]	-448713.3	0.0
Topographic	1	-1.84 [-2.38 – -1.29]	7.22 [5.29 – 8.96]	0.74 [-0.68 – 2.11]		0.20 [0.20 – 0.21]	-430510.5	18202.8
RSF	1	-0.46 [-0.62 – -0.31]	0.84 [0.41 – 1.24]			0.21 [0.20 – 0.21]	-397468.6	51244.6
Anthropogenic	1	1.39 [1.02 – 1.77]	1.56 [1.16 – 1.99]	-2.07 [-2.74 – -1.49]	-1.25 [-1.54 – -0.94]	0.21 [0.20 – 0.21]	-383565.2	65148.0
Phenology	1	-0.30 [-0.55 – -0.06]	-1.24 [-2.67 – -0.00]	-1.68 [-2.40 – -1.03]	4.91 [3.61 – 6.09]	0.21 [0.20 – 0.21]	-376359.7	72353.6
Climate	1	0.03 [-2.77 – 2.41]	6.41 [2.88 – 10.28]	-0.87 [-3.73 – 2.43]		0.21 [0.20 – 0.21]	-373775.7	74937.6
Habitat	2	1.22 [0.99 – 1.43]	0.97 [0.21 – 1.77]	-3.97 [-4.49 – -3.42]		0.21 [0.20 – 0.21]	-447567.4	0.0
Topographic	2	-1.85 [-2.37 – -1.30]	7.17 [5.37 – 9.01]	0.79 [-0.57 – 2.12]		0.21 [0.20 – 0.21]	-432491.7	15075.7
RSF	2	-0.46 [-0.62 – -0.31]	0.85 [0.44 – 1.25]			0.21 [0.20 – 0.21]	-396482.2	51085.2
Phenology	2	0.62 [-0.13 – 1.40]	-1.94 [-3.53 – -0.52]	-5.21 [-8.13 – -2.40]	3.68 [2.07 – 5.26]	0.21 [0.20 – 0.21]	-394850.0	52717.4
Anthropogenic	2	1.36 [0.99 – 1.75]	1.58 [1.21 – 1.97]	-2.04 [-2.71 – -1.42]	-1.26 [-1.53 – -0.96]	0.20 [0.20 – 0.21]	-384116.1	63451.3
Climate	2	0.03 [-2.59 – 2.22]	6.41 [2.95 – 10.19]	-0.90 [-3.44 – 2.19]		0.21 [0.20 – 0.21]	-375468.4	72099.0

Additionally, the posterior means and CIs across replicates return nearly completely overlapping estimates (Figure S6.2).

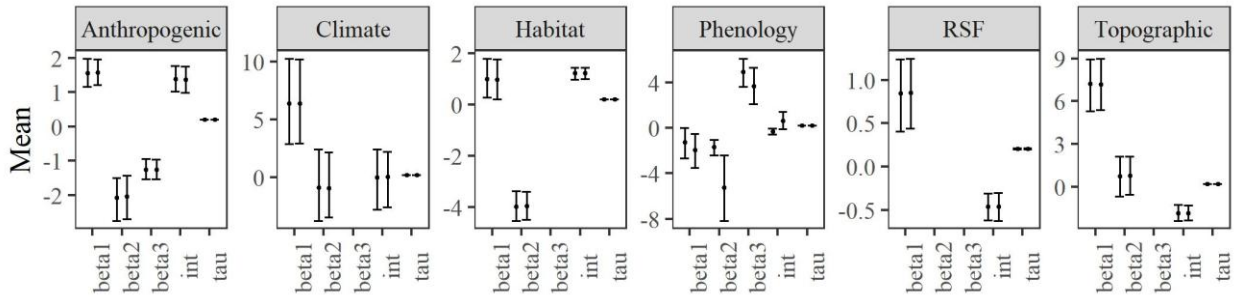

Figure S6.2. 95% posterior means and credible intervals of parameters for each multivariable hypothesis.

APPENDIX VII

Table S7.1. All covariate estimates, 80% credible intervals ([80% CI]), and DIC (deviance information criterion) comparison for univariable models of genetic connectivity for the Gunnison Basin extent for the Gunnison sage-grouse. GR = Gelman-Rubin statistic. See Table 3.1 in main text for the variable names corresponding to abbreviations (Cov.). MW=moving window radius in meters, Form=quadratic (Q), or linear (L), GR=Gelman-Rubin diagnostic. Models are ranked by DIC within each covariate.

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
D12	3000	L	1.45 [1.43 – 1.48]	0.99	2.74 [2.48 – 3.03]	0.99	-2.86 [-3.92 – -1.88]	1.00			-11348.50
	3000	Q	1.45 [1.43 – 1.47]	1.01	2.74 [2.48 – 3.03]	1.03	-3.48 [-5.29 – -1.71]	1.00	1.47 [-1.99 – 4.81]	1.00	-11298.93
	1000	L	1.45 [1.43 – 1.48]	0.99	2.40 [2.20 – 2.62]	1.00	-3.18 [-4.78 – -1.56]	0.99			-11251.12
	1000	Q	1.45 [1.43 – 1.48]	0.99	2.41 [2.21 – 2.62]	1.02	-3.10 [-5.11 – -1.11]	1.00	-0.34 [-4.02 – 3.29]	0.92	-11234.57
	564	Q	1.45 [1.43 – 1.48]	1.02	2.28 [2.10 – 2.47]	1.03	-2.52 [-4.85 – -0.01]	1.02	-0.73 [-4.60 – 3.08]	1.00	-11206.80
	564	L	1.45 [1.43 – 1.48]	1.02	2.28 [2.10 – 2.47]	1.00	-2.75 [-4.77 – -0.56]	0.99			-11206.42
	6400	L	1.45 [1.43 – 1.48]	1.02	2.78 [2.45 – 3.12]	1.00	-1.98 [-2.87 – -1.06]	1.02			-11131.31
	20000	Q	1.45 [1.43 – 1.48]	0.98	2.39 [1.18 – 3.58]	0.97	0.47 [-2.55 – 3.60]	0.97	-1.07 [-3.42 – 1.26]	0.98	-11120.59
	20000	L	1.45 [1.43 – 1.48]	1.01	2.72 [1.71 – 3.65]	1.00	-0.77 [-2.00 – 0.58]	1.01			-11078.39
	15000	Q	1.45 [1.43 – 1.48]	1.03	2.67 [1.68 – 3.67]	1.04	1.09 [-1.84 – 3.95]	1.05	-2.7 [-5.18 – -0.14]	1.07	-11052.66
	6400	Q	1.45 [1.43 – 1.48]	1.00	2.94 [2.57 – 3.33]	1.03	-3.62 [-5.63 – -1.58]	1.02	2.59 [-0.23 – 5.40]	0.99	-11025.45
	10000	L	1.45 [1.43 – 1.48]	1.02	2.92 [2.50 – 3.36]	1.03	-1.77 [-2.70 – -0.87]	1.03			-11014.94
	10000	Q	1.45 [1.43 – 1.48]	1.00	2.97 [2.45 – 3.48]	1.00	-2.11 [-4.48 – 0.31]	1.00	0.50 [-2.56 – 3.41]	1.01	-11000.56
	15000	L	1.45 [1.43 – 1.48]	1.01	3.28 [2.51 – 4.12]	1.01	-1.73 [-2.95 – -0.56]	1.02			-10960.11
DI12		L	1.45 [1.43 – 1.48]	1.01	1.45 [1.19 – 1.72]	0.99	5.49 [3.62 – 7.54]	0.99			-11132.45
		Q	1.45 [1.43 – 1.48]	0.99	1.46 [1.19 – 1.73]	1.01	5.08 [2.90 – 7.40]	1.00	1.75 [-2.09 – 5.62]	0.98	-11129.02
D14	15000	Q	1.45 [1.43 – 1.48]	1.01	1.41 [0.66 – 2.13]	0.99	3.58 [0.95 – 6.28]	1.00	-3.20 [-5.29 – -1.11]	1.00	-11389.27
	20000	Q	1.45 [1.43 – 1.48]	1.01	1.42 [0.67 – 2.19]	0.97	2.93 [0.27 – 5.48]	0.98	-2.38 [-4.47 – -0.28]	0.98	-11321.36
	564	L	1.45 [1.43 – 1.48]	1.00	2.18 [2.01 – 2.34]	0.97	-0.98 [-4.54 – 2.59]	0.99			-11256.36
	1000	L	1.45 [1.43 – 1.48]	0.97	2.20 [2.03 – 2.38]	1.00	-1.65 [-5.04 – 1.76]	1.00			-11244.51
	20000	L	1.45 [1.43 – 1.48]	1.02	2.14 [1.71 – 2.59]	0.98	0.02 [-0.64 – 0.70]	0.98			-11243.99

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	564	Q	1.45 [1.43 – 1.48]	1.00	2.18 [2.01 – 2.35]	1.00	-1.03 [-4.67 – 2.55]	0.96	0.08 [-3.92 – 4.17]	0.97	-11243.03
	1000	Q	1.45 [1.43 – 1.48]	0.95	2.20 [2.03 – 2.38]	0.98	-1.69 [-5.16 – 1.79]	0.99	0.10 [-4.02 – 3.94]	0.96	-11220.25
	3000	Q	1.45 [1.43 – 1.48]	0.98	2.47 [2.21 – 2.73]	1.01	-3.71 [-6.24 – -1.19]	1.02	0.56 [-3.72 – 4.64]	0.99	-11137.60
	3000	L	1.45 [1.43 – 1.48]	0.98	2.47 [2.21 – 2.74]	1.03	-3.58 [-6.15 – -1.06]	1.04			-11133.50
	6400	L	1.45 [1.43 – 1.48]	1.01	2.37 [2.13 – 2.62]	0.97	-0.93 [-1.78 – -0.06]	0.97			-11123.59
	10000	L	1.45 [1.43 – 1.48]	0.99	2.42 [2.12 – 2.72]	0.98	-0.69 [-1.31 – -0.01]	0.99			-11123.53
	15000	L	1.45 [1.43 – 1.48]	0.99	2.37 [2.01 – 2.75]	0.99	-0.37 [-0.95 – 0.21]	1.01			-11123.51
	10000	Q	1.45 [1.43 – 1.48]	0.98	2.45 [1.91 – 2.97]	1.03	-0.86 [-3.32 – 1.72]	1.03	0.17 [-2.27 – 2.53]	1.04	-11122.42
	6400	Q	1.45 [1.43 – 1.48]	0.99	2.63 [2.27 – 2.98]	1.03	-3.13 [-5.24 – -0.89]	1.02	2.80 [0.19 – 5.28]	1.03	-11109.11
DI14		Q	1.45 [1.43 – 1.48]	1.00	1.89 [1.61 – 2.17]	0.97	2.48 [-0.07 – 5.17]	0.99	0.78 [-3.03 – 4.57]	1.01	-11094.34
		L	1.45 [1.43 – 1.48]	1.00	1.88 [1.60 – 2.17]	0.98	2.75 [0.17 – 5.19]	0.98			-11089.03
D47	564	Q	1.45 [1.43 – 1.48]	0.99	2.06 [1.67 – 2.44]	1.01	0.69 [-1.91 – 3.27]	1.01	-0.05 [-3.78 – 3.86]	1.03	-11274.92
	564	L	1.45 [1.43 – 1.48]	1.00	2.07 [1.68 – 2.46]	1.00	0.60 [-1.92 – 3.19]	0.99			-11266.89
	20000	Q	1.45 [1.43 – 1.48]	0.99	2.23 [1.10 – 3.31]	1.02	-0.41 [-3.26 – 2.57]	1.02	0.37 [-1.77 – 2.51]	1.03	-11242.03
	20000	L	1.45 [1.43 – 1.48]	1.02	2.13 [1.35 – 2.88]	1.01	0.03 [-0.96 – 1.09]	1.01			-11226.00
	1000	L	1.45 [1.43 – 1.48]	1.03	2.13 [1.70 – 2.57]	1.00	0.13 [-1.95 – 2.29]	1.00			-11215.62
	1000	Q	1.45 [1.43 – 1.48]	1.00	2.13 [1.69 – 2.56]	1.01	0.16 [-2.25 – 2.53]	0.98	0.12 [-3.80 – 3.81]	0.97	-11210.66
	15000	L	1.45 [1.43 – 1.48]	1.02	2.41 [1.69 – 3.11]	1.00	-0.37 [-1.34 – 0.65]	1.00			-11170.65
	15000	Q	1.45 [1.43 – 1.48]	1.03	2.56 [1.54 – 3.58]	1.02	-0.90 [-3.87 – 2.05]	1.03	0.43 [-1.90 – 2.75]	1.03	-11133.38
	3000	Q	1.45 [1.43 – 1.48]	1.01	2.47 [1.78 – 3.14]	1.01	-0.75 [-3.39 – 1.90]	1.01	0.03 [-2.82 – 2.91]	1.00	-11128.52
	3000	L	1.45 [1.43 – 1.48]	1.00	2.46 [1.93 – 3.03]	1.05	-0.73 [-2.00 – 0.48]	1.06			-11124.10
	6400	Q	1.45 [1.43 – 1.48]	0.96	2.87 [2.01 – 3.79]	0.96	-0.91 [-3.81 – 1.85]	0.99	-0.52 [-2.96 – 2.04]	1.01	-11023.39
	6400	L	1.45 [1.43 – 1.48]	0.98	3.00 [2.33 – 3.64]	0.99	-1.46 [-2.54 – -0.35]	0.99			-11013.49
	10000	L	1.45 [1.43 – 1.48]	1.02	3.06 [2.37 – 3.75]	0.96	-1.27 [-2.2 – -0.33]	0.96			-10973.00
	10000	Q	1.45 [1.43 – 1.48]	0.99	2.83 [1.83 – 3.87]	0.98	-0.50 [-3.44 – 2.39]	0.97	-0.61 [-2.65 – 1.54]	0.97	-10968.34
DI47		L	1.45 [1.43 – 1.48]	1.02	2.15 [1.97 – 2.32]	1.01	0.29 [-3.69 – 4.17]	0.98			-11277.36
		Q	1.45 [1.43 – 1.48]	1.04	2.15 [1.98 – 2.33]	1.01	0.30 [-3.71 – 4.26]	1.01	0.00 [-4.10 – 4.06]	0.99	-11232.39
DD	564	Q	1.45 [1.43 – 1.48]	1.01	2.15 [2.01 – 2.30]	0.99	0.20 [-3.76 – 4.33]	1.00	0.11 [-4.05 – 4.04]	1.00	-11263.39

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	3000	Q	1.45 [1.43 – 1.48]	1.03	2.14 [1.99 – 2.29]	1.01	1.43 [-2.06 – 4.87]	0.99	0.92 [-3.16 – 4.59]	1.00	-11245.65
	1000	L	1.45 [1.43 – 1.48]	1.00	2.15 [2.01 – 2.30]	1.01	0.25 [-3.91 – 4.26]	0.99			-11244.89
	1000	Q	1.45 [1.43 – 1.48]	1.01	2.15 [2.01 – 2.30]	1.00	0.36 [-3.66 – 4.33]	0.99	0.16 [-3.95 – 4.12]	1.02	-11244.43
	6400	L	1.45 [1.43 – 1.48]	0.99	2.12 [1.96 – 2.28]	1.01	0.64 [-0.40 – 2.04]	1.03			-11242.52
	564	L	1.45 [1.43 – 1.48]	1.02	2.15 [2.01 – 2.30]	0.99	0.28 [-3.86 – 4.16]	0.99			-11241.08
	10000	Q	1.45 [1.43 – 1.48]	1.03	2.31 [2.13 – 2.50]	1.02	-4.04 [-5.83 – -2.15]	1.05	4.14 [2.06 – 6.20]	1.04	-11240.92
	3000	L	1.45 [1.43 – 1.48]	0.98	2.14 [1.99 – 2.29]	0.97	1.74 [-1.70 – 5.20]	0.93			-11232.60
	6400	Q	1.45 [1.43 – 1.48]	0.99	2.13 [1.97 – 2.29]	0.97	-1.03 [-3.45 – 1.42]	0.97	2.78 [-0.14 – 5.83]	1.02	-11223.03
	10000	L	1.45 [1.43 – 1.48]	1.02	2.22 [2.05 – 2.39]	1.00	-0.33 [-0.77 – 0.13]	0.98			-11184.61
	15000	Q	1.45 [1.43 – 1.48]	0.99	2.19 [1.98 – 2.40]	1.02	2.97 [0.64 – 5.41]	0.96	-3.36 [-5.83 – -1.00]	0.96	-11181.45
	15000	L	1.45 [1.43 – 1.48]	1.00	2.29 [2.09 – 2.49]	0.98	-0.37 [-0.71 – -0.01]	0.98			-11151.22
	20000	L	1.45 [1.43 – 1.48]	0.98	2.29 [2.04 – 2.55]	1.01	-0.29 [-0.73 – 0.14]	1.01			-11144.87
	20000	Q	1.45 [1.43 – 1.48]	1.03	2.28 [2.03 – 2.56]	1.00	-0.25 [-2.21 – 1.65]	0.98	-0.03 [-2.22 – 2.20]	0.97	-11125.28
DAG	3000	Q	1.45 [1.43 – 1.48]	1.00	2.54 [2.33 – 2.75]	0.99	-2.22 [-4.05 – -0.42]	1.01	-0.54 [-3.22 – 2.17]	1.02	-11572.27
	3000	L	1.45 [1.43 – 1.48]	0.97	2.54 [2.35 – 2.75]	1.03	-2.52 [-3.34 – -1.78]	1.00			-11530.63
	1000	Q	1.45 [1.43 – 1.48]	1.02	2.36 [2.19 – 2.55]	1.01	-1.96 [-3.93 – -0.02]	1.05	-0.03 [-3.05 – 3.05]	1.06	-11237.54
	1000	L	1.45 [1.43 – 1.48]	1.00	2.37 [2.19 – 2.55]	0.98	-1.98 [-2.86 – -1.08]	0.98			-11216.18
	564	Q	1.45 [1.43 – 1.48]	1.01	2.35 [2.17 – 2.53]	1.00	-1.80 [-3.83 – 0.33]	0.99	-0.20 [-3.33 – 2.83]	0.98	-11209.18
	564	L	1.45 [1.43 – 1.48]	0.98	2.35 [2.17 – 2.52]	0.99	-1.89 [-2.81 – -0.98]	1.00			-11200.92
	6400	Q	1.45 [1.43 – 1.48]	0.99	2.60 [2.33 – 2.89]	0.98	-0.98 [-2.51 – 0.49]	0.98	-0.60 [-2.19 – 1.05]	0.98	-11184.10
	6400	L	1.45 [1.43 – 1.48]	1.00	2.66 [2.42 – 2.91]	1.00	-1.49 [-2.02 – -0.99]	1.00			-11146.03
	20000	L	1.45 [1.43 – 1.48]	1.00	2.83 [2.47 – 3.19]	1.01	-1.35 [-1.96 – -0.71]	1.01			-10963.57
	10000	L	1.45 [1.43 – 1.48]	0.99	2.62 [2.36 – 2.91]	1.02	-1.10 [-1.63 – -0.59]	1.01			-10933.76
	10000	Q	1.45 [1.43 – 1.48]	1.00	2.72 [2.40 – 3.06]	1.01	-2.16 [-3.71 – -0.55]	1.02	1.26 [-0.56 – 3.00]	1.03	-10929.74
	20000	Q	1.45 [1.43 – 1.48]	1.00	2.95 [2.50 – 3.44]	0.97	-2.18 [-4.26 – -0.28]	0.98	0.94 [-1.07 – 3.06]	0.98	-10925.76
	15000	Q	1.45 [1.43 – 1.48]	0.99	2.87 [2.49 – 3.31]	0.98	-2.19 [-3.84 – -0.48]	0.98	1.17 [-0.43 – 2.70]	0.98	-10924.93
	15000	L	1.45 [1.43 – 1.48]	1.02	2.70 [2.40 – 3.04]	1.01	-0.99 [-1.48 – -0.52]	1.01			-10923.25
DA	20000	Q	1.45 [1.43 – 1.48]	0.99	2.08 [0.86 – 3.20]	0.99	0.35 [-2.59 – 3.36]	0.99	-0.34 [-2.48 – 1.84]	0.98	-11262.67

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	564	L	1.45 [1.43 – 1.48]	1.00	2.11 [1.75 – 2.48]	0.97	0.33 [-2.36 – 3.16]	0.96			-11260.81
	564	Q	1.45 [1.43 – 1.48]	0.97	2.11 [1.73 – 2.47]	0.99	0.33 [-2.33 – 3.25]	0.99	0.11 [-3.82 – 3.98]	0.99	-11246.34
	20000	L	1.45 [1.43 – 1.48]	1.00	2.15 [1.24 – 3.00]	1.03	0.01 [-1.14 – 1.22]	1.03			-11237.11
	1000	Q	1.45 [1.43 – 1.48]	0.99	2.19 [1.80 – 2.57]	1.01	-0.28 [-2.94 – 2.47]	1.00	0.13 [-3.83 – 3.96]	1.00	-11233.24
	1000	L	1.45 [1.43 – 1.48]	1.01	2.19 [1.79 – 2.58]	1.00	-0.21 [-2.83 – 2.49]	1.00			-11224.48
	3000	L	1.45 [1.43 – 1.48]	0.99	2.61 [2.11 – 3.14]	1.01	-1.58 [-3.26 – 0.07]	1.02			-11102.07
	15000	Q	1.45 [1.43 – 1.48]	1.00	2.53 [1.48 – 3.57]	0.96	-0.36 [-3.25 – 2.66]	0.93	-0.28 [-2.54 – 1.97]	0.94	-11099.03
	3000	Q	1.45 [1.43 – 1.48]	0.99	2.68 [2.13 – 3.22]	1.01	-2.02 [-4.43 – 0.46]	1.02	0.70 [-2.63 – 3.96]	1.03	-11077.93
	15000	L	1.45 [1.43 – 1.48]	0.99	2.63 [1.88 – 3.36]	0.98	-0.68 [-1.68 – 0.37]	0.97			-11072.22
	6400	L	1.45 [1.43 – 1.48]	1.00	2.94 [2.38 – 3.49]	1.03	-1.68 [-2.81 – -0.53]	1.04			-11002.62
	6400	Q	1.45 [1.43 – 1.48]	1.01	3.13 [2.35 – 3.88]	1.03	-2.55 [-5.23 – 0.19]	1.02	0.91 [-1.65 – 3.56]	1.02	-10983.33
	10000	L	1.45 [1.43 – 1.48]	0.99	3.07 [2.45 – 3.69]	1.02	-1.44 [-2.36 – -0.52]	1.02			-10957.85
	10000	Q	1.45 [1.43 – 1.48]	0.99	2.95 [2.00 – 3.92]	1.01	-1.00 [-3.83 – 1.81]	1.01	-0.37 [-2.50 – 1.84]	1.00	-10951.45
DIA		Q	1.45 [1.43 – 1.48]	1.01	2.15 [1.93 – 2.35]	0.96	0.23 [-3.49 – 3.94]	0.96	0.19 [-3.85 – 4.11]	0.97	-11238.47
		L	1.45 [1.43 – 1.48]	1.01	2.14 [1.94 – 2.35]	0.98	0.30 [-3.57 – 4.09]	0.96			-11236.47
DB	564	Q	1.45 [1.43 – 1.48]	1.02	2.11 [1.75 – 2.48]	0.96	0.40 [-2.43 – 3.24]	0.97	0.02 [-4.00 – 3.98]	1.01	-11256.80
	564	L	1.45 [1.43 – 1.48]	0.97	2.12 [1.76 – 2.49]	1.04	0.28 [-2.42 – 3.09]	1.04			-11230.52
	20000	Q	1.45 [1.43 – 1.48]	0.98	2.15 [0.97 – 3.30]	1.00	0.31 [-2.63 – 3.28]	0.99	-0.37 [-2.53 – 1.80]	1.00	-11224.67
	1000	Q	1.45 [1.43 – 1.48]	1.01	2.19 [1.79 – 2.60]	0.98	-0.34 [-3.14 – 2.49]	0.96	0.30 [-3.65 – 4.18]	1.01	-11223.91
	1000	L	1.45 [1.43 – 1.48]	1.05	2.19 [1.80 – 2.58]	1.00	-0.24 [-2.87 – 2.44]	1.00			-11205.82
	20000	L	1.45 [1.43 – 1.48]	1.00	2.28 [1.36 – 3.16]	0.99	-0.17 [-1.35 – 1.05]	0.99			-11191.12
	15000	Q	1.45 [1.43 – 1.48]	0.98	2.55 [1.48 – 3.54]	1.01	-0.34 [-3.14 – 2.55]	1.00	-0.28 [-2.49 – 1.90]	0.99	-11106.58
	3000	L	1.45 [1.43 – 1.48]	1.01	2.64 [2.13 – 3.13]	0.99	-1.65 [-3.23 – 0.01]	0.99			-11106.46
	3000	Q	1.45 [1.43 – 1.48]	1.00	2.66 [2.10 – 3.22]	1.02	-1.88 [-4.43 – 0.59]	1.00	0.62 [-2.89 – 3.93]	0.99	-11105.52
	15000	L	1.45 [1.43 – 1.48]	0.97	2.63 [1.88 – 3.35]	0.99	-0.68 [-1.71 – 0.38]	0.99			-11102.54
	6400	L	1.45 [1.43 – 1.48]	1.00	2.92 [2.37 – 3.49]	1.02	-1.67 [-2.81 – -0.52]	1.02			-10999.14
	6400	Q	1.45 [1.43 – 1.48]	0.98	3.14 [2.39 – 3.89]	0.95	-2.65 [-5.28 – 0.01]	0.96	0.99 [-1.48 – 3.59]	0.98	-10986.66
	10000	L	1.45 [1.43 – 1.48]	1.01	3.10 [2.48 – 3.69]	0.97	-1.48 [-2.35 – -0.56]	0.97			-10943.73

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	10000	Q	1.45 [1.43 – 1.48]	1.00	2.98 [2.01 – 3.94]	1.02	-1.09 [-3.86 – 1.71]	1.01	-0.26 [-2.46 – 1.92]	1.00	-10939.56
DIB		L	1.45 [1.43 – 1.48]	1.00	2.15 [1.93 – 2.37]	1.01	0.19 [-3.69 – 3.93]	1.00			-11258.02
		Q	1.45 [1.43 – 1.48]	1.00	2.15 [1.94 – 2.36]	0.99	0.10 [-3.59 – 3.85]	1.03	0.11 [-3.92 – 4.22]	0.90	-11253.60
DID		Q	1.45 [1.43 – 1.48]	0.98	1.98 [1.58 – 2.39]	0.99	1.21 [-0.99 – 3.33]	1.00	-1.49 [-4.29 – 1.35]	1.03	-11242.11
		L	1.45 [1.43 – 1.48]	0.99	2.11 [1.79 – 2.44]	1.00	0.14 [-0.68 – 0.97]	1.00			-11203.27
DIOG		L	1.45 [1.43 – 1.48]	0.97	1.68 [1.41 – 1.96]	0.99	2.24 [1.09 – 3.36]	0.98			-11049.61
		Q	1.45 [1.43 – 1.48]	1.00	1.71 [1.44 – 1.99]	1.01	1.73 [-0.14 – 3.55]	1.03	1.09 [-2.22 – 4.49]	1.00	-11041.68
DP	1000	Q	1.45 [1.43 – 1.48]	0.95	2.15 [2.01 – 2.30]	0.99	0.22 [-3.86 – 4.10]	0.98	0.17 [-3.82 – 4.10]	0.99	-11258.69
	1000	L	1.45 [1.43 – 1.48]	1.00	2.15 [2.01 – 2.30]	1.02	0.14 [-3.89 – 4.30]	1.05			-11254.59
	3000	Q	1.45 [1.43 – 1.48]	0.97	2.15 [2.01 – 2.30]	1.00	-0.06 [-4.08 – 3.76]	0.98	0.41 [-3.51 – 4.37]	1.02	-11253.77
	3000	L	1.45 [1.43 – 1.48]	0.98	2.15 [2.01 – 2.31]	0.97	0.04 [-3.97 – 3.80]	1.02			-11253.11
	10000	Q	1.45 [1.43 – 1.48]	1.03	2.29 [2.12 – 2.48]	1.03	-4.35 [-6.24 – -2.46]	0.96	4.90 [2.58 – 7.25]	0.96	-11230.49
	6400	Q	1.45 [1.43 – 1.48]	1.02	2.14 [1.98 – 2.30]	1.04	-0.64 [-3.17 – 1.94]	1.06	2.40 [-1.13 – 5.83]	1.01	-11217.10
	6400	L	1.45 [1.43 – 1.48]	1.01	2.14 [1.98 – 2.30]	0.99	0.42 [-1.11 – 2.16]	1.00			-11212.87
	10000	L	1.45 [1.43 – 1.48]	0.97	2.22 [2.05 – 2.40]	0.97	-0.42 [-0.93 – 0.15]	1.00			-11195.91
	15000	Q	1.45 [1.43 – 1.48]	1.00	2.23 [2.03 – 2.44]	1.00	1.82 [-0.64 – 4.28]	1.03	-2.31 [-4.83 – 0.18]	1.03	-11161.47
	20000	L	1.45 [1.43 – 1.48]	1.00	2.25 [2.03 – 2.45]	0.99	-0.21 [-0.57 – 0.16]	0.99			-11157.46
	20000	Q	1.45 [1.43 – 1.48]	1.01	2.21 [1.99 – 2.44]	1.04	0.65 [-1.93 – 3.19]	1.00	-0.93 [-3.59 – 1.78]	1.00	-11144.29
	15000	L	1.45 [1.43 – 1.48]	0.99	2.30 [2.11 – 2.50]	0.97	-0.44 [-0.80 – -0.06]	0.99			-11130.00
DIP		Q	1.45 [1.43 – 1.48]	1.00	2.15 [1.83 – 2.47]	1.00	-0.08 [-2.12 – 1.88]	1.02	0.42 [-2.88 – 3.76]	1.02	-11219.54
		L	1.45 [1.43 – 1.48]	1.01	2.13 [1.84 – 2.43]	1.01	0.13 [-0.89 – 1.13]	1.01			-11216.47
AS	3000	Q	1.45 [1.43 – 1.48]	1.01	1.62 [1.11 – 2.12]	1.01	1.58 [-0.68 – 3.82]	0.98	-0.52 [-2.98 – 2.06]	0.97	-11426.40
	3000	L	1.45 [1.43 – 1.48]	1.02	1.68 [1.29 – 2.09]	1.01	1.12 [0.22 – 2.06]	1.00			-11414.06
	6400	L	1.45 [1.43 – 1.48]	1.00	1.87 [1.39 – 2.35]	1.01	0.57 [-0.38 – 1.55]	1.01			-11344.87
	564	Q	1.45 [1.43 – 1.48]	0.98	1.90 [1.57 – 2.25]	0.97	1.18 [-0.91 – 3.19]	0.98	-0.22 [-3.50 – 3.20]	0.98	-11325.04
	1000	Q	1.45 [1.43 – 1.48]	1.01	1.86 [1.51 – 2.20]	0.99	1.37 [-0.72 – 3.40]	1.00	-0.41 [-3.61 – 2.95]	1.01	-11325.02
	564	L	1.45 [1.43 – 1.48]	1.04	1.92 [1.60 – 2.25]	1.05	1.02 [-0.24 – 2.34]	1.02			-11318.98
	1000	L	1.45 [1.43 – 1.48]	1.02	1.88 [1.55 – 2.22]	0.98	1.11 [-0.07 – 2.35]	0.97			-11313.41

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	15000	L	1.45 [1.43 – 1.48]	1.02	1.96 [1.48 – 2.46]	1.02	0.32 [-0.46 – 1.11]	1.02			-11288.79
	6400	Q	1.45 [1.43 – 1.48]	1.05	1.96 [1.26 – 2.63]	1.02	0.16 [-2.37 – 2.75]	1.04	0.41 [-2.00 – 2.93]	1.04	-11286.10
	20000	L	1.45 [1.43 – 1.48]	1.00	2.04 [1.49 – 2.59]	1.00	0.17 [-0.61 – 0.98]	0.99			-11270.60
	15000	Q	1.45 [1.43 – 1.48]	1.03	2.36 [1.58 – 3.10]	1.00	-1.36 [-3.92 – 1.22]	1.01	1.48 [-0.72 – 3.68]	1.01	-11269.82
	10000	L	1.45 [1.43 – 1.48]	0.98	2.01 [1.53 – 2.49]	0.96	0.27 [-0.55 – 1.12]	0.96			-11255.91
	10000	Q	1.45 [1.43 – 1.48]	0.99	2.27 [1.58 – 2.98]	0.99	-0.93 [-3.45 – 1.62]	0.99	1.19 [-1.18 – 3.46]	0.99	-11235.73
	20000	Q	1.45 [1.43 – 1.48]	1.02	2.26 [1.42 – 3.13]	0.99	-0.73 [-3.47 – 1.93]	1.00	0.75 [-1.36 – 2.95]	1.00	-11220.32
BS	3000	L	1.45 [1.43 – 1.48]	1.00	1.69 [1.29 – 2.07]	1.00	1.12 [0.24 – 2.05]	0.99			-11442.00
	3000	Q	1.46 [1.43 – 1.48]	1.00	1.61 [1.11 – 2.10]	1.04	1.57 [-0.54 – 3.87]	1.04	-0.54 [-2.99 – 1.98]	1.04	-11433.94
	1000	L	1.45 [1.43 – 1.48]	1.00	1.87 [1.54 – 2.20]	1.00	1.14 [-0.05 – 2.43]	0.97			-11338.53
	6400	L	1.45 [1.43 – 1.48]	1.00	1.87 [1.39 – 2.35]	0.99	0.57 [-0.36 – 1.56]	1.00			-11333.88
	564	L	1.46 [1.43 – 1.48]	1.00	1.91 [1.59 – 2.25]	1.03	1.02 [-0.26 – 2.36]	1.03			-11324.03
	1000	Q	1.45 [1.43 – 1.48]	1.00	1.86 [1.52 – 2.21]	0.98	1.32 [-0.77 – 3.37]	0.97	-0.40 [-3.61 – 3.02]	0.99	-11301.57
	15000	L	1.45 [1.43 – 1.48]	1.02	1.96 [1.47 – 2.46]	0.99	0.32 [-0.47 – 1.10]	1.00			-11298.81
	6400	Q	1.45 [1.43 – 1.48]	0.98	1.98 [1.26 – 2.64]	0.99	0.12 [-2.41 – 2.70]	1.00	0.49 [-1.95 – 2.93]	1.00	-11294.95
	564	Q	1.45 [1.43 – 1.48]	0.95	1.90 [1.58 – 2.24]	0.96	1.17 [-0.84 – 3.19]	0.98	-0.12 [-3.52 – 3.19]	1.01	-11284.64
	10000	L	1.45 [1.43 – 1.48]	0.99	2.00 [1.54 – 2.48]	1.00	0.27 [-0.54 – 1.11]	0.99			-11281.53
	20000	L	1.45 [1.43 – 1.48]	1.00	2.04 [1.49 – 2.60]	0.98	0.17 [-0.63 – 0.97]	0.98			-11255.78
	15000	Q	1.45 [1.43 – 1.48]	1.02	2.36 [1.59 – 3.10]	1.00	-1.38 [-3.89 – 1.22]	1.00	1.5 [-0.68 – 3.71]	1.00	-11237.16
	10000	Q	1.45 [1.43 – 1.48]	0.97	2.28 [1.56 – 2.99]	0.98	-0.96 [-3.52 – 1.61]	0.99	1.2 [-1.12 – 3.55]	0.99	-11230.03
	20000	Q	1.45 [1.43 – 1.48]	0.98	2.26 [1.41 – 3.11]	0.98	-0.71 [-3.35 – 1.96]	0.99	0.71 [-1.4 – 2.89]	1.01	-11218.42
CON	20000	Q	1.45 [1.43 – 1.48]	1.01	2.19 [1.82 – 2.59]	0.98	0.32 [-1.72 – 2.35]	1.03	-1.19 [-4.02 – 1.61]	1.04	-11267.11
	20000	L	1.45 [1.43 – 1.48]	1.00	2.29 [1.95 – 2.63]	1.02	-0.46 [-1.49 – 0.65]	1.02			-11239.44
	15000	Q	1.45 [1.43 – 1.48]	1.05	2.08 [1.76 – 2.40]	1.01	0.57 [-1.38 – 2.59]	0.99	-0.61 [-3.87 – 2.62]	0.99	-11196.94
	15000	L	1.45 [1.43 – 1.48]	0.99	2.10 [1.82 – 2.41]	0.98	0.23 [-1.00 – 1.49]	0.98			-11177.19
	10000	L	1.45 [1.43 – 1.48]	1.01	1.97 [1.74 – 2.21]	0.98	1.35 [-0.05 – 2.73]	0.97			-11047.46
	10000	Q	1.45 [1.43 – 1.48]	1.00	1.96 [1.72 – 2.21]	1.05	1.37 [-0.57 – 3.23]	1.06	0.03 [-3.56 – 3.77]	1.03	-11037.42
	6400	L	1.45 [1.43 – 1.48]	0.97	1.90 [1.68 – 2.13]	1.01	2.52 [0.77 – 4.18]	0.99			-10941.94

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	6400	Q	1.45 [1.43 – 1.48]	1.03	1.90 [1.68 – 2.12]	1.00	2.57 [0.59 – 4.53]	0.99	-0.12 [-3.98 – 3.76]	0.99	-10910.57
	564	L	1.45 [1.43 – 1.48]	1.00	2.04 [1.87 – 2.24]	1.01	2.38 [-0.10 – 5.05]	1.00			-10900.99
	1000	Q	1.45 [1.43 – 1.48]	1.02	2.03 [1.86 – 2.22]	1.00	2.54 [-0.18 – 5.31]	0.98	-0.19 [-4.13 – 3.79]	1.04	-10890.58
	564	Q	1.45 [1.43 – 1.48]	1.05	2.05 [1.87 – 2.23]	1.02	2.42 [-0.39 – 5.04]	1.04	0.02 [-3.75 – 4.01]	1.01	-10887.80
	1000	L	1.45 [1.43 – 1.48]	0.97	2.04 [1.86 – 2.23]	1.00	2.47 [0.04 – 5.10]	0.99			-10878.63
	3000	Q	1.45 [1.43 – 1.47]	1.02	1.94 [1.74 – 2.15]	0.96	3.52 [0.92 – 5.96]	0.96	-0.35 [-4.18 – 3.53]	1.03	-10810.15
	3000	L	1.45 [1.43 – 1.48]	1.01	1.94 [1.74 – 2.14]	1.00	3.30 [1.02 – 5.67]	1.01			-10801.69
LS	6400	Q	1.45 [1.43 – 1.48]	1.01	2.29 [2.12 – 2.46]	1.00	-3.50 [-5.99 – -0.94]	0.97	1.79 [-1.81 – 5.25]	0.96	-11330.62
	6400	L	1.45 [1.43 – 1.48]	0.96	2.27 [2.11 – 2.44]	1.01	-2.80 [-4.27 – -1.01]	0.99			-11323.20
	10000	L	1.45 [1.43 – 1.48]	0.98	2.33 [2.13 – 2.53]	1.00	-1.42 [-2.42 – -0.36]	0.99			-11295.73
	10000	Q	1.45 [1.43 – 1.48]	1.00	2.37 [2.16 – 2.59]	1.00	-2.38 [-4.45 – -0.26]	1.01	1.91 [-1.66 – 5.37]	1.02	-11284.53
	564	Q	1.45 [1.43 – 1.48]	0.98	2.15 [2.01 – 2.30]	1.00	-0.36 [-4.38 – 3.87]	1.00	-0.02 [-3.99 – 3.85]	0.96	-11281.03
	20000	Q	1.45 [1.43 – 1.48]	0.98	2.37 [2.07 – 2.69]	1.04	-1.74 [-3.79 – 0.25]	1.01	1.48 [-2.40 – 5.41]	0.96	-11263.98
	1000	L	1.45 [1.43 – 1.48]	0.99	2.15 [2.01 – 2.30]	0.97	-0.53 [-4.41 – 3.65]	0.97			-11263.88
	20000	L	1.45 [1.43 – 1.48]	0.99	2.38 [2.06 – 2.69]	1.02	-1.42 [-3.16 – 0.34]	1.02			-11261.80
	564	L	1.45 [1.43 – 1.48]	0.98	2.15 [2.01 – 2.30]	1.02	-0.30 [-4.24 – 3.85]	0.97			-11254.14
	1000	Q	1.45 [1.43 – 1.48]	0.99	2.15 [2.01 – 2.30]	1.02	-0.45 [-4.50 – 3.78]	1.01	-0.21 [-4.27 – 3.87]	1.03	-11251.92
	3000	Q	1.45 [1.43 – 1.48]	1.00	2.15 [2.01 – 2.30]	0.98	0.08 [-4.03 – 4.12]	1.02	0.08 [-3.99 – 3.99]	1.00	-11235.62
	3000	L	1.45 [1.43 – 1.48]	1.01	2.16 [2.01 – 2.31]	1.02	-0.59 [-2.57 – 2.98]	0.98			-11226.92
	15000	Q	1.45 [1.43 – 1.48]	1.01	2.25 [2.00 – 2.51]	1.03	-0.75 [-2.68 – 1.15]	1.01	0.19 [-3.79 – 3.93]	0.98	-11198.71
	15000	L	1.45 [1.43 – 1.48]	0.98	2.25 [2.00 – 2.51]	1.00	-0.77 [-2.37 – 0.87]	1.00			-11188.43
CC	20000	Q	1.45 [1.43 – 1.48]	0.98	1.85 [1.42 – 2.30]	0.95	1.48 [-0.62 – 3.60]	0.96	-1.25 [-3.38 – 1.01]	0.95	-11284.18
	20000	L	1.45 [1.43 – 1.48]	1.01	2.03 [1.70 – 2.36]	1.00	0.36 [-0.50 – 1.34]	1.02			-11260.32
	15000	L	1.45 [1.43 – 1.48]	1.00	2.20 [1.91 – 2.48]	1.01	-0.15 [-0.99 – 0.77]	1.01			-11211.27
	564	L	1.45 [1.43 – 1.48]	1.02	2.14 [1.95 – 2.33]	0.99	0.11 [-1.61 – 2.59]	0.98			-11208.81
	6400	L	1.45 [1.43 – 1.48]	0.98	2.22 [1.95 – 2.48]	0.97	-0.26 [-1.15 – 0.69]	0.96			-11198.64
	1000	L	1.45 [1.43 – 1.48]	0.98	2.19 [2.03 – 2.36]	1.03	-0.54 [-1.48 – 0.67]	1.03			-11198.09
	564	Q	1.45 [1.43 – 1.48]	0.98	2.14 [1.94 – 2.33]	0.99	1.06 [-1.63 – 3.71]	1.04	-1.16 [-4.21 – 2.37]	1.02	-11185.28

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	15000	Q	1.45 [1.43 – 1.48]	1.03	2.14 [1.76 – 2.51]	1.01	0.32 [-1.70 – 2.39]	1.01	-0.53 [-2.81 – 1.74]	1.02	-11175.77
	10000	L	1.45 [1.43 – 1.48]	0.98	2.22 [1.95 – 2.49]	0.96	-0.24 [-1.04 – 0.63]	0.95			-11173.15
	1000	Q	1.45 [1.43 – 1.48]	1.02	2.18 [2.00 – 2.36]	0.97	0.25 [-2.13 – 2.69]	0.99	-0.88 [-3.74 – 2.04]	1.02	-11171.02
	10000	Q	1.45 [1.43 – 1.48]	0.98	2.33 [1.99 – 2.67]	1.00	-1.27 [-3.35 – 0.75]	1.01	1.53 [-1.15 – 4.24]	1.00	-11143.32
	6400	Q	1.45 [1.43 – 1.48]	0.99	2.35 [2.04 – 2.66]	1.00	-1.74 [-3.71 – 0.28]	1.01	2.32 [-0.61 – 5.22]	1.00	-11102.04
	3000	Q	1.45 [1.43 – 1.48]	0.98	2.36 [2.17 – 2.55]	0.97	-3.38 [-5.51 – -1.24]	0.98	2.39 [-1.19 – 5.82]	0.96	-11093.93
	3000	L	1.45 [1.43 – 1.48]	1.02	2.33 [2.14 – 2.51]	1.03	-2.30 [-3.71 – -0.85]	1.01			-11074.07
PBS	3000	L	1.45 [1.43 – 1.48]	1.02	0.58 [-0.21 – 1.32]	1.02	2.97 [1.55 – 4.52]	1.01			-12222.98
	3000	Q	1.46 [1.43 – 1.48]	0.99	0.85 [-0.04 – 1.66]	0.99	1.45 [-1.40 – 4.39]	0.98	1.81 [-1.15 – 4.68]	0.99	-12126.34
	6400	L	1.45 [1.43 – 1.48]	0.99	0.99 [0.08 – 1.82]	0.99	1.66 [0.49 – 2.96]	0.99			-11800.34
	6400	Q	1.45 [1.43 – 1.48]	1.01	1.66 [0.55 – 2.72]	1.01	-1.00 [-3.91 – 2.03]	1.03	2.32 [-0.05 – 4.58]	1.03	-11611.97
	1000	Q	1.46 [1.43 – 1.48]	0.99	1.36 [0.78 – 1.90]	0.99	3.09 [0.84 – 5.43]	1.00	-1.99 [-4.76 – 1.20]	1.01	-11603.61
	1000	L	1.45 [1.43 – 1.48]	1.04	1.52 [0.89 – 2.06]	1.00	1.75 [0.27 – 3.55]	1.00			-11570.64
	564	Q	1.45 [1.43 – 1.48]	0.99	1.50 [1.01 – 1.95]	1.00	3.21 [1.15 – 5.26]	1.01	-2.86 [-5.37 – 0.24]	1.06	-11489.31
	564	L	1.45 [1.43 – 1.48]	1.03	1.64 [1.11 – 2.16]	0.99	1.51 [0.06 – 3.18]	0.99			-11463.42
	10000	L	1.45 [1.43 – 1.48]	1.00	1.92 [1.17 – 2.69]	0.98	0.30 [-0.71 – 1.34]	0.98			-11322.99
	20000	L	1.45 [1.43 – 1.48]	0.99	2.07 [1.41 – 2.72]	1.00	0.11 [-0.76 – 1.02]	1.00			-11282.44
	15000	L	1.45 [1.43 – 1.48]	0.99	2.03 [1.37 – 2.65]	0.98	0.18 [-0.69 – 1.11]	0.99			-11281.68
	10000	Q	1.45 [1.43 – 1.48]	1.01	2.31 [1.25 – 3.36]	0.98	-1.11 [-3.93 – 1.85]	0.98	1.12 [-1.12 – 3.25]	0.97	-11232.23
	15000	Q	1.45 [1.43 – 1.48]	1.01	2.47 [1.51 – 3.46]	0.98	-1.51 [-4.41 – 1.35]	1.00	1.44 [-0.83 – 3.69]	1.01	-11208.62
	20000	Q	1.45 [1.43 – 1.48]	0.98	2.39 [1.41 – 3.35]	1.02	-1.08 [-3.95 – 1.78]	1.01	0.97 [-1.20 – 3.23]	1.00	-11202.56
PSB	3000	L	1.45 [1.43 – 1.48]	1.01	1.09 [0.35 – 1.79]	0.97	1.80 [0.63 – 3.06]	0.97			-11924.25
	3000	Q	1.45 [1.43 – 1.48]	0.97	1.19 [0.27 – 2.06]	0.99	1.17 [-1.57 – 4.13]	1.02	0.69 [-1.98 – 3.25]	1.03	-11885.62
	6400	L	1.45 [1.43 – 1.48]	0.99	1.61 [0.85 – 2.36]	0.98	0.83 [-0.28 – 1.97]	0.97			-11472.26
	1000	Q	1.45 [1.43 – 1.48]	0.99	1.48 [0.86 – 2.05]	0.96	3.30 [0.92 – 5.73]	0.99	-3.20 [-5.69 – -0.43]	0.98	-11456.50
	1000	L	1.45 [1.43 – 1.48]	0.96	1.76 [1.21 – 2.30]	0.95	0.88 [-0.29 – 2.14]	0.93			-11429.38
	564	Q	1.45 [1.43 – 1.48]	1.01	1.53 [1.02 – 2.06]	1.02	3.53 [1.36 – 5.67]	1.03	-3.81 [-6.17 – -1.21]	1.04	-11425.56
	6400	Q	1.45 [1.43 – 1.48]	0.97	1.94 [0.95 – 2.91]	1.02	-0.47 [-3.34 – 2.31]	1.00	1.13 [-1.14 – 3.49]	1.00	-11404.32

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	564	L	1.46 [1.43 – 1.48]	1.03	1.83 [1.30 – 2.34]	1.00	0.77 [-0.40 – 2.08]	1.00			-11400.41
	10000	L	1.45 [1.43 – 1.48]	1.00	2.18 [1.50 – 2.82]	1.03	-0.04 [-0.94 – 0.93]	1.03			-11240.45
	15000	L	1.45 [1.43 – 1.48]	1.00	2.11 [1.51 – 2.71]	0.98	0.07 [-0.80 – 0.94]	0.98			-11230.90
	20000	L	1.45 [1.43 – 1.48]	1.00	2.13 [1.54 – 2.75]	1.03	0.02 [-0.82 – 0.86]	1.03			-11219.68
	20000	Q	1.45 [1.43 – 1.48]	1.01	2.40 [1.45 – 3.34]	1.02	-0.99 [-3.82 – 1.82]	1.03	0.80 [-1.32 – 3.02]	1.03	-11210.91
	10000	Q	1.45 [1.43 – 1.48]	0.99	2.47 [1.50 – 3.45]	0.99	-1.11 [-4.03 – 1.66]	1.00	0.91 [-1.19 – 3.14]	1.02	-11192.84
	15000	Q	1.45 [1.43 – 1.48]	0.99	2.52 [1.61 – 3.43]	0.98	-1.47 [-4.29 – 1.27]	0.98	1.28 [-0.87 – 3.53]	0.97	-11178.52
SBHT	3000	L	1.46 [1.43 – 1.48]	1.01	-0.11 [-1.03 – 0.78]	0.99	3.57 [2.20 – 5.07]	1.00			-12567.86
	3000	Q	1.46 [1.43 – 1.48]	0.98	0.61 [-0.48 – 1.68]	0.99	0.62 [-2.48 – 3.75]	0.99	2.61 [0.15 – 5.21]	0.98	-12394.56
	6400	L	1.45 [1.43 – 1.48]	0.98	0.54 [-0.50 – 1.50]	1.02	2.27 [0.93 – 3.73]	1.03			-11980.42
	1000	Q	1.46 [1.43 – 1.48]	1.00	1.07 [0.39 – 1.73]	0.98	2.47 [0.08 – 4.93]	0.96	0.11 [-2.96 – 3.55]	0.98	-11838.25
	1000	L	1.46 [1.43 – 1.48]	1.02	1.13 [0.44 – 1.75]	0.99	2.39 [0.94 – 4.10]	0.99			-11814.54
	6400	Q	1.45 [1.43 – 1.48]	0.99	1.44 [0.22 – 2.53]	1.02	-0.98 [-3.91 – 2.11]	1.00	2.72 [0.42 – 4.90]	0.99	-11680.06
	564	Q	1.46 [1.43 – 1.48]	0.96	1.26 [0.68 – 1.79]	0.95	2.65 [0.43 – 4.97]	0.97	-0.79 [-3.95 – 2.68]	1.00	-11678.93
	564	L	1.46 [1.43 – 1.48]	1.01	1.30 [0.71 – 1.87]	0.98	2.17 [0.78 – 3.74]	0.99			-11673.67
	10000	L	1.45 [1.43 – 1.48]	0.99	1.61 [0.91 – 2.35]	1.01	0.72 [-0.26 – 1.69]	1.01			-11414.41
	15000	L	1.45 [1.43 – 1.48]	1.01	1.67 [1.02 – 2.31]	0.99	0.67 [-0.19 – 1.56]	0.99			-11368.97
	20000	L	1.45 [1.43 – 1.48]	1.02	1.73 [1.05 – 2.37]	1.01	0.62 [-0.27 – 1.54]	1.00			-11318.18
	10000	Q	1.45 [1.43 – 1.48]	1.03	2.34 [1.30 – 3.36]	1.01	-1.85 [-4.71 – 1.06]	1.00	2.03 [-0.15 – 4.14]	0.99	-11251.97
	20000	Q	1.45 [1.43 – 1.48]	1.01	2.31 [1.32 – 3.27]	0.99	-1.59 [-4.39 – 1.35]	0.98	1.77 [-0.46 – 3.94]	0.98	-11239.07
	15000	Q	1.45 [1.43 – 1.48]	1.01	2.48 [1.50 – 3.47]	0.99	-2.29 [-5.18 – 0.57]	1.00	2.37 [0.17 – 4.57]	1.00	-11224.63
B		L	1.45 [1.43 – 1.48]	0.97	1.99 [1.84 – 2.15]	0.99	2.26 [1.25 – 3.65]	1.05			-11244.24
		Q	1.45 [1.43 – 1.48]	1.02	1.99 [1.84 – 2.15]	1.00	1.70 [-0.53 – 4.06]	1.04	1.18 [-1.77 – 4.46]	1.06	-11204.94
N		L	1.45 [1.43 – 1.48]	1.02	1.88 [1.64 – 2.12]	1.03	1.00 [0.33 – 1.79]	1.02			-11450.70
		Q	1.45 [1.43 – 1.48]	1.00	1.94 [1.68 – 2.20]	1.02	-0.15 [-2.02 – 1.74]	1.01	1.62 [-0.74 – 4.05]	1.02	-11379.26
W		Q	1.45 [1.43 – 1.48]	1.01	1.99 [1.84 – 2.15]	1.00	1.35 [-1.15 – 3.93]	0.96	1.74 [-1.43 – 5.07]	1.00	-11274.51
		L	1.45 [1.43 – 1.48]	1.02	1.99 [1.84 – 2.15]	0.99	2.32 [1.28 – 3.89]	0.96			-11264.93
DRI	10000	L	1.45 [1.43 – 1.48]	0.98	1.14 [0.46 – 1.85]	0.96	1.38 [0.42 – 2.32]	0.97			-11416.54

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	1000	L	1.45 [1.43 – 1.48]	1.01	1.24 [0.46 – 2.00]	1.00	1.43 [0.26 – 2.65]	1.00			-11414.47
	3000	L	1.45 [1.43 – 1.48]	0.98	1.44 [0.64 – 2.21]	0.98	1.03 [-0.07 – 2.17]	0.97			-11394.49
	15000	L	1.45 [1.43 – 1.48]	1.00	1.00 [0.28 – 1.72]	1.01	1.57 [0.61 – 2.56]	1.01			-11386.57
	6400	L	1.45 [1.43 – 1.48]	0.95	1.30 [0.58 – 2.04]	0.97	1.17 [0.19 – 2.17]	0.97			-11385.09
	20000	L	1.45 [1.43 – 1.48]	1.00	0.91 [0.18 – 1.65]	0.98	1.67 [0.70 – 2.66]	0.98			-11346.82
	1000	Q	1.45 [1.43 – 1.48]	1.03	1.98 [1.00 – 2.95]	1.02	-1.65 [-4.58 – 1.28]	1.04	2.85 [0.38 – 5.41]	1.04	-11299.16
	10000	Q	1.45 [1.43 – 1.48]	1.02	2.30 [1.21 – 3.37]	0.99	-2.52 [-5.45 – 0.46]	1.00	2.99 [0.84 – 5.19]	1.01	-11274.45
	15000	Q	1.45 [1.43 – 1.48]	1.00	2.19 [1.06 – 3.23]	1.00	-2.32 [-5.07 – 0.73]	1.01	2.91 [0.70 – 4.94]	1.01	-11264.35
	6400	Q	1.45 [1.43 – 1.48]	0.99	2.36 [1.29 – 3.45]	1.02	-2.52 [-5.55 – 0.39]	1.03	2.97 [0.75 – 5.15]	1.03	-11242.83
	3000	Q	1.45 [1.43 – 1.48]	0.99	2.27 [1.23 – 3.31]	1.03	-2.11 [-5.07 – 0.91]	1.01	2.59 [0.26 – 4.98]	0.99	-11224.24
	20000	Q	1.45 [1.43 – 1.48]	1.02	2.01 [0.87 – 3.18]	0.98	-1.79 [-4.88 – 1.18]	0.99	2.55 [0.48 – 4.70]	1.00	-11208.79
GDD	15000	L	1.45 [1.43 – 1.48]	1.02	0.63 [-0.37 – 1.59]	0.97	2.57 [0.95 – 4.27]	0.98			-11511.39
	10000	L	1.45 [1.43 – 1.48]	1.01	0.93 [-0.20 – 2.00]	1.02	1.89 [0.25 – 3.65]	1.02			-11507.08
	20000	L	1.45 [1.43 – 1.48]	1.01	0.55 [-0.31 – 1.44]	1.00	3.09 [1.39 – 4.74]	1.00			-11458.18
	15000	Q	1.45 [1.43 – 1.48]	1.01	1.19 [0.06 – 2.27]	1.01	-0.06 [-3.01 – 3.04]	1.02	2.83 [0.12 – 5.48]	1.02	-11448.64
	10000	Q	1.45 [1.43 – 1.48]	0.98	1.46 [0.23 – 2.61]	0.99	-0.53 [-3.51 – 2.60]	0.99	2.41 [-0.10 – 4.95]	1.00	-11437.73
	6400	L	1.45 [1.43 – 1.48]	1.00	1.34 [0.09 – 2.44]	0.98	1.21 [-0.41 – 3.07]	0.99			-11407.01
	1000	Q	1.45 [1.43 – 1.48]	0.99	1.64 [0.22 – 2.99]	0.98	0.03 [-3.13 – 3.07]	1.02	1.22 [-1.65 – 4.08]	1.02	-11405.93
	6400	Q	1.45 [1.43 – 1.48]	1.02	1.60 [0.28 – 2.85]	1.00	-0.35 [-3.40 – 2.72]	1.00	1.69 [-0.88 – 4.26]	0.99	-11385.71
	1000	L	1.45 [1.43 – 1.48]	1.01	1.57 [0.19 – 2.88]	0.99	0.91 [-1.09 – 3.05]	0.99			-11364.07
	20000	Q	1.45 [1.43 – 1.48]	1.01	1.01 [0.01 – 1.98]	1.00	0.71 [-2.20 – 3.69]	1.03	2.76 [-0.05 – 5.68]	1.03	-11364.03
	3000	L	1.45 [1.43 – 1.48]	1.02	1.82 [0.47 – 3.09]	1.03	0.52 [-1.38 – 2.53]	1.04			-11329.31
	3000	Q	1.45 [1.43 – 1.48]	0.97	1.87 [0.53 – 3.19]	0.99	-0.07 [-2.92 – 2.89]	0.98	0.75 [-1.80 – 3.22]	1.00	-11273.65
MAR	3000	L	1.45 [1.43 – 1.48]	0.98	2.29 [2.04 – 2.54]	1.00	-1.83 [-4.48 – 0.82]	1.01			-11292.08
	3000	Q	1.45 [1.43 – 1.48]	1.00	2.29 [2.04 – 2.55]	0.99	-1.86 [-4.61 – 0.86]	0.98	0.46 [-3.58 – 4.41]	0.98	-11290.52
	1000	L	1.45 [1.43 – 1.48]	0.96	2.28 [2.03 – 2.54]	0.94	-1.74 [-4.47 – 1.05]	0.94			-11284.13
	6400	Q	1.45 [1.43 – 1.48]	1.01	2.33 [2.11 – 2.58]	0.98	-2.41 [-4.69 – -0.12]	0.96	0.82 [-3.17 – 4.67]	0.98	-11280.00
	6400	L	1.45 [1.43 – 1.48]	1.01	2.34 [2.10 – 2.58]	0.98	-2.30 [-4.52 – -0.04]	0.99			-11268.44

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	1000	Q	1.45 [1.43 – 1.48]	0.99	2.28 [2.03 – 2.55]	1.01	-1.74 [-4.55 – 1.08]	1.04	0.37 [-3.70 – 4.48]	0.98	-11260.54
	10000	L	1.45 [1.43 – 1.48]	1.01	2.38 [2.15 – 2.61]	0.98	-2.44 [-4.32 – -0.54]	0.99			-11255.13
	10000	Q	1.45 [1.43 – 1.48]	0.98	2.38 [2.15 – 2.61]	0.99	-2.49 [-4.35 – -0.54]	0.98	0.83 [-3.06 – 4.91]	1.00	-11252.41
	15000	L	1.45 [1.43 – 1.48]	1.01	2.42 [2.18 – 2.67]	1.02	-2.27 [-3.79 – -0.68]	1.00			-11247.02
	15000	Q	1.45 [1.43 – 1.48]	0.99	2.43 [2.19 – 2.68]	0.98	-2.76 [-4.65 – -0.87]	0.99	1.95 [-1.83 – 5.71]	1.02	-11241.90
	20000	Q	1.45 [1.43 – 1.48]	1.00	2.45 [2.20 – 2.72]	1.02	-2.62 [-4.43 – -0.77]	1.04	2.34 [-1.24 – 6.04]	1.05	-11178.64
	20000	L	1.45 [1.43 – 1.48]	1.02	2.43 [2.18 – 2.70]	0.96	-1.88 [-3.28 – -0.51]	0.99			-11167.81
MMT	15000	L	1.45 [1.43 – 1.48]	1.01	0.69 [-0.36 – 1.74]	1.02	2.10 [0.62 – 3.62]	1.02			-11507.11
	10000	L	1.45 [1.43 – 1.48]	0.99	0.90 [-0.32 – 2.07]	0.99	1.63 [0.13 – 3.23]	0.99			-11498.40
	6400	L	1.45 [1.43 – 1.48]	1.03	1.16 [-0.13 – 2.42]	0.98	1.31 [-0.31 – 2.94]	0.99			-11479.73
	6400	Q	1.45 [1.43 – 1.48]	0.99	1.64 [0.20 – 2.99]	1.14	-0.89 [-4.02 – 2.17]	1.16	2.05 [-0.21 – 4.28]	1.11	-11420.63
	10000	Q	1.45 [1.43 – 1.48]	1.00	1.58 [0.19 – 2.88]	0.96	-0.95 [-4.06 – 2.23]	0.97	2.14 [-0.14 – 4.53]	1.00	-11411.25
	15000	Q	1.45 [1.43 – 1.48]	1.01	1.38 [0.07 – 2.57]	0.99	-0.68 [-3.75 – 2.59]	1.00	2.51 [-0.01 – 4.97]	1.00	-11404.27
	20000	L	1.45 [1.43 – 1.48]	0.96	0.67 [-0.28 – 1.62]	0.97	2.41 [0.87 – 3.93]	0.97			-11401.25
	3000	Q	1.45 [1.43 – 1.48]	1.01	1.69 [0.20 – 3.10]	0.97	-0.29 [-3.37 – 2.81]	1.00	1.21 [-1.35 – 3.73]	1.00	-11378.80
	1000	Q	1.45 [1.43 – 1.48]	1.00	1.63 [0.02 – 3.13]	1.02	-0.14 [-3.32 – 3.02]	1.04	1.12 [-1.49 – 3.79]	1.00	-11378.15
	3000	L	1.45 [1.43 – 1.48]	0.98	1.52 [0.01 – 2.94]	0.98	0.82 [-1.01 – 2.80]	0.98			-11374.60
	1000	L	1.45 [1.43 – 1.48]	1.00	1.56 [0.01 – 3.02]	0.98	0.79 [-1.11 – 2.82]	0.98			-11367.21
	20000	Q	1.45 [1.43 – 1.48]	1.02	1.26 [0.16 – 2.36]	1.02	-0.15 [-3.19 – 2.92]	1.02	2.50 [-0.02 – 5.10]	1.02	-11366.10
BD	1000	L	1.45 [1.43 – 1.48]	0.99	1.40 [0.99 – 1.81]	1.01	4.09 [1.95 – 6.23]	1.02			-11235.94
	20000	L	1.45 [1.43 – 1.48]	1.02	1.65 [1.35 – 1.99]	0.99	3.25 [1.25 – 5.24]	0.99			-11228.66
	1000	Q	1.45 [1.43 – 1.48]	1.02	1.42 [1.01 – 1.83]	1.01	3.52 [1.16 – 5.94]	1.02	2.08 [-1.68 – 5.84]	0.99	-11223.46
	3000	L	1.45 [1.43 – 1.48]	0.98	1.38 [1.08 – 1.72]	1.00	2.77 [1.65 – 3.85]	1.00			-11221.49
	15000	Q	1.45 [1.43 – 1.48]	1.02	1.31 [0.93 – 1.72]	1.00	3.28 [1.15 – 5.35]	1.02	0.02 [-3.61 – 3.58]	1.03	-11212.48
	20000	Q	1.45 [1.43 – 1.48]	1.02	1.66 [1.34 – 2.00]	0.99	3.23 [1.02 – 5.49]	0.99	-0.04 [-3.89 – 3.83]	1.00	-11210.39
	15000	L	1.45 [1.43 – 1.48]	0.99	1.31 [0.96 – 1.70]	1.00	3.29 [1.86 – 4.66]	1.01			-11201.57
	3000	Q	1.45 [1.43 – 1.48]	1.01	1.45 [1.12 – 1.80]	0.99	1.98 [0.00 – 4.03]	1.03	1.50 [-1.75 – 4.85]	1.03	-11199.91
	10000	L	1.45 [1.43 – 1.48]	1.01	1.26 [0.94 – 1.58]	1.05	3.09 [2.04 – 4.18]	1.03			-11193.90

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	10000	Q	1.45 [1.43 – 1.48]	1.01	1.30 [0.97 – 1.67]	1.04	2.55 [0.54 – 4.61]	1.02	0.95 [-2.39 – 4.35]	0.99	-11177.32
	6400	L	1.45 [1.43 – 1.48]	1.01	1.52 [1.27 – 1.78]	0.99	2.56 [1.60 – 3.53]	1.00			-11147.70
	6400	Q	1.45 [1.43 – 1.48]	1.02	1.54 [1.28 – 1.82]	0.98	2.15 [0.31 – 3.78]	0.96	1.05 [-2.01 – 4.40]	0.99	-11128.36
BDR	1000	Q	1.45 [1.43 – 1.48]	1.00	2.49 [2.23 – 2.75]	0.99	-1.64 [-3.66 – 0.46]	1.02	-0.87 [-4.21 – 2.29]	1.04	-11435.40
	1000	L	1.45 [1.43 – 1.48]	0.99	2.52 [2.29 – 2.75]	1.01	-2.11 [-3.10 – -1.13]	0.99			-11418.83
	3000	Q	1.46 [1.43 – 1.48]	1.01	2.50 [2.22 – 2.81]	1.02	-1.03 [-3.05 – 0.95]	1.00	-1.39 [-4.37 – 1.67]	1.00	-11407.14
	3000	L	1.45 [1.43 – 1.48]	1.00	2.56 [2.31 – 2.83]	1.01	-1.83 [-2.73 – -0.94]	1.02			-11367.93
	20000	Q	1.46 [1.43 – 1.48]	0.98	2.25 [1.94 – 2.58]	0.98	-1.07 [-2.94 – 0.80]	0.97	1.81 [-0.77 – 4.28]	1.00	-11245.67
	6400	L	1.45 [1.43 – 1.48]	0.98	2.35 [2.09 – 2.62]	0.98	-0.81 [-1.69 – 0.08]	0.99			-11225.46
	15000	L	1.45 [1.43 – 1.48]	1.00	2.20 [1.95 – 2.47]	1.06	-0.16 [-0.99 – 0.64]	1.06			-11222.34
	20000	L	1.45 [1.43 – 1.48]	0.99	2.12 [1.87 – 2.40]	0.98	0.10 [-0.64 – 0.88]	0.97			-11222.07
	15000	Q	1.45 [1.43 – 1.48]	1.02	2.34 [2.01 – 2.69]	0.99	-1.38 [-3.49 – 0.64]	0.98	1.82 [-0.93 – 4.61]	0.97	-11221.08
	6400	Q	1.45 [1.43 – 1.48]	1.03	2.53 [2.24 – 2.83]	1.01	-3.10 [-5.09 – -1.07]	1.00	4.04 [0.83 – 7.26]	1.01	-11208.28
	10000	L	1.45 [1.43 – 1.48]	1.01	2.29 [2.03 – 2.57]	0.99	-0.49 [-1.25 – 0.31]	0.99			-11203.14
	10000	Q	1.45 [1.43 – 1.48]	0.99	2.60 [2.23 – 2.96]	0.97	-3.13 [-5.31 – -0.91]	0.98	3.83 [0.82 – 6.77]	0.98	-11192.60
GU	1000	Q	1.45 [1.43 – 1.48]	0.98	2.48 [1.83 – 3.15]	0.98	-0.28 [-2.87 – 2.30]	1.00	-2.20 [-5.45 – 1.34]	0.98	-11354.40
	3000	Q	1.45 [1.43 – 1.48]	0.98	2.43 [1.86 – 3.00]	1.02	-0.61 [-3.08 – 1.95]	1.03	-1.43 [-4.94 – 2.18]	0.97	-11312.59
	1000	L	1.45 [1.43 – 1.48]	0.99	2.60 [1.98 – 3.23]	1.02	-1.44 [-3.40 – 0.54]	1.01			-11269.13
	3000	L	1.45 [1.43 – 1.48]	0.98	2.45 [1.92 – 3.02]	0.96	-1.11 [-3.04 – 0.82]	0.95			-11259.52
	6400	L	1.45 [1.43 – 1.48]	1.01	2.01 [1.62 – 2.40]	0.98	0.79 [-1.13 – 2.72]	0.99			-11184.05
	6400	Q	1.45 [1.43 – 1.48]	1.01	2.04 [1.64 – 2.43]	0.97	0.34 [-1.91 – 2.63]	0.97	1.10 [-2.53 – 4.87]	0.98	-11174.72
	20000	L	1.45 [1.43 – 1.48]	1.01	1.96 [1.70 – 2.23]	1.03	1.36 [-0.24 – 3.01]	1.04			-11169.06
	20000	Q	1.45 [1.43 – 1.48]	0.97	1.98 [1.71 – 2.26]	0.96	1.02 [-1.03 – 2.94]	0.97	1.23 [-2.45 – 4.95]	0.97	-11148.29
	15000	L	1.45 [1.43 – 1.48]	0.99	1.89 [1.62 – 2.16]	1.02	1.88 [0.28 – 3.52]	1.00			-11130.30
	15000	Q	1.45 [1.43 – 1.48]	1.01	1.90 [1.63 – 2.17]	1.01	1.58 [-0.41 – 3.59]	1.00	1.20 [-2.58 – 4.89]	1.00	-11124.59
	10000	L	1.45 [1.43 – 1.48]	0.99	1.88 [1.61 – 2.16]	0.97	2.00 [0.23 – 3.90]	0.97			-11112.90
	10000	Q	1.45 [1.43 – 1.48]	1.02	1.90 [1.63 – 2.17]	1.02	1.61 [-0.41 – 3.64]	1.04	1.53 [-2.22 – 5.23]	1.02	-11077.69
GUR	3000	Q	1.45 [1.43 – 1.48]	1.00	2.57 [2.31 – 2.87]	0.97	-1.98 [-3.98 – -0.07]	0.98	-1.35 [-4.93 – 2.28]	0.97	-11465.67

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	1000	Q	1.45 [1.43 – 1.48]	0.99	2.65 [2.32 – 2.98]	1.03	-2.34 [-4.52 – -0.13]	1.05	-0.71 [-4.08 – 2.73]	1.04	-11461.27
	3000	L	1.45 [1.43 – 1.48]	1.00	2.61 [2.35 – 2.89]	0.99	-2.57 [-3.80 – -1.41]	1.00			-11437.66
	1000	L	1.45 [1.43 – 1.48]	1.00	2.67 [2.38 – 2.98]	1.04	-2.65 [-3.94 – -1.44]	1.03			-11424.21
	6400	L	1.45 [1.43 – 1.48]	1.00	2.36 [2.09 – 2.64]	1.00	-1.04 [-2.15 – 0.13]	1.01			-11270.12
	20000	Q	1.45 [1.43 – 1.48]	0.99	2.16 [1.85 – 2.48]	1.00	-0.88 [-2.85 – 1.02]	1.00	2.12 [-0.64 – 5.05]	0.99	-11213.93
	20000	L	1.45 [1.43 – 1.48]	0.99	2.04 [1.77 – 2.31]	0.96	0.42 [-0.38 – 1.25]	0.96			-11213.46
	15000	Q	1.45 [1.43 – 1.48]	1.04	2.21 [1.90 – 2.55]	0.99	-0.72 [-2.73 – 1.31]	1.01	1.35 [-1.68 – 4.39]	1.00	-11212.44
	10000	L	1.45 [1.43 – 1.48]	0.95	2.28 [2.00 – 2.57]	1.00	-0.49 [-1.40 – 0.48]	1.00			-11211.09
	6400	Q	1.45 [1.43 – 1.48]	1.03	2.44 [2.16 – 2.76]	1.02	-2.26 [-4.29 – -0.27]	1.01	2.78 [-0.81 – 6.33]	1.02	-11204.22
	15000	L	1.45 [1.43 – 1.48]	0.97	2.14 [1.88 – 2.42]	1.00	0.06 [-0.86 – 0.97]	1.00			-11197.01
	10000	Q	1.45 [1.43 – 1.48]	1.00	2.46 [2.13 – 2.82]	1.01	-2.22 [-4.39 – -0.08]	1.00	2.93 [-0.27 – 5.97]	0.98	-11192.88
S	1000	L	1.45 [1.43 – 1.48]	1.01	1.07 [0.50 – 1.66]	0.98	2.46 [1.17 – 3.76]	0.97			-11430.30
	3000	L	1.45 [1.43 – 1.48]	1.01	1.06 [0.53 – 1.61]	0.98	2.03 [1.04 – 3.04]	0.99			-11410.66
	1000	Q	1.45 [1.43 – 1.48]	1.01	1.24 [0.59 – 1.90]	0.96	1.32 [-1.23 – 3.86]	1.00	1.54 [-1.43 – 4.64]	1.02	-11405.10
	10000	L	1.45 [1.43 – 1.48]	1.02	1.22 [0.64 – 1.84]	1.00	1.44 [0.50 – 2.39]	1.00			-11384.64
	3000	Q	1.45 [1.43 – 1.48]	1.01	1.31 [0.58 – 2.02]	0.99	0.84 [-1.82 – 3.59]	1.00	1.25 [-1.40 – 3.86]	1.00	-11376.34
	6400	L	1.45 [1.43 – 1.48]	0.99	1.14 [0.60 – 1.69]	0.98	1.56 [0.74 – 2.41]	0.98			-11350.31
	6400	Q	1.45 [1.43 – 1.48]	0.98	1.92 [0.99 – 2.87]	1.02	-1.38 [-4.36 – 1.58]	1.02	2.46 [0.13 – 4.84]	1.01	-11292.10
	15000	L	1.45 [1.43 – 1.48]	1.01	1.70 [1.11 – 2.34]	0.97	0.71 [-0.27 – 1.65]	0.98			-11289.12
	10000	Q	1.45 [1.43 – 1.48]	0.98	1.93 [0.96 – 2.87]	1.02	-1.28 [-4.35 – 1.78]	1.02	2.40 [-0.14 – 4.93]	1.00	-11285.69
	15000	Q	1.45 [1.43 – 1.48]	1.00	2.01 [1.10 – 2.91]	1.00	-0.59 [-3.46 – 2.32]	1.02	1.21 [-1.28 – 3.72]	1.02	-11278.11
	20000	Q	1.45 [1.43 – 1.48]	0.97	2.03 [1.21 – 2.87]	1.01	-0.26 [-3.10 – 2.58]	0.99	0.84 [-1.92 – 3.52]	0.97	-11260.88
	20000	L	1.45 [1.43 – 1.48]	0.98	1.85 [1.27 – 2.47]	0.96	0.56 [-0.55 – 1.62]	0.96			-11242.75
CTI	20000	Q	1.45 [1.43 – 1.48]	0.99	2.20 [0.85 – 3.48]	0.99	0.65 [-2.50 – 3.70]	0.98	-0.83 [-3.14 – 1.58]	0.98	-11210.15
	3000	Q	1.45 [1.43 – 1.48]	0.99	2.93 [2.35 – 3.54]	1.04	-0.98 [-3.57 – 1.55]	1.04	-2.40 [-5.27 – 0.50]	1.03	-11199.44
	20000	L	1.45 [1.43 – 1.48]	1.04	2.40 [1.27 – 3.50]	1.04	-0.33 [-1.71 – 1.13]	1.04			-11179.09
	3000	L	1.45 [1.43 – 1.48]	1.01	3.24 [2.79 – 3.73]	1.00	-2.88 [-4.00 – -1.78]	1.00			-11087.75
	564	Q	1.45 [1.43 – 1.48]	0.96	2.79 [2.23 – 3.31]	1.04	-2.39 [-4.98 – 0.27]	1.02	-1.77 [-5.55 – 1.96]	0.98	-11079.34

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	1000	L	1.45 [1.43 – 1.48]	1.03	2.85 [2.35 – 3.34]	0.98	-3.00 [-4.91 – -0.99]	0.99			-11077.61
	1000	Q	1.45 [1.43 – 1.48]	0.99	2.80 [2.27 – 3.32]	1.02	-2.28 [-4.78 – 0.27]	1.01	-1.69 [-5.32 – 1.90]	1.00	-11068.83
	564	L	1.45 [1.43 – 1.48]	0.99	2.81 [2.29 – 3.35]	0.98	-3.01 [-5.34 – -0.70]	0.97			-11063.22
	6400	Q	1.45 [1.43 – 1.48]	0.99	2.99 [2.13 – 3.88]	1.03	0.02 [-2.74 – 2.66]	1.03	-1.90 [-4.00 – 0.29]	1.02	-11012.14
	15000	Q	1.45 [1.43 – 1.48]	0.97	2.71 [1.48 – 3.98]	1.00	1.20 [-1.85 – 4.26]	1.02	-2.27 [-4.54 – 0.03]	1.01	-10988.41
	15000	L	1.45 [1.43 – 1.48]	1.00	3.46 [2.45 – 4.49]	0.97	-1.60 [-2.86 – -0.39]	0.97			-10887.82
	6400	L	1.45 [1.43 – 1.48]	1.02	3.57 [3.01 – 4.15]	1.02	-2.26 [-3.10 – -1.41]	1.01			-10885.18
	10000	Q	1.45 [1.43 – 1.48]	0.99	3.20 [2.08 – 4.33]	0.97	0.29 [-2.71 – 3.28]	0.98	-2.13 [-4.31 – 0.06]	0.99	-10796.29
	10000	L	1.45 [1.43 – 1.48]	1.06	3.97 [3.16 – 4.82]	1.04	-2.45 [-3.51 – -1.40]	1.04			-10741.96
SL	20000	L	1.45 [1.43 – 1.48]	1.01	1.85 [1.53 – 2.18]	1.03	1.72 [-0.03 – 3.38]	1.05			-11178.55
	20000	Q	1.45 [1.43 – 1.48]	1.01	1.86 [1.52 – 2.20]	0.99	1.46 [-0.62 – 3.52]	1.00	0.92 [-2.92 – 4.54]	1.02	-11171.99
	15000	L	1.45 [1.43 – 1.48]	0.98	1.77 [1.51 – 2.05]	0.99	2.64 [1.00 – 4.36]	1.00			-11079.26
	15000	Q	1.45 [1.43 – 1.48]	1.01	1.78 [1.52 – 2.06]	1.00	2.29 [0.34 – 4.27]	1.01	1.30 [-2.49 – 5.23]	1.04	-11066.24
	564	L	1.45 [1.43 – 1.48]	0.99	1.70 [1.33 – 2.10]	0.99	2.70 [0.51 – 4.84]	0.97			-10985.78
	564	Q	1.45 [1.43 – 1.48]	1.02	1.72 [1.35 – 2.12]	1.01	2.31 [-0.09 – 4.75]	0.99	1.09 [-2.65 – 4.74]	1.00	-10963.78
	1000	L	1.45 [1.43 – 1.48]	0.99	1.59 [1.20 – 2.02]	0.97	3.16 [0.87 – 5.21]	0.98			-10956.52
	1000	Q	1.45 [1.43 – 1.48]	0.99	1.61 [1.22 – 2.03]	0.96	2.81 [0.39 – 5.23]	0.97	0.86 [-2.96 – 4.67]	0.99	-10952.96
	3000	L	1.45 [1.43 – 1.48]	0.97	0.91 [0.48 – 1.38]	0.97	4.78 [3.04 – 6.38]	0.97			-10941.40
	3000	Q	1.45 [1.43 – 1.48]	1.02	0.92 [0.45 – 1.40]	0.97	4.60 [2.25 – 6.97]	0.97	0.33 [-3.19 – 3.92]	1.00	-10910.22
	10000	Q	1.45 [1.43 – 1.48]	1.01	1.57 [1.32 – 1.84]	1.01	3.62 [1.72 – 5.57]	1.01	1.14 [-2.57 – 4.98]	1.03	-10857.07
	10000	L	1.45 [1.43 – 1.48]	0.99	1.56 [1.31 – 1.82]	1.01	4.05 [2.45 – 5.50]	1.00			-10852.83
	6400	L	1.45 [1.43 – 1.48]	0.96	1.19 [0.86 – 1.53]	0.96	4.80 [3.21 – 6.36]	0.96			-10843.64
	6400	Q	1.45 [1.43 – 1.48]	0.99	1.22 [0.86 – 1.58]	0.99	4.46 [2.26 – 6.63]	0.97	0.78 [-2.88 – 4.44]	0.97	-10809.50
TRI	6400	L	1.45 [1.43 – 1.48]	0.97	2.15 [2.01 – 2.30]	0.99	0.42 [-3.63 – 4.64]	1.01			-11272.28
	564	Q	1.45 [1.43 – 1.48]	1.00	2.15 [2.01 – 2.30]	0.98	0.29 [-3.69 – 4.40]	1.00	0.01 [-4.14 – 4.12]	1.01	-11267.66
	3000	Q	1.45 [1.43 – 1.48]	0.99	2.15 [2.01 – 2.30]	1.00	0.41 [-3.69 – 4.54]	0.97	0.02 [-4.03 – 4.18]	0.99	-11262.68
	15000	Q	1.45 [1.43 – 1.48]	0.99	2.15 [2.00 – 2.30]	1.01	0.27 [-3.83 – 4.32]	0.99	-0.01 [-4.11 – 4.01]	1.03	-11261.88
	15000	L	1.45 [1.43 – 1.48]	0.99	2.15 [2.01 – 2.30]	0.99	0.17 [-3.86 – 4.08]	0.99			-11261.60

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	10000	L	1.45 [1.43 – 1.48]	0.99	2.15 [2.00 – 2.30]	1.03	0.51 [-3.67 – 4.71]	1.00			-11260.44
	3000	L	1.45 [1.43 – 1.48]	0.98	2.15 [2.01 – 2.30]	1.01	0.36 [-3.70 – 4.34]	0.98			-11254.68
	20000	Q	1.45 [1.43 – 1.48]	0.97	2.15 [2.01 – 2.30]	0.97	0.00 [-4.07 – 4.10]	1.01	0.01 [-4.02 – 3.98]	1.01	-11252.41
	10000	Q	1.45 [1.43 – 1.48]	1.01	2.15 [2.00 – 2.30]	1.02	0.49 [-3.62 – 4.49]	1.00	-0.03 [-4.04 – 4.13]	1.02	-11250.98
	20000	L	1.45 [1.43 – 1.48]	0.97	2.15 [2.01 – 2.30]	1.03	-0.01 [-3.86 – 4.14]	1.02			-11248.33
	1000	Q	1.45 [1.43 – 1.48]	1.00	2.15 [2.01 – 2.30]	1.00	0.22 [-3.81 – 4.49]	0.98	-0.03 [-4.11 – 4.31]	1.01	-11238.49
	1000	L	1.45 [1.43 – 1.48]	0.98	2.15 [2.01 – 2.30]	0.97	0.24 [-3.87 – 4.43]	1.00			-11229.35
	564	L	1.45 [1.43 – 1.48]	1.03	2.16 [2.01 – 2.30]	0.98	0.25 [-3.75 – 4.18]	1.00			-11228.65
	6400	Q	1.45 [1.43 – 1.48]	1.01	2.15 [2.01 – 2.30]	1.02	0.62 [-3.54 – 4.64]	1.01	-0.01 [-4.08 – 4.10]	1.00	-11224.07

APPENDIX VIII

Table S8.1. Pearson correlation coefficient (*r*) of variables which were highly correlated in the Gunnison Basin (Extent = GB) and range-wide (Extent = RW). Multivariable genetic connectivity analyses for the Gunnison sage-grouse retained only the variable which had the lowest DIC (deviance information criterion).

Extent	Variable 1	Variable 2	*r*	DIC Var. 1	DIC Var. 2
GB	all sagebrush	big sagebrush	0.95	-11426.40	-11442.00
GB	all sagebrush	percent sagebrush	0.72	-11426.40	-11924.25
GB	all sagebrush	percent big sagebrush	0.70	-11426.40	-12222.98
GB	all sagebrush	shrub height	0.71	-11426.40	-12567.86
GB	big sagebrush	percent sagebrush	0.84	-11442.00	-11924.25
GB	big sagebrush	percent big sagebrush	0.80	-11442.00	-12222.98
GB	big sagebrush	shrub height	0.83	-11442.00	-12567.86
GB	green-up rate	brown-down rate	0.81	-11465.67	-11435.40
GB	brown-down	season length	0.73	-11235.94	-11430.30
GB	nest	brood	0.96	-11450.70	-11244.24
GB	nest	winter	0.70	-11450.70	-11274.51
GB	brood	winter	0.74	-11244.24	-11274.50
GB	slope	compound topographic index	-0.93	-11178.55	-11210.15
GB	distanct to roads class 4-7	distance to all roads	0.82	-11277.36	-11238.47
GB	distanct to roads class 4-7	distance to BLM roads	0.81	-11277.36	-11258.02
GB	distanct to all roads	distance to BLM roads	0.97	-11238.47	-11258.02
GB	density of development	population density	0.82	-11263.39	-11258.69
GB	density of roads 4-7	density of BLM roads	0.81	-11274.92	-11256.80
GB	dryness index	growing degree day	0.75	-11416.54	-11511.39
GB	dryness index	mean annual rainfall	-0.82	-11416.50	-11292.08
GB	dryness index	mean maximum temperature	0.80	-11416.50	-11507.11
GB	growing degree day	mean maximum temperature	0.96	-11511.39	-11507.10
GB	shrub height	mean annual rainfall	-0.70	-11292.08	-12567.86
RW	density of class 2 roads	density of class 1 & 2 roads	0.70	-46946.64	-47118.66
RW	distance to class 1,2 & 4 roads	distance to all roads	0.84	-46308.20	-46463.03
RW	distance to class 2 roads	distance to class 1 & 2 roads	0.91	-44565.59	-44889.42
RW	dryness index	growing degree dats	0.72	-47166.09	-44559.81
RW	mean annual rainfall	growing degree dats	-0.82	-48055.12	-44559.81
RW	mean maximum temperature	growing degree dats	0.98	-46224.93	-44559.81
RW	dryness index	mean maximum temperature	0.73	-47166.09	-46224.93
RW	mean annual rainfall	mean maximum	-0.81	-48055.12	-46224.93

Extent	Variable 1	Variable 2	*r*	DIC Var. 1	DIC Var. 2
		temperature			
RW	percentage big sagebrush cover	percentage sagebrush cover	0.87	-46157.70	46552.80
RW	percentage big sagebrush cover	shrub height	0.88	-46157.70	-47447.00
RW	percentage sagebrush cover	shrub height	0.91	-46552.80	-47447.00
RW	proportion big sagebrush cover	proportion of sagebrush cover	0.92	-47874.20	-48258.80
RW	green-up	brown-down	0.87	-45874.36	-45653.00
RW	green-up rate	brown-down rate	0.91	-48002.20	-48421.40
RW	season length	brown-down	0.82	-46379.80	-45653.00
RW	compoung topographic index	slope	-0.89	-47373.90	-47248.50
RW	brown-down rate	mean annual rainfall	0.70	-48421.40	-48055.12

APPENDIX IX

Table S9.1. Deviance information criterion (DIC) ranking, deviance (Dbar), and penalty for increased complexity (Dhat) for all multivariable genetic connectivity models for the Gunnison Basin extent of the Gunnison sage-grouse. See Table 3.1 in main text for the variable names corresponding to abbreviations.

Model	DIC	ΔDIC	Dbar	Dhat
Anthropogenic Change				
int + DAG + D14 + DAG	-11715.84	0.00	28976.48	40692.32
int + DAG + DAG	-11715.46	0.37	28977.25	40692.72
int + DAG + DIB + DAG	-11706.46	9.37	28977.18	40683.64
int + D47 + D14 + DAG	-11693.45	22.39	28976.39	40669.83
int + D14 + DAG	-11679.56	36.28	28976.59	40656.15
int + DAG + D14 + DAG + DIB	-11673.70	42.13	28976.71	40650.42
int + DIB + D14 + DAG	-11671.89	43.94	28976.74	40648.63
int + DAG + D47 + D14 + DAG	-11667.73	48.11	28976.51	40644.24
int + DAG + DIB	-11666.98	48.86	28977.31	40644.29
int + D47 + DAG + DA	-11664.74	51.10	28977.56	40642.29
int + D47 + DAG	-11664.63	51.20	28977.02	40641.65
int + D47 + D14 + DAG + DA	-11663.63	52.21	28976.94	40640.56
int + DAG + D47 + DAG	-11663.04	52.80	28976.85	40639.89
int + DAG + D12 + D14 + DAG	-11659.38	56.45	28974.49	40633.87
int + D47 + D12 + D14 + DAG	-11652.48	63.36	28974.26	40626.74
int + DAG + D12 + DAG	-11650.62	65.22	28973.80	40624.42
int + DAG + DA	-11647.80	68.04	28977.78	40625.57
int + D14 + DAG + DA	-11633.71	82.12	28976.63	40610.34
int + DAG + D47 + D12 + D14 + DAG	-11630.72	85.11	28974.16	40604.88
int + D12 + DAG	-11629.09	86.75	28974.04	40603.13
int + D12 + D14 + DAG	-11628.65	87.19	28974.48	40603.13
int + DAG + D47 + D14 + DAG + DA	-11627.04	88.79	28976.58	40603.62

Model	DIC	ΔDIC	Dbar	Dhat
int + DAG + DAG + DA	-11621.04	94.79	28977.83	40598.87
int + DAG + D47 + DAG + DA	-11608.39	107.45	28977.69	40586.08
int + DAG + D14 + DAG + DA	-11604.67	111.17	28976.42	40581.08
int + DAG + D47 + D12 + DAG	-11599.94	115.90	28973.44	40573.38
int + D47 + D12 + DAG	-11599.79	116.05	28973.58	40573.36
int + D47 + D12 + DAG + DA	-11595.83	120.01	28974.28	40570.11
int + D12 + DAG + DA	-11594.34	121.50	28974.40	40568.73
int + DAG + D12 + DAG + DA	-11588.69	127.14	28974.44	40563.13
int + DAG + D47 + D12 + DAG + DA	-11587.82	128.02	28974.32	40562.14
int + DAG + D47 + D12	-11357.48	358.36	28978.87	40336.35
int + DAG + D12	-11354.67	361.17	28978.48	40333.15
int + D47 + D12	-11340.76	375.08	28978.95	40319.71
int + DAG + D12 + DA	-11313.85	401.98	28979.21	40293.06
int + DAG + D47 + D12 + DA	-11307.85	407.99	28979.39	40287.25
int + D47 + D12 + DA	-11305.73	410.11	28979.37	40285.10
int + D12 + DA	-11294.79	421.05	28979.29	40274.08
int + D12 + D14	-11261.55	454.29	28978.60	40240.15
int + D47 + D12 + D14	-11258.34	457.50	28978.73	40237.07
int + DAG + D47 + D12 + D14	-11256.90	458.94	28978.55	40235.44
int + DAG + D47	-11256.56	459.28	28992.43	40248.99
int + DAG + D12 + D14 + DA	-11254.77	461.06	28979.09	40233.86
int + DAG + DIB	-11248.83	467.01	28992.48	40241.31
int + DAG + D12 + D14	-11245.53	470.31	28978.41	40223.94
int + D47 + D12 + D14 + DA	-11243.64	472.20	28979.50	40223.14
int + D12 + D14 + DA	-11236.58	479.25	28979.45	40216.04
int + DAG + DA	-11229.28	486.56	28993.28	40222.56
int + DAG + D47 + DA	-11224.74	491.10	28993.34	40218.08
int + DI47 + DIP	-11223.37	492.47	28993.41	40216.78

Model	DIC	ΔDIC	Dbar	Dhat
int + DI47 + DID + DIP	-11220.41	495.43	28993.70	40214.11
int + DAG + D47 + D12 + D14 + DA	-11214.81	501.03	28979.50	40194.31
int + D47 + DA	-11208.92	506.92	28993.39	40202.31
int + DID + DIP	-11197.58	518.26	28993.76	40191.34
int + DI47 + DID	-11191.97	523.87	28993.50	40185.47
int + DI47 + DI14 + DIP	-11171.05	544.78	28992.60	40163.65
int + DI47 + DI14	-11169.70	546.14	28991.67	40161.37
int + DI47 + DI14 + DID	-11165.96	549.88	28992.54	40158.49
int + DI14 + DIP	-11164.02	551.82	28992.62	40156.64
int + DAG + D14	-11155.21	560.63	28991.67	40146.88
int + DI14 + DID	-11152.29	563.55	28992.44	40144.73
int + DI12 + DID + DIP	-11148.55	567.29	28975.86	40124.41
int + DI14 + DID + DIP	-11142.85	572.99	28993.20	40136.04
int + DI47 + DI14 + DID + DIP	-11137.65	578.19	28993.09	40130.74
int + D14 + DIB	-11135.97	579.87	28991.92	40127.89
int + DAG + D14 + DIB	-11135.59	580.24	28991.74	40127.33
int + DAG + D14 + DA	-11135.03	580.80	28992.59	40127.62
int + D14 + DA	-11134.28	581.56	28992.72	40127.00
int + DI47 + DI12 + DIP	-11134.25	581.58	28975.72	40109.97
int + D47 + D14 + DA	-11133.99	581.84	28992.70	40126.69
int + DI12 + DI14 + DID + DIP	-11125.50	590.33	28975.13	40100.64
int + DI47 + DI12	-11122.92	592.92	28974.82	40097.74
int + D47 + D14	-11115.48	600.36	28991.99	40107.47
int + DI12 + DID	-11114.12	601.72	28975.89	40090.01
int + DAG + D47 + D14	-11113.26	602.58	28991.84	40105.09
int + DI47 + DI12 + DID + DIP	-11111.90	603.93	28976.24	40088.14
int + DI47 + DI12 + DI14 + DIP	-11108.48	607.36	28975.21	40083.69
int + DI47 + DI12 + DI14 + DID + DIOG	-11026.00	689.84	28976.15	40002.16

Model	DIC	ΔDIC	Dbar	Dhat
int + DI47 + DI12 + DI14 + DID + DIP	-11106.62	609.22	28975.40	40082.01
int + DI12 + DI14	-11103.72	612.11	28974.20	40077.92
int + DAG + D47 + D14 + DA	-11103.55	612.29	28992.89	40096.44
int + DI47 + DI12 + DID + DIP + DIOG	-11102.81	613.03	28976.91	40079.71
int + DI47 + DI12 + DID	-11101.31	614.52	28975.69	40077.00
int + DI12 + DI14 + DIP	-11098.96	616.88	28975.05	40074.01
int + DI47 + DI12 + DI14 + DID	-11094.23	621.60	28975.19	40069.43
int + DI47 + DI12 + DI14	-11091.38	624.46	28974.21	40065.59
int + DI12 + DIOG	-11085.08	630.76	28975.83	40060.91
int + DI12 + DI14 + DID	-11084.09	631.74	28974.84	40058.93
int + DI12 + DIP	-11082.12	633.72	28975.67	40057.79
int + DI47 + DIOG	-11076.84	639.00	28986.86	40063.70
int + DI47 + DI12 + DIOG	-11075.42	640.42	28975.88	40051.30
int + DI47 + DI12 + DIOG + DIP	-11073.89	641.94	28976.59	40050.48
int + DI12 + DIOG + DIP	-11061.92	653.91	28976.50	40038.43
int + DI12 + DID + DIP + DIOG	-11056.81	659.02	28977.15	40033.96
int + DI47 + DIOG + DIP	-11044.69	671.14	28986.59	40031.28
int + DI12 + DI14 + DIP + DIOG	-11036.27	679.56	28975.97	40012.25
int + DI47 + DI12 + DI14 + DIOG	-11034.73	681.10	28975.25	40009.99
int + DID + DIOG	-11034.54	681.30	28986.04	40020.58
int + DIOG + DIP	-11032.09	683.74	28986.78	40018.87
int + DI12 + DID + DIOG	-11031.55	684.29	28976.67	40008.22
int + DI12 + DI14 + DIOG	-11026.77	689.06	28975.18	40001.96
int + DI47 + DI12 + DID + DIOG	-11025.86	689.98	28976.22	40002.08
int + DI47 + DID + DIOG + DIP	-11020.76	695.08	28986.59	40007.35
int + DI47 + DI12 + DI14 + DIP + DIOG	-11015.66	700.17	28976.51	39992.17
int + DI47 + DI14 + DIOG	-11014.96	700.88	28986.00	40000.96
int + DI14 + DIOG	-11012.87	702.97	28986.25	39999.12

Model	DIC	ΔDIC	Dbar	Dhat
int + DI47 + DID + DIOG	-11004.75	711.09	28986.09	39990.84
int + DID + DIOG + DIP	-11001.41	714.42	28986.74	39988.15
int + DI12 + DI14 + DID + DIOG	-10998.82	717.02	28975.94	39974.76
int + DI47 + DI14 + DIOG + DIP	-10996.77	719.07	28986.39	39983.16
int + DI14 + DIOG + DIP	-10992.94	722.90	28986.05	39978.99
int + DI14 + DID + DIOG	-10978.02	737.82	28985.72	39963.73
int + DI47 + DI14 + DID + DIP + DIOG	-10967.84	748.00	28986.34	39954.18
int + DI47 + DI14 + DID + DIOG	-10964.55	751.29	28985.57	39950.12
int + DI14 + DID + DIP + DIOG	-10943.74	772.10	28986.41	39930.15
Temperature-moisture Regime				
int + GDD + MAR	-11539.43	0.00	28988.62	40528.05
int + MAR + MMT	-11509.81	29.61	28990.01	40499.82
Habitat Composition and Configuration				
int + SBHT + LS	-12604.15	0.00	28979.76	41583.92
int + SBHT + LS + CC	-12588.72	15.43	28980.30	41569.02
int + SBHT + LS + CON	-12576.29	27.86	28980.65	41556.94
int + SBHT + LS + CON + CC	-12554.81	49.35	28981.24	41536.05
int + SBHT + CC	-12545.70	58.45	28980.33	41526.03
int + SBHT + CON	-12527.20	76.96	28980.64	41507.84
int + SBHT + CON + CC	-12526.80	77.35	28981.15	41507.95
int + LS + CON	-11280.02	1324.13	28992.31	40272.33
int + LS + CON + CC	-11258.90	1345.25	28993.29	40252.20
int + CON + CC	-11255.24	1348.92	28993.44	40248.68
int + LS + CC	-11244.20	1359.96	28993.23	40237.42
Phenology				
int + GUR + SL	-11455.68	0.00	28985.72	40441.41
int + GUR + GU + SL	-11420.62	35.06	28985.11	40405.73
int + GUR + GU	-11387.54	68.14	28984.82	40372.37

Model	DIC	ΔDIC	Dbar	Dhat
int + GUR + BD	-11356.17	99.51	28984.15	40340.32
int + BDR + BD	-11345.98	109.70	28984.67	40330.65
int + BDR + GU	-11327.59	128.09	28985.35	40312.94
int + GUR + BD + GU	-11308.58	147.10	28984.08	40292.66
int + BDR + BD + GU	-11287.43	168.25	28984.28	40271.71
int + TRI + SLOPE	-11010.29	445.39	28980.08	39990.37
int + CTI + TRI	-10992.18	463.50	28980.98	39973.17
int + CTI + TRI + SLOPE	-10978.58	477.11	28991.00	39969.57
Terrain Morphology				
int + CTI	-11210.15	0.00	28992.97	40203.12
int + CTI + SLOPE	-10972.43	237.72	28990.83	39963.26
Presence-Absence				
int + PAS	-11150.28		28993.43	40143.71
Resource Selection				
int + N	-11450.70		28989.98	40440.68

APPENDIX X

Table S10.1. Deviance information criterion (DIC) ranking, deviance (Dbar), and penalty for increased complexity (Dhat) for all multiple hypothesis genetic connectivity models for the Gunnison Basin extent for the Gunnison sage-grouse. See Table 3.1 in main text for the variable names corresponding to abbreviations.

Model	DIC	ΔDIC	Dbar	Dhat
int + SBHT + LS + N	-12642.39	0.00	28980.64	41623.02
int + SBHT + LS + GDD + MAR	-12627.86	14.53	28979.46	41607.32
int + SBHT + LS + GUR + GDD + MAR	-12583.42	58.97	28979.51	41562.93
int + SBHT + LS + N + GDD + MAR	-12576.49	65.90	28980.51	41557.00
int + SBHT + LS + GUR	-12512.66	129.72	28979.11	41491.77
int + SBHT + LS + N + GUR	-12510.58	131.80	28979.87	41490.45
int + SBHT + LS + N + GUR + GDD + MAR	-12484.99	157.40	28980.02	41465.01
int + DD + D14 + DAG + SBHT + LS + GDD + MAR	-12350.39	292.00	28975.65	41326.04
int + DD + D14 + DAG + SBHT + LS + GUR	-12278.29	364.09	28974.25	41252.54
int + DD + D14 + DAG + SBHT + LS	-12273.12	369.26	28975.17	41248.29
int + DD + D14 + DAG + SBHT + LS + N	-12240.67	401.71	28975.68	41216.35
int + DD + D14 + DAG + SBHT + LS + GUR + GDD + MAR	-12226.41	415.97	28973.52	41199.93
int + DD + D14 + DAG + SBHT + LS + N + GUR + GDD + MAR	-12194.96	447.42	28975.05	41170.01
int + DD + D14 + DAG + SBHT + LS + N + GUR	-12191.22	451.17	28975.69	41166.91
int + DD + D14 + DAG + SBHT + LS + N + GDD + MAR	-12170.48	471.91	28976.11	41146.59
int + DD + D14 + DAG + SBHT + LS + TRI + GDD + MAR	-12142.41	499.98	28974.14	41116.54
int + SBHT + LS + TRI + GUR	-12052.56	589.83	28974.72	41027.28
int + SBHT + LS + TRI + GDD + MAR	-12034.87	607.52	28974.32	41009.18
int + SBHT + LS + TRI + GUR + GDD + MAR	-12022.66	619.73	28974.69	40997.35
int + DD + D14 + DAG + SBHT + LS + TRI	-12012.88	629.50	28973.00	40985.88
int + SBHT + LS + TRI	-12003.88	638.50	28973.97	40977.85
int + DD + D14 + DAG + SBHT + LS + TRI + GUR	-11949.90	692.48	28971.43	40921.34
int + SBHT + LS + N + TRI + GDD + MAR	-11922.00	720.39	28974.84	40896.84

Model	DIC	ΔDIC	Dbar	Dhat
int + SBHT + LS + N + TRI + GUR + GDD + MAR	-11886.42	755.96	28975.07	40861.49
int + SBHT + LS + N + TRI + GUR	-11883.54	758.85	28974.61	40858.15
int + DD + D14 + DAG + SBHT + LS + N + TRI + GDD + MAR	-11878.42	763.97	28973.13	40851.55
int + SBHT + LS + N + TRI	-11841.11	801.28	28974.42	40815.53
int + DD + D14 + DAG + SBHT + LS + N + TRI + GUR	-11822.15	820.23	28971.63	40793.78
int + DD + D14 + DAG + GDD + MAR	-11811.29	831.10	28976.05	40787.34
int + DD + D14 + DAG + N + GDD + MAR	-11806.76	835.63	28976.65	40783.41
int + DD + D14 + DAG + SBHT + LS + N + TRI	-11803.20	839.19	28972.45	40775.65
int + DD + D14 + DAG + GUR + GDD + MAR	-11785.44	856.95	28973.74	40759.17
int + DD + D14 + DAG + N + GUR + GDD + MAR	-11744.83	897.56	28975.20	40720.02
int + DD + D14 + DAG + N + GUR	-11717.94	924.44	28977.19	40695.13
int + DD + D14 + DAG + N	-11712.67	929.72	28977.52	40690.19
int + DD + D14 + DAG + GUR	-11676.26	966.13	28976.57	40652.83
int + DD + D14 + DAG + TRI + GUR + GDD + MAR	-11649.19	993.20	28973.17	40622.36
int + DD + D14 + DAG + TRI + GDD + MAR	-11602.41	1039.98	28974.85	40577.26
int + N + GDD + MAR	-11594.63	1047.76	28989.32	40583.95
int + GUR + GDD + MAR	-11570.54	1071.84	28985.19	40555.74
int + N + GUR + GDD + MAR	-11554.84	1087.54	28986.14	40540.98
int + N + GUR	-11484.02	1158.37	28986.15	40470.17
int + DD + D14 + DAG + N + TRI + GUR + GDD + MAR	-11480.71	1161.67	28973.75	40454.46
int + DD + D14 + DAG + N + TRI + GDD + MAR	-11471.44	1170.94	28975.19	40446.63
int + DD + D14 + DAG + TRI + GUR	-11468.23	1174.16	28973.83	40442.05
int + DD + D14 + DAG + N + TRI + GUR	-11414.48	1227.90	28974.57	40389.06
int + DD + D14 + DAG + N + TRI	-11389.43	1252.96	28975.06	40364.49
int + TRI + GUR + GDD + MAR	-11195.92	1446.46	28980.35	40176.27
int + N + TRI + GUR + GDD + MAR	-11141.82	1500.57	28980.62	40122.44
int + TRI + GUR	-11138.94	1503.45	28979.20	40118.13
int + TRI + GDD + MAR	-11093.14	1549.25	28981.32	40074.46

Model	DIC	ΔDIC	Dbar	Dhat
int + N + TRI + GDD + MAR	-11075.47	1566.92	28982.40	40057.87
int + N + TRI + GUR	-11055.97	1586.42	28979.65	40035.62
int + N + TRI	-11008.45	1633.93	28981.33	39989.79
int + DD + D14 + DAG + TRI	-10897.10	1745.32	29604.15	40501.22

APPENDIX XI

Table S11.1. All covariate estimates, 80% credible intervals ([80% CI]), and DIC (deviance information criterion) comparison for univariable genetic connectivity models for the range-wide extent of Gunnison sage-grouse. See Table 3.1 in main text for the variable names corresponding to abbreviations (Cov.). MW=moving window radius, Form=quadratic (Q), or linear (L), GR=Gelman-Rubin diagnostic. Models are ranked by DIC within each covariate.

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
D2	1000	L	1.29 [1.25 – 1.32]	1.03	0.84 [0.63 – 1.04]	1.01	0.43 [-3.56 – 4.51]	1.00			-46946.65
	1000	Q	1.29 [1.25 – 1.32]	1.01	0.83 [0.63 – 1.04]	1.00	0.50 [-3.50 – 4.44]	1.03	0.06 [-4.03 – 4.08]	0.99	-46913.13
	20000	L	1.29 [1.25 – 1.32]	1.01	-0.11 [-0.86 – 0.62]	1.00	3.70 [0.95 – 6.62]	1.01			-45933.41
	20000	Q	1.29 [1.25 – 1.32]	1.03	-0.15 [-0.89 – 0.59]	1.00	3.54 [0.63 – 6.53]	0.99	0.96 [-2.94 – 4.94]	1.02	-45719.39
	3000	Q	1.28 [1.25 – 1.32]	1.01	0.79 [0.57 – 1.01]	1.02	1.92 [-1.62 – 5.55]	0.99	0.44 [-3.60 – 4.46]	1.01	-45287.24
	3000	L	1.29 [1.25 – 1.32]	1.01	0.79 [0.56 – 1.00]	1.00	2.07 [-1.36 – 5.63]	0.99			-45140.70
	15000	L	1.29 [1.26 – 1.32]	1.00	0.22 [-0.32 – 0.76]	0.98	3.63 [0.70 – 6.74]	0.99			-44755.62
	15000	Q	1.29 [1.25 – 1.32]	1.01	0.19 [-0.36 – 0.74]	1.03	3.55 [0.50 – 6.76]	1.01	0.93 [-3.08 – 4.92]	1.01	-44704.39
	6400	L	1.28 [1.25 – 1.32]	0.98	0.70 [0.44 – 0.96]	1.01	2.55 [-0.60 – 5.85]	1.00			-44241.30
	10000	Q	1.29 [1.25 – 1.32]	1.01	0.60 [0.29 – 0.92]	1.03	2.77 [-0.29 – 5.82]	1.03	0.42 [-3.60 – 4.49]	1.03	-44182.11
	10000	L	1.29 [1.26 – 1.32]	1.02	0.61 [0.29 – 0.93]	1.05	2.78 [-0.29 – 5.87]	1.03			-44142.68
	6400	Q	1.29 [1.25 – 1.32]	0.96	0.70 [0.43 – 0.96]	1.00	2.51 [-0.70 – 5.85]	0.99	0.35 [-3.79 – 4.39]	0.98	-43973.05
DI2		L	1.29 [1.25 – 1.32]	0.98	1.28 [0.74 – 1.81]	1.00	-2.57 [-5.41 – 0.29]	0.99			-44565.59
		Q	1.28 [1.25 – 1.32]	1.00	1.30 [0.77 – 1.84]	0.99	-2.47 [-5.46 – 0.53]	0.98	-1.01 [-4.98 – 2.90]	1.03	-44516.38
D4	20000	L	1.29 [1.25 – 1.32]	1.00	0.64 [0.28 – 0.99]	0.97	0.72 [-0.34 – 1.80]	0.99			-46851.54
	20000	Q	1.28 [1.25 – 1.32]	0.99	0.58 [0.18 – 0.98]	1.02	1.34 [-1.13 – 3.79]	1.02	-0.81 [-3.99 – 2.37]	1.00	-46762.17
	1000	Q	1.28 [1.25 – 1.32]	0.99	0.75 [0.49 – 1.00]	1.01	2.12 [-1.69 – 5.83]	1.02	0.41 [-3.56 – 4.42]	0.98	-45662.41
	1000	L	1.28 [1.25 – 1.32]	0.99	0.75 [0.49 – 1.00]	0.98	2.09 [-1.68 – 5.87]	0.97			-45543.37
	15000	L	1.29 [1.25 – 1.32]	1.01	-0.04 [-0.73 – 0.64]	1.00	2.78 [0.73 – 4.89]	1.00			-43471.90
	15000	Q	1.29 [1.25 – 1.32]	1.02	0.00 [-0.71 – 0.65]	0.99	2.33 [-0.27 – 4.99]	0.99	1.00 [-2.60 – 4.44]	0.99	-43136.27
	3000	L	1.28 [1.25 – 1.32]	0.99	0.57 [0.23 – 0.90]	1.00	3.05 [0.08 – 6.26]	1.00			-42957.05
	6400	L	1.29 [1.25 – 1.32]	1.02	0.38 [-0.06 – 0.81]	1.02	3.47 [0.58 – 6.55]	1.02			-42808.24

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	3000	Q	1.28 [1.25 – 1.32]	1.01	0.56 [0.22 – 0.89]	0.98	3.04 [-0.09 – 6.34]	1.00	0.89 [-3.02 – 4.91]	1.01	-42709.97
	10000	L	1.28 [1.25 – 1.32]	1.01	0.11 [-0.45 – 0.69]	1.01	3.41 [0.88 – 5.98]	1.00			-42643.94
	10000	Q	1.29 [1.25 – 1.32]	1.00	0.12 [-0.46 – 0.69]	1.00	3.08 [0.25 – 5.90]	1.01	1.25 [-2.50 – 5.15]	1.04	-42364.71
	6400	Q	1.28 [1.25 – 1.32]	0.99	0.38 [-0.06 – 0.81]	0.99	3.34 [0.35 – 6.45]	0.98	1.10 [-2.81 – 5.00]	1.01	-42305.30
DI4		Q	1.29 [1.25 – 1.32]	0.99	1.00 [0.65 – 1.34]	0.99	-2.11 [-6.00 – 1.63]	0.99	-0.39 [-4.50 – 3.63]	0.99	-46369.30
		L	1.28 [1.25 – 1.32]	0.99	1.00 [0.65 – 1.33]	0.99	-2.14 [-5.96 – 1.64]	1.00			-46264.86
D5	3000	Q	1.29 [1.25 – 1.32]	1.01	0.85 [0.61 – 1.08]	0.98	-0.23 [-3.61 – 3.18]	0.97	0.12 [-3.89 – 4.15]	0.99	-47083.29
	1000	L	1.29 [1.25 – 1.32]	0.97	0.84 [0.63 – 1.04]	0.99	0.10 [-3.80 – 4.05]	0.99			-47012.67
	3000	L	1.29 [1.25 – 1.32]	0.99	0.84 [0.61 – 1.07]	0.99	-0.23 [-3.49 – 3.24]	0.99			-47037.06
	6400	Q	1.29 [1.25 – 1.32]	0.98	0.93 [0.62 – 1.24]	0.97	-1.28 [-4.47 – 1.93]	0.99	-0.12 [-4.15 – 3.91]	1.00	-47383.67
	10000	L	1.29 [1.25 – 1.32]	0.98	1.09 [0.72 – 1.45]	1.00	-2.58 [-5.51 – 0.49]	1.00			-47562.26
	6400	L	1.28 [1.25 – 1.32]	1.01	0.93 [0.63 – 1.23]	1.02	-1.28 [-4.36 – 1.91]	1.00			-47413.85
	20000	L	1.29 [1.25 – 1.32]	1.02	1.38 [0.87 – 1.89]	1.01	-3.49 [-6.52 – -0.47]	1.00			-46034.95
	20000	Q	1.29 [1.26 – 1.32]	0.97	1.40 [0.90 – 1.90]	1.01	-3.31 [-6.32 – -0.26]	1.00	-1.57 [-5.42 – 2.42]	1.03	-45988.02
	1000	Q	1.29 [1.25 – 1.32]	1.00	0.84 [0.63 – 1.04]	0.98	0.00 [-4.02 – 4.04]	1.01	0.06 [-4.02 – 4.11]	1.01	-47267.44
	15000	Q	1.29 [1.25 – 1.32]	1.01	1.15 [0.71 – 1.59]	1.00	-2.24 [-5.25 – 0.87]	1.01	-0.94 [-4.94 – 2.97]	1.01	-47805.18
	10000	Q	1.29 [1.25 – 1.32]	0.98	1.09 [0.73 – 1.45]	1.00	-2.45 [-5.35 – 0.66]	1.01	-0.86 [-4.80 – 3.20]	1.00	-47539.17
	15000	L	1.28 [1.25 – 1.32]	0.99	1.14 [0.70 – 1.56]	1.01	-2.35 [-5.25 – 0.70]	1.02			-47579.10
DI5		L	1.28 [1.25 – 1.32]	0.99	0.47 [-0.07 – 1.05]	1.01	2.04 [-0.92 – 4.85]	1.00			-47012.82
		Q	1.29 [1.25 – 1.32]	1.01	0.47 [-0.06 – 1.02]	0.99	1.83 [-1.14 – 4.73]	0.99	0.79 [-3.11 – 4.52]	0.98	-46881.87
D12	1000	L	1.29 [1.25 – 1.32]	1.01	0.84 [0.63 – 1.04]	1.00	0.26 [-3.81 – 4.32]	1.01			-47118.66
	1000	Q	1.29 [1.25 – 1.32]	1.02	0.84 [0.63 – 1.04]	1.02	0.30 [-3.73 – 4.28]	0.99	-0.07 [-4.16 – 4.01]	1.02	-46996.01
	3000	Q	1.29 [1.25 – 1.32]	0.98	0.81 [0.58 – 1.03]	1.02	1.17 [-2.85 – 5.12]	1.04	-0.18 [-4.13 – 3.88]	1.01	-46520.31
	20000	L	1.28 [1.25 – 1.32]	0.99	0.20 [-0.46 – 0.89]	0.98	3.31 [-0.10 – 6.74]	0.99			-46271.97
	3000	L	1.28 [1.25 – 1.32]	1.01	0.81 [0.59 – 1.03]	1.01	1.24 [-2.81 – 5.08]	0.98			-46203.36
	20000	Q	1.29 [1.25 – 1.32]	0.99	0.18 [-0.50 – 0.89]	0.99	3.40 [-0.04 – 6.82]	0.99	0.30 [-3.83 – 4.49]	1.01	-45711.76
	6400	L	1.29 [1.25 – 1.32]	1.00	0.74 [0.48 – 1.00]	1.02	2.10 [-1.43 – 5.62]	1.01			-45291.37
	15000	L	1.29 [1.25 – 1.32]	1.01	0.42 [-0.08 – 0.92]	1.01	3.18 [-0.28 – 6.67]	1.01			-45234.98

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	6400	Q	1.29 [1.25 – 1.32]	0.99	0.73 [0.47 – 1.00]	1.00	2.21 [-1.31 – 5.8]	1.00	0.05 [-4.10 – 4.16]	0.99	-45199.37
	15000	Q	1.29 [1.25 – 1.32]	1.01	0.41 [-0.09 – 0.93]	1.02	3.13 [-0.25 – 6.61]	1.03	0.25 [-3.88 – 4.50]	1.02	-45125.04
	10000	L	1.28 [1.25 – 1.32]	0.98	0.66 [0.35 – 0.98]	0.97	2.55 [-0.99 – 6.00]	0.97			-44907.59
	10000	Q	1.29 [1.25 – 1.32]	1.01	0.65 [0.34 – 0.98]	1.03	2.58 [-0.91 – 6.04]	1.01	0.07 [-4.09 – 4.30]	0.99	-44803.11
DI12		Q	1.28 [1.25 – 1.32]	1.01	1.33 [0.75 – 1.89]	1.01	-2.19 [-5.00 – 0.67]	1.03	-0.94 [-4.94 – 2.98]	1.02	-44889.42
		L	1.29 [1.25 – 1.32]	1.00	1.31 [0.74 – 1.86]	1.00	-2.33 [-4.94 – 0.28]	1.00			-44537.12
D124	1000	L	1.28 [1.25 – 1.32]	1.01	0.76 [0.50 – 1.01]	1.02	1.91 [-1.85 – 5.79]	1.02			-46033.98
	1000	Q	1.28 [1.25 – 1.32]	0.98	0.76 [0.50 – 1.01]	1.00	1.92 [-1.83 – 5.84]	1.00	0.33 [-3.72 – 4.41]	1.01	-45766.28
	20000	L	1.29 [1.25 – 1.32]	1.00	-0.20 [-0.96 – 0.54]	0.98	2.84 [0.89 – 4.83]	0.98			-44368.51
	20000	Q	1.28 [1.25 – 1.32]	1.03	-0.19 [-0.95 – 0.55]	1.02	2.47 [-0.11 – 5.04]	1.02	0.79 [-2.62 – 4.29]	1.01	-44234.34
	15000	L	1.29 [1.25 – 1.32]	1.00	-0.06 [-0.74 – 0.64]	0.99	3.06 [0.76 – 5.35]	1.00			-43399.98
	3000	L	1.28 [1.25 – 1.32]	0.99	0.58 [0.27 – 0.90]	1.00	3.09 [0.02 – 6.32]	1.00			-43073.27
	15000	Q	1.28 [1.25 – 1.32]	1.00	-0.03 [-0.72 – 0.65]	1.00	2.62 [0.01 – 5.32]	0.99	1.05 [-2.58 – 4.68]	1.00	-42989.74
	10000	L	1.29 [1.25 – 1.32]	0.99	0.14 [-0.41 – 0.69]	1.00	3.58 [0.92 – 6.40]	0.99			-42698.73
	3000	Q	1.28 [1.25 – 1.32]	1.00	0.59 [0.26 – 0.91]	1.00	2.97 [-0.17 – 6.34]	0.99	0.90 [-3.15 – 4.92]	0.99	-42688.84
	6400	L	1.28 [1.25 – 1.32]	1.01	0.41 [0.00 – 0.82]	1.04	3.52 [0.51 – 6.70]	1.05			-42576.38
	10000	Q	1.28 [1.25 – 1.32]	1.03	0.14 [-0.42 – 0.68]	0.99	3.34 [0.54 – 6.19]	1.01	1.22 [-2.61 – 5.13]	0.99	-42389.38
	6400	Q	1.28 [1.25 – 1.32]	1.02	0.41 [-0.02 – 0.81]	1.00	3.41 [0.40 – 6.66]	1.00	0.97 [-3.00 – 4.94]	1.00	-42336.37
DI124		L	1.29 [1.25 – 1.32]	1.01	0.98 [0.64 – 1.32]	1.03	-2.02 [-5.83 – 1.90]	1.03			-46308.24
		Q	1.29 [1.25 – 1.32]	1.04	0.98 [0.64 – 1.32]	1.00	-1.95 [-5.89 – 1.85]	1.02	-0.39 [-4.44 – 3.69]	1.02	-46285.13
DD	20000	L	1.28 [1.25 – 1.32]	1.00	0.83 [0.57 – 1.09]	0.99	-0.15 [-3.53 – 3.85]	0.98			-47303.89
	1000	Q	1.29 [1.25 – 1.32]	0.99	0.83 [0.62 – 1.03]	0.99	0.83 [-3.25 – 4.76]	1.03	0.25 [-3.76 – 4.35]	0.99	-46922.73
	20000	Q	1.28 [1.25 – 1.32]	1.01	0.83 [0.56 – 1.09]	1.02	0.18 [-3.38 – 4.10]	0.98	-0.82 [-4.78 – 3.29]	1.01	-46919.49
	1000	L	1.29 [1.25 – 1.32]	0.99	0.84 [0.63 – 1.04]	1.00	0.85 [-3.27 – 4.73]	0.99			-46784.10
	15000	Q	1.28 [1.25 – 1.32]	1.01	0.81 [0.59 – 1.04]	1.02	0.92 [-2.80 – 4.81]	1.03	-0.36 [-4.31 – 3.81]	1.01	-46475.40
	15000	L	1.28 [1.25 – 1.32]	1.00	0.81 [0.58 – 1.04]	0.98	0.82 [-2.81 – 4.76]	1.01			-46324.87
	10000	L	1.29 [1.25 – 1.32]	0.99	0.81 [0.60 – 1.02]	1.01	1.41 [-2.10 – 5.12]	0.98			-45910.75
	10000	Q	1.29 [1.25 – 1.32]	0.99	0.81 [0.59 – 1.02]	1.00	1.40 [-2.09 – 5.14]	0.99	-0.02 [-4.12 – 4.05]	0.96	-45832.54

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	6400	L	1.29 [1.25 – 1.32]	0.99	0.81 [0.60 – 1.02]	0.99	1.78 [-1.68 – 5.33]	1.01			-45468.85
	6400	Q	1.29 [1.25 – 1.32]	1.01	0.81 [0.60 – 1.01]	1.00	1.76 [-1.65 – 5.40]	1.00	0.28 [-3.83 – 4.41]	1.02	-45317.53
	3000	Q	1.29 [1.25 – 1.32]	0.99	0.81 [0.6 0- 1.01]	0.99	2.04 [-1.09 – 5.49]	1.01	0.55 [-3.41 – 4.59]	0.97	-44536.15
	3000	L	1.28 [1.25 – 1.32]	1.02	0.81 [0.60 – 1.01]	1.01	2.12 [-1.00 – 5.51]	1.00			-44511.54
DAG	20000	L	1.29 [1.25 – 1.32]	0.99	0.63 [0.31 – 0.94]	1.01	1.69 [-0.23 – 4.00]	0.99			-48123.18
	20000	Q	1.29 [1.25 – 1.32]	0.98	0.63 [0.31 – 0.92]	0.99	2.13 [-0.18 – 4.50]	0.98	-0.87 [-4.71 – 2.93]	0.99	-47833.98
	15000	L	1.29 [1.25 – 1.32]	1.01	0.62 [0.33 – 0.92]	1.00	2.36 [-0.07 – 5.04]	1.00			-46917.87
	15000	Q	1.29 [1.25 – 1.32]	0.98	0.63 [0.32 – 0.93]	1.00	2.49 [-0.04 – 5.17]	1.00	-0.30 [-4.34 – 3.81]	1.01	-46726.04
	10000	L	1.29 [1.25 – 1.32]	1.02	0.68 [0.41 – 0.94]	1.00	2.62 [-0.24 – 5.71]	0.99			-46470.99
	6400	L	1.28 [1.25 – 1.32]	1.00	0.71 [0.47 – 0.96]	0.98	2.75 [-0.55 – 6.13]	0.99			-46330.01
	10000	Q	1.28 [1.25 – 1.32]	1.00	0.67 [0.41 – 0.94]	1.00	2.67 [-0.22 – 5.72]	1.00	0.14 [-3.90 – 4.23]	1.01	-46226.48
	6400	Q	1.29 [1.25 – 1.32]	0.99	0.72 [0.47 – 0.97]	1.01	2.76 [-0.58 – 6.12]	0.98	0.27 [-3.76 – 4.37]	1.02	-45972.62
	3000	Q	1.29 [1.25 – 1.32]	1.01	0.73 [0.49 – 0.96]	1.02	2.80 [-0.46 – 6.16]	0.99	0.59 [-3.46 – 4.62]	1.02	-44924.96
	3000	L	1.28 [1.25 – 1.32]	1.01	0.73 [0.50 – 0.97]	1.00	2.86 [-0.49 – 6.25]	1.00			-44920.76
	1000	L	1.29 [1.25 – 1.32]	0.99	0.72 [0.50 – 0.95]	1.01	2.90 [-0.28 – 6.05]	0.99			-44711.18
	1000	Q	1.29 [1.25 – 1.32]	1.02	0.72 [0.49 – 0.96]	1.02	2.78 [-0.40 – 6.05]	1.01	0.91 [-3.07 – 4.89]	1.00	-44445.53
DA	10000	L	1.29 [1.25 – 1.32]	1.00	0.55 [0.13 – 0.95]	1.01	1.19 [-0.27 – 2.71]	1.01			-45969.70
	10000	Q	1.29 [1.25 – 1.32]	1.02	0.53 [0.11 – 0.95]	0.98	1.50 [-0.78 – 3.87]	0.97	-0.55 [-4.11 – 2.92]	0.98	-45901.87
	1000	L	1.28 [1.25 – 1.32]	0.99	0.75 [0.49 – 1.01]	1.00	2.01 [-1.72 – 5.72]	0.99			-45870.04
	1000	Q	1.28 [1.25 – 1.32]	1.00	0.75 [0.49 – 1.00]	1.00	1.96 [-1.85 – 5.73]	1.00	0.44 [-3.65 – 4.43]	1.02	-45775.27
	20000	L	1.29 [1.25 – 1.32]	0.98	-0.18 [-0.96 – 0.58]	1.01	2.76 [0.77 – 4.84]	1.01			-44548.37
	20000	Q	1.28 [1.25 – 1.32]	0.99	-0.17 [-0.95 – 0.60]	0.99	2.39 [-0.30 – 5.02]	0.99	0.84 [-2.57 – 4.32]	0.98	-44229.18
	15000	L	1.29 [1.25 – 1.32]	1.00	-0.04 [-0.75 – 0.67]	1.01	2.95 [0.68 – 5.32]	1.01			-43674.35
	15000	Q	1.28 [1.25 – 1.32]	1.01	-0.05 [-0.77 – 0.66]	0.98	2.59 [-0.12 – 5.35]	1.00	1.16 [-2.51 – 4.8]	1.01	-43076.41
	3000	L	1.29 [1.25 – 1.32]	1.00	0.59 [0.26 – 0.91]	0.98	2.92 [-0.07 – 6.17]	1.00			-43051.15
	6400	L	1.28 [1.25 – 1.32]	1.01	0.41 [-0.02 – 0.83]	1.01	3.33 [0.42 – 6.50]	1.01			-42942.93
	3000	Q	1.29 [1.25 – 1.32]	1.00	0.57 [0.24 – 0.91]	1.01	2.93 [-0.21 – 6.24]	1.00	0.91 [-2.98 – 4.83]	1.00	-42755.39
	6400	Q	1.28 [1.25 – 1.32]	0.99	0.41 [-0.01 – 0.85]	0.98	3.18 [0.12 – 6.36]	1.00	0.94 [-3.07 – 4.94]	0.98	-42572.24

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
DIA		Q	1.29 [1.25 – 1.32]	0.99	0.96 [0.62 – 1.30]	1.02	-1.79 [-5.67 – 2.08]	1.01	-0.29 [-4.34 – 3.76]	1.02	-46463.03
		L	1.28 [1.25 – 1.32]	0.99	0.96 [0.62 – 1.30]	1.00	-1.81 [-5.64 – 2.11]	0.98			-46357.50
DLD	10000	Q	1.28 [1.25 – 1.32]	0.99	0.77 [0.09 – 1.41]	1.03	0.18 [-2.53 – 2.90]	1.02	0.33 [-3.43 – 4.17]	1.00	-48052.90
	10000	L	1.28 [1.25 – 1.32]	1.02	0.74 [0.08 – 1.40]	0.99	0.36 [-2.08 – 2.76]	0.99			-47969.55
	6400	Q	1.29 [1.25 – 1.32]	0.98	0.77 [0.17 – 1.37]	1.01	0.28 [-2.65 – 3.16]	1.02	0.17 [-3.75 – 4.10]	1.00	-47923.20
	15000	Q	1.28 [1.25 – 1.32]	0.98	0.83 [0.08 – 1.57]	1.00	-0.13 [-2.73 – 2.48]	1.00	0.29 [-3.13 – 3.79]	1.02	-47768.60
	6400	L	1.28 [1.25 – 1.32]	0.99	0.79 [0.17 – 1.38]	1.00	0.23 [-2.62 – 3.15]	0.99			-47512.84
	15000	L	1.29 [1.25 – 1.32]	1.00	0.85 [0.10 – 1.57]	0.98	-0.05 [-1.91 – 1.86]	0.99			-47333.67
	1000	Q	1.29 [1.25 – 1.32]	1.01	0.86 [0.46 – 1.26]	0.99	-0.28 [-3.81 – 3.21]	1.00	-0.03 [-4.14 – 3.98]	0.99	-46978.70
	1000	L	1.28 [1.25 – 1.32]	1.02	0.86 [0.45 – 1.25]	0.98	-0.27 [-3.73 – 3.28]	0.99			-46972.38
	3000	L	1.29 [1.25 – 1.32]	1.00	0.92 [0.40 – 1.43]	1.00	-0.54 [-3.69 – 2.57]	0.99			-46486.97
	3000	Q	1.28 [1.25 – 1.32]	1.00	0.92 [0.40 – 1.44]	1.00	-0.53 [-3.71 – 2.61]	1.00	-0.10 [-4.09 – 3.85]	0.99	-46411.66
	20000	L	1.29 [1.25 – 1.32]	1.02	1.33 [0.93 – 1.73]	1.03	-3.01 [-5.11 – -0.87]	1.04			-39893.21
	20000	Q	1.29 [1.25 – 1.32]	0.98	1.33 [0.93 – 1.73]	1.02	-2.67 [-4.96 – -0.34]	1.01	-1.41 [-5.43 – 2.39]	1.01	-39715.29
DILD		L	1.28 [1.25 – 1.32]	0.98	0.80 [0.56 – 1.04]	0.99	1.06 [-2.88 – 4.97]	0.99			-46736.90
		Q	1.29 [1.26 – 1.32]	1.00	0.80 [0.56 – 1.04]	1.01	1.07 [-2.89 – 4.92]	1.01	0.29 [-3.77 – 4.29]	1.01	-46566.38
DP	1000	L	1.29 [1.25 – 1.32]	0.98	0.84 [0.63 – 1.04]	0.99	0.07 [-3.96 – 4.21]	0.98			-47237.49
	3000	Q	1.28 [1.25 – 1.32]	0.99	0.83 [0.63 – 1.03]	0.96	0.44 [-3.57 – 4.50]	0.99	-0.04 [-4.05 – 4.05]	1.00	-47177.37
	1000	Q	1.29 [1.25 – 1.32]	0.99	0.84 [0.64 – 1.04]	0.99	0.13 [-4.01 – 4.13]	0.99	0.06 [-3.98 – 4.16]	0.97	-47048.62
	3000	L	1.29 [1.25 – 1.32]	1.00	0.83 [0.63 – 1.03]	1.01	0.43 [-3.59 – 4.52]	0.98			-46984.11
	20000	Q	1.29 [1.25 – 1.32]	0.99	0.82 [0.60 – 1.04]	1.00	0.66 [-3.04 – 4.60]	1.01	-0.50 [-4.50 – 3.64]	1.01	-46792.30
	20000	L	1.28 [1.25 – 1.32]	1.00	0.82 [0.60 – 1.04]	0.99	0.53 [-3.13 – 4.44]	1.01			-46754.88
	6400	L	1.29 [1.25 – 1.32]	1.00	0.83 [0.62 – 1.03]	1.01	1.22 [-2.61 – 5.05]	0.99			-46668.27
	15000	Q	1.28 [1.25 – 1.32]	0.98	0.82 [0.61 – 1.02]	0.98	0.95 [-2.81 – 4.95]	1.01	-0.19 [-4.24 – 3.96]	1.00	-46594.13
	10000	Q	1.28 [1.25 – 1.32]	1.01	0.82 [0.62 – 1.02]	1.00	1.15 [-2.67 – 5.02]	0.99	-0.02 [-4.16 – 4.05]	1.03	-46545.75
	6400	Q	1.28 [1.25 – 1.32]	0.99	0.83 [0.62 – 1.02]	1.00	1.13 [-2.64 – 5.00]	1.00	0.11 [-3.99 – 4.14]	0.96	-46497.17
	10000	L	1.29 [1.25 – 1.32]	1.01	0.82 [0.62 – 1.03]	0.99	1.03 [-2.68 – 4.91]	0.99			-46452.14
	15000	L	1.29 [1.25 – 1.32]	1.00	0.82 [0.61 – 1.03]	0.99	0.90 [-2.80 – 4.86]	0.98			-46438.06

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
DIP		Q	1.29 [1.25 – 1.32]	1.00	1.44 [0.94 – 1.95]	0.99	-2.96 [-5.75 – -0.19]	0.99	-1.41 [-5.23 – 2.40]	1.02	-41696.59
		L	1.29 [1.25 – 1.32]	1.01	1.45 [0.94 – 1.95]	1.00	-3.33 [-5.87 – -0.81]	1.00			-41696.10
DOG	1000	L	1.28 [1.25 – 1.32]	1.00	0.75 [0.50 – 1.01]	0.99	1.96 [-1.84 – 5.76]	0.99			-45992.40
	10000	L	1.29 [1.25 – 1.32]	1.00	0.56 [0.13 – 0.96]	0.99	1.17 [-0.33 – 2.70]	0.98			-45984.71
	10000	Q	1.28 [1.25 – 1.32]	1.01	0.53 [0.10 – 0.95]	1.01	1.53 [-0.81 – 3.87]	1.02	-0.63 [-4.08 – 2.83]	1.01	-45922.07
	1000	Q	1.29 [1.25 – 1.32]	0.98	0.75 [0.49 – 1.01]	0.98	2.00 [-1.86 – 5.78]	0.99	0.44 [-3.59 – 4.50]	1.00	-45886.41
	20000	L	1.28 [1.25 – 1.32]	1.00	-0.19 [-0.96 – 0.57]	1.01	2.79 [0.79 – 4.78]	1.01			-44556.93
	20000	Q	1.28 [1.25 – 1.32]	1.01	-0.17 [-0.94 – 0.58]	0.99	2.37 [-0.28 – 5.02]	0.99	0.87 [-2.59 – 4.38]	1.02	-43890.49
	15000	L	1.28 [1.25 – 1.32]	1.01	-0.05 [-0.77 – 0.65]	1.03	3.01 [0.71 – 5.32]	1.04			-43612.68
	6400	L	1.28 [1.25 – 1.32]	1.01	0.41 [-0.02 – 0.84]	0.99	3.35 [0.40 – 6.54]	0.98			-43143.62
	3000	L	1.28 [1.25 – 1.32]	0.99	0.58 [0.25 – 0.91]	0.98	2.97 [-0.09 – 6.26]	0.98			-43074.05
	15000	Q	1.29 [1.25 – 1.32]	1.02	-0.03 [-0.74 – 0.67]	1.00	2.54 [-0.18 – 5.19]	1.00	1.16 [-2.40 – 4.81]	0.99	-42964.50
	3000	Q	1.28 [1.25 – 1.32]	1.01	0.58 [0.24 – 0.91]	1.00	2.92 [-0.27 – 6.17]	1.01	0.85 [-3.04 – 4.80]	1.02	-42857.85
	6400	Q	1.29 [1.25 – 1.32]	1.01	0.42 [-0.02 – 0.83]	1.03	3.17 [0.16 – 6.35]	1.04	1.06 [-2.93 – 5.03]	1.01	-42550.35
DIOG		L	1.29 [1.25 – 1.32]	0.98	1.30 [0.94 – 1.62]	1.01	-2.35 [-3.69 – -0.86]	1.03			-44540.65
		Q	1.28 [1.25 – 1.32]	0.99	1.23 [0.88 – 1.58]	1.00	-1.27 [-3.58 – 0.98]	1.00	-2.01 [-5.50 – 1.54]	1.01	-44445.81
DRI	3000	Q	1.29 [1.25 – 1.32]	0.99	0.89 [0.20 – 1.58]	0.99	-0.13 [-2.97 – 2.72]	1.00	-0.32 [-4.19 – 3.44]	0.97	-47166.08
	1000	Q	1.28 [1.25 – 1.32]	0.99	0.88 [0.21 – 1.56]	1.00	-0.11 [-3.03 – 2.84]	1.00	-0.31 [-4.16 – 3.59]	1.00	-47134.77
	1000	L	1.29 [1.25 – 1.32]	1.01	0.87 [0.19 – 1.56]	1.04	-0.16 [-3.02 – 2.70]	1.04			-47108.77
	6400	L	1.29 [1.25 – 1.32]	1.02	0.92 [0.23 – 1.62]	1.00	-0.35 [-2.90 – 2.23]	1.00			-47023.97
	6400	Q	1.29 [1.25 – 1.32]	1.01	0.91 [0.23 – 1.61]	0.98	-0.13 [-2.91 – 2.61]	0.99	-0.50 [-4.30 – 3.25]	1.00	-46998.32
	3000	L	1.29 [1.25 – 1.32]	0.99	0.88 [0.19 – 1.58]	1.00	-0.19 [-2.94 – 2.50]	1.00			-46967.20
	10000	Q	1.28 [1.25 – 1.32]	1.00	1.00 [0.33 – 1.69]	1.02	-0.41 [-3.19 – 2.28]	1.02	-0.61 [-4.34 – 3.18]	1.02	-46858.31
	10000	L	1.29 [1.25 – 1.32]	0.97	0.99 [0.32 – 1.68]	0.99	-0.59 [-3.03 – 1.82]	0.99			-46816.68
	15000	L	1.28 [1.25 – 1.32]	0.98	1.08 [0.41 – 1.75]	0.97	-0.92 [-3.30 – 1.47]	0.96			-46640.21
	15000	Q	1.29 [1.26 – 1.32]	0.99	1.09 [0.42 – 1.77]	1.02	-0.73 [-3.43 – 2.02]	1.01	-0.76 [-4.47 – 3.02]	1.00	-46575.86
	20000	L	1.29 [1.25 – 1.32]	0.99	1.19 [0.53 – 1.86]	1.00	-1.29 [-3.58 – 1.00]	1.00			-45853.64
	20000	Q	1.29 [1.25 – 1.32]	1.00	1.18 [0.51 – 1.84]	0.98	-0.99 [-3.60 – 1.70]	0.98	-0.80 [-4.54 – 2.93]	1.00	-45794.24

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
GDD	1000	L	1.28 [1.25 – 1.32]	0.99	1.64 [-0.01 – 3.32]	0.99	-1.19 [-3.70 – 1.25]	0.99			-44559.81
	3000	L	1.29 [1.25 – 1.32]	1.01	1.78 [0.36 – 3.17]	1.01	-1.54 [-3.79 – 0.77]	1.01			-43665.34
	1000	Q	1.29 [1.25 – 1.32]	1.00	1.65 [0.04 – 3.39]	1.01	0.09 [-3.19 – 3.26]	1.04	-1.88 [-4.81 – 1.11]	1.00	-43491.70
	6400	L	1.28 [1.25 – 1.32]	1.00	1.77 [0.52 – 3.04]	0.97	-1.60 [-3.73 – 0.49]	0.98			-43345.80
	10000	L	1.28 [1.25 – 1.32]	1.00	1.85 [0.66 – 3.02]	0.99	-1.71 [-3.68 – 0.27]	0.99			-42822.52
	3000	Q	1.29 [1.25 – 1.32]	0.99	1.71 [0.35 – 3.11]	1.01	-0.14 [-3.25 – 2.95]	1.02	-1.98 [-4.88 – 1.00]	0.99	-42790.64
	6400	Q	1.28 [1.25 – 1.32]	0.99	1.66 [0.37 – 2.91]	0.98	-0.19 [-3.27 – 2.93]	1.00	-1.88 [-4.87 – 1.15]	1.00	-42634.37
	10000	Q	1.29 [1.25 – 1.32]	1.01	1.64 [0.45 – 2.82]	0.99	-0.20 [-3.21 – 2.82]	0.98	-1.80 [-4.71 – 1.08]	0.96	-42570.36
	15000	L	1.29 [1.25 – 1.32]	0.97	1.86 [0.77 – 2.91]	0.99	-1.75 [-3.49 – 0.09]	0.98			-42456.91
	15000	Q	1.28 [1.25 – 1.32]	1.00	1.66 [0.53 – 2.76]	1.00	-0.33 [-3.39 – 2.74]	1.01	-1.68 [-4.52 – 1.27]	1.01	-42212.73
	20000	L	1.29 [1.25 – 1.32]	1.01	1.90 [0.96 – 2.84]	1.01	-1.84 [-3.43 – -0.25]	1.01			-41467.46
	20000	Q	1.28 [1.25 – 1.32]	0.98	1.65 [0.65 – 2.65]	0.99	-0.40 [-3.29 – 2.56]	0.99	-1.58 [-4.41 – 1.23]	0.99	-41448.16
MAR	20000	L	1.28 [1.25 – 1.32]	1.01	0.49 [-0.16 – 1.14]	1.00	1.35 [-1.11 – 3.73]	0.99			-48055.12
	20000	Q	1.28 [1.25 – 1.32]	1.01	0.50 [-0.16 – 1.16]	1.01	1.03 [-1.78 – 3.83]	1.00	0.84 [-2.78 – 4.42]	0.96	-47814.09
	15000	L	1.29 [1.25 – 1.32]	1.00	0.69 [0.05 – 1.33]	1.00	0.60 [-1.92 – 3.07]	1.00			-47710.26
	15000	Q	1.29 [1.25 – 1.32]	0.98	0.70 [0.07 – 1.34]	0.98	0.28 [-2.45 – 3.06]	0.97	0.77 [-2.92 – 4.44]	0.99	-47401.78
	10000	Q	1.29 [1.25 – 1.32]	1.00	0.87 [0.24 – 1.52]	1.01	-0.30 [-3.21 – 2.60]	1.00	0.35 [-3.44 – 4.11]	0.98	-47110.86
	10000	L	1.29 [1.25 – 1.32]	1.00	0.86 [0.25 – 1.50]	0.99	-0.14 [-2.84 – 2.42]	0.99			-47020.98
	1000	L	1.29 [1.25 – 1.32]	0.98	0.95 [0.41 – 1.50]	0.99	-0.68 [-3.84 – 2.32]	1.00			-46632.54
	6400	L	1.29 [1.25 – 1.32]	1.01	0.95 [0.34 – 1.57]	1.00	-0.54 [-3.45 – 2.17]	1.00			-46580.07
	1000	Q	1.28 [1.25 – 1.32]	0.99	0.96 [0.40 – 1.52]	0.97	-0.77 [-3.95 – 2.42]	0.98	0.01 [-4.01 – 3.94]	1.00	-46397.92
	3000	Q	1.29 [1.25 – 1.32]	0.99	0.97 [0.39 – 1.56]	1.01	-0.79 [-3.94 – 2.34]	1.02	0.04 [-3.90 – 3.94]	0.99	-46382.57
	6400	Q	1.29 [1.25 – 1.32]	1.02	0.96 [0.35 – 1.59]	0.98	-0.63 [-3.72 – 2.26]	0.98	0.16 [-3.77 – 4.01]	1.01	-46372.57
	3000	L	1.29 [1.25 – 1.32]	1.02	0.98 [0.41 – 1.56]	0.99	-0.77 [-3.82 – 2.19]	1.00			-46223.01
MMT	1000	L	1.29 [1.25 – 1.32]	0.99	1.16 [-0.34 – 2.74]	0.99	-0.54 [-3.18 – 1.95]	0.99			-46224.93
	3000	L	1.29 [1.25 – 1.32]	1.01	1.19 [-0.24 – 2.70]	1.01	-0.62 [-3.21 – 1.81]	1.01			-46172.68
	6400	L	1.29 [1.25 – 1.32]	0.99	1.30 [-0.05 – 2.75]	0.99	-0.80 [-3.29 – 1.53]	0.99			-45577.95
	1000	Q	1.29 [1.25 – 1.32]	0.99	1.24 [-0.29 – 2.83]	1.02	0.17 [-3.00 – 3.25]	1.01	-1.36 [-4.67 – 1.98]	0.99	-45355.43

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	3000	Q	1.28 [1.25 – 1.32]	1.01	1.28 [-0.18 – 2.83]	0.99	0.10 [-3.01 – 3.14]	1.00	-1.42 [-4.71 – 1.91]	0.99	-45124.59
	6400	Q	1.29 [1.25 – 1.32]	0.97	1.37 [-0.01 – 2.83]	1.02	-0.04 [-3.11 – 2.92]	0.99	-1.50 [-4.65 – 1.61]	0.96	-44631.03
	10000	L	1.29 [1.25 – 1.32]	1.00	1.50 [0.24 – 2.78]	0.98	-1.17 [-3.44 – 1.02]	0.98			-44554.07
	10000	Q	1.28 [1.25 – 1.32]	1.01	1.46 [0.21 – 2.77]	1.00	-0.22 [-3.33 – 2.83]	1.00	-1.47 [-4.57 – 1.68]	0.99	-43880.59
	15000	L	1.28 [1.25 – 1.32]	0.97	1.66 [0.50 – 2.85]	0.98	-1.44 [-3.52 – 0.54]	0.98			-43632.95
	15000	Q	1.29 [1.25 – 1.32]	1.00	1.54 [0.37 – 2.70]	1.00	-0.32 [-3.34 – 2.71]	0.99	-1.43 [-4.44 – 1.47]	1.00	-43530.03
	20000	L	1.29 [1.25 – 1.32]	1.01	1.80 [0.78 – 2.86]	0.98	-1.70 [-3.57 – 0.08]	0.98			-42576.84
	20000	Q	1.29 [1.25 – 1.32]	1.00	1.65 [0.57 – 2.73]	1.01	-0.50 [-3.43 – 2.47]	1.00	-1.56 [-4.49 – 1.35]	0.97	-42280.46
AS	1000	Q	1.29 [1.26 – 1.32]	1.00	0.46 [-0.02 – 0.95]	1.01	1.45 [-1.37 – 4.18]	1.00	1.65 [-1.99 – 5.49]	1.00	-48258.84
	1000	L	1.29 [1.25 – 1.32]	0.99	0.48 [0.01 – 0.95]	1.01	1.85 [-0.35 – 4.36]	0.99			-48072.77
	3000	L	1.29 [1.25 – 1.32]	0.98	0.34 [-0.19 – 0.85]	0.97	2.42 [0.15 – 5.03]	0.99			-47501.89
	3000	Q	1.29 [1.25 – 1.32]	1.03	0.34 [-0.19 – 0.85]	1.00	1.99 [-0.71 – 4.77]	1.00	1.63 [-2.17 – 5.51]	1.00	-47361.27
	20000	L	1.29 [1.25 – 1.32]	1.02	0.62 [-0.13 – 1.33]	1.02	0.62 [-1.34 – 2.79]	1.03			-46844.58
	20000	Q	1.29 [1.25 – 1.32]	0.99	0.61 [-0.16 – 1.35]	1.00	0.46 [-2.29 – 3.22]	0.99	0.58 [-2.73 – 3.92]	0.99	-46762.49
	6400	L	1.29 [1.25 – 1.32]	0.99	0.18 [-0.40 – 0.75]	0.99	2.60 [0.43 – 4.97]	0.99			-46680.12
	6400	Q	1.29 [1.25 – 1.32]	0.99	0.19 [-0.39 – 0.78]	1.00	2.00 [-0.72 – 4.73]	0.98	1.72 [-1.92 – 5.35]	1.00	-46354.79
	15000	L	1.29 [1.25 – 1.32]	1.00	0.33 [-0.35 – 0.98]	0.99	1.71 [-0.36 – 4.03]	0.99			-46073.48
	10000	L	1.28 [1.25 – 1.32]	1.02	0.19 [-0.46 – 0.80]	1.00	2.46 [0.25 – 4.94]	1.01			-45920.82
	15000	Q	1.29 [1.25 – 1.32]	0.99	0.35 [-0.36 – 1.02]	1.01	1.28 [-1.42 – 4.06]	1.02	1.14 [-2.44 – 4.55]	1.02	-45790.18
	10000	Q	1.29 [1.25 – 1.32]	1.03	0.20 [-0.46 – 0.82]	1.01	1.97 [-0.74 – 4.84]	1.01	1.40 [-2.17 – 5.05]	0.99	-45227.35
BS	1000	L	1.29 [1.25 – 1.32]	0.98	0.46 [-0.03 – 0.94]	0.98	2.06 [-0.31 – 4.72]	0.97			-47874.24
	3000	L	1.28 [1.25 – 1.32]	0.99	0.32 [-0.19 – 0.80]	0.98	2.60 [0.36 – 5.22]	0.98			-47759.59
	1000	Q	1.29 [1.25 – 1.32]	1.02	0.45 [-0.05 – 0.92]	1.02	1.65 [-1.06 – 4.55]	1.03	1.52 [-2.24 – 5.35]	0.99	-47673.83
	3000	Q	1.29 [1.25 – 1.32]	1.02	0.32 [-0.20 – 0.81]	1.01	2.14 [-0.48 – 4.99]	1.00	1.62 [-2.20 – 5.42]	1.00	-47401.11
	20000	L	1.29 [1.25 – 1.32]	0.99	0.58 [-0.18 – 1.30]	1.00	0.75 [-1.24 – 2.98]	0.99			-46553.29
	20000	Q	1.29 [1.25 – 1.32]	1.00	0.59 [-0.17 – 1.31]	1.00	0.50 [-2.22 – 3.26]	0.99	0.65 [-2.66 – 3.99]	1.00	-46498.90
	15000	L	1.28 [1.25 – 1.32]	0.98	0.30 [-0.37 – 0.93]	1.05	1.81 [-0.23 – 4.14]	1.06			-46255.93
	6400	L	1.28 [1.25 – 1.32]	0.99	0.17 [-0.40 – 0.72]	0.99	2.74 [0.61 – 5.15]	0.99			-46119.11

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	10000	L	1.29 [1.25 – 1.32]	1.00	0.15 [-0.47 – 0.76]	1.00	2.64 [0.38 – 5.1]	1.00			-45792.29
	15000	Q	1.29 [1.25 – 1.32]	1.02	0.32 [-0.37 – 0.97]	1.04	1.43 [-1.26 – 4.21]	1.05	1.08 [-2.37 – 4.53]	1.03	-45682.53
	6400	Q	1.28 [1.25 – 1.32]	1.01	0.18 [-0.40 – 0.74]	0.99	2.15 [-0.46 – 4.90]	0.98	1.71 [-1.98 – 5.37]	1.00	-45619.23
	10000	Q	1.28 [1.25 – 1.32]	1.02	0.17 [-0.47 – 0.78]	1.02	2.17 [-0.56 – 4.94]	1.02	1.31 [-2.23 – 4.87]	1.00	-45336.36
CON	3000	L	1.29 [1.25 – 1.32]	1.02	0.91 [0.44 – 1.43]	1.02	-0.26 [-1.86 – 1.24]	1.02			-46682.32
	1000	L	1.28 [1.25 – 1.32]	0.98	0.89 [0.44 – 1.36]	1.00	-0.21 [-1.75 – 1.37]	1.01			-46634.97
	1000	Q	1.29 [1.25 – 1.32]	0.99	0.89 [0.43 – 1.36]	0.98	-0.14 [-2.68 – 2.43]	1.00	-0.07 [-3.30 – 3.14]	1.04	-46624.40
	3000	Q	1.29 [1.25 – 1.32]	1.01	0.92 [0.43 – 1.44]	1.03	-0.18 [-2.69 – 2.30]	1.04	-0.20 [-3.46 – 3.03]	1.01	-46528.27
	6400	Q	1.29 [1.25 – 1.32]	1.01	1.08 [0.54 – 1.65]	1.02	-0.92 [-3.37 – 1.52]	1.02	0.36 [-2.92 – 3.48]	1.03	-45725.12
	6400	L	1.29 [1.25 – 1.32]	0.99	1.07 [0.54 – 1.63]	1.02	-0.67 [-2.27 – 0.77]	1.01			-45680.12
	10000	L	1.29 [1.25 – 1.32]	1.01	1.27 [0.65 – 1.90]	1.03	-1.09 [-2.65 – 0.39]	1.03			-44342.19
	10000	Q	1.29 [1.25 – 1.32]	1.00	1.28 [0.67 – 1.92]	0.97	-1.25 [-3.75 – 1.17]	1.00	0.23 [-3.03 – 3.45]	0.99	-44134.18
	20000	Q	1.29 [1.25 – 1.32]	1.00	1.80 [0.95 – 2.72]	0.99	-1.15 [-4.00 – 1.58]	0.99	-1.58 [-4.72 – 1.57]	0.99	-43133.84
	15000	Q	1.28 [1.25 – 1.32]	0.96	1.67 [0.88 – 2.53]	0.99	-1.39 [-4.07 – 1.33]	1.00	-1.19 [-4.57 – 2.10]	1.00	-42976.88
	15000	L	1.29 [1.25 – 1.32]	0.99	1.68 [0.92 – 2.53]	0.97	-1.98 [-3.93 – -0.29]	0.98			-42558.57
	20000	L	1.29 [1.25 – 1.32]	1.00	1.89 [1.07 – 2.76]	1.00	-2.22 [-4.02 – -0.55]	1.00			-42368.13
LS	1000	L	1.28 [1.25 – 1.32]	1.01	0.84 [0.61 – 1.06]	0.98	-0.13 [-2.41 – 2.56]	1.01			-46988.84
	1000	Q	1.28 [1.25 – 1.32]	1.02	0.84 [0.61 – 1.06]	1.00	-0.32 [-2.99 – 2.71]	1.01	0.94 [-2.89 – 4.68]	1.00	-46933.82
	3000	Q	1.28 [1.25 – 1.32]	0.99	0.91 [0.66 – 1.16]	1.02	-1.28 [-3.60 – 1.17]	1.01	0.78 [-3.14 – 4.59]	1.00	-45099.29
	3000	L	1.29 [1.25 – 1.32]	1.02	0.92 [0.67 – 1.16]	1.01	-1.12 [-3.15 – 1.17]	1.02			-44809.61
	6400	L	1.28 [1.25 – 1.32]	1.00	1.11 [0.83 – 1.39]	0.99	-2.67 [-4.48 – -0.71]	1.01			-41116.07
	6400	Q	1.28 [1.25 – 1.32]	1.00	1.12 [0.83 – 1.40]	1.03	-2.38 [-4.46 – -0.24]	1.03	-1.16 [-5.08 – 2.84]	1.02	-40854.23
	10000	L	1.28 [1.25 – 1.32]	1.02	1.21 [0.90 – 1.49]	1.02	-2.96 [-4.65 – -1.14]	1.02			-40426.84
	20000	L	1.29 [1.25 – 1.32]	0.98	1.32 [0.99 – 1.64]	0.99	-3.14 [-4.84 – -1.36]	1.00			-40389.27
	10000	Q	1.28 [1.25 – 1.32]	0.96	1.20 [0.89 – 1.49]	0.98	-2.43 [-4.50 – -0.28]	0.97	-1.53 [-5.33 – 2.23]	0.94	-40328.90
	20000	Q	1.29 [1.25 – 1.32]	1.01	1.30 [0.97 – 1.62]	1.01	-2.60 [-4.70 – -0.45]	0.98	-1.55 [-5.23 – 2.22]	0.99	-40327.44
	15000	L	1.29 [1.25 – 1.32]	0.98	1.25 [0.94 – 1.55]	1.00	-2.96 [-4.53 – -1.32]	0.99			-40253.69
	15000	Q	1.28 [1.25 – 1.32]	1.01	1.25 [0.93 – 1.54]	0.99	-2.38 [-4.45 – -0.29]	1.00	-1.57 [-5.25 – 2.10]	1.00	-40091.67

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
CC	3000	Q	1.29 [1.26 – 1.32]	0.97	0.84 [0.63 – 1.03]	1.00	-0.13 [-4.12 – 3.93]	0.99	-0.08 [-4.13 – 3.99]	0.99	-47248.05
	1000	Q	1.28 [1.25 – 1.32]	1.00	0.84 [0.63 – 1.03]	1.00	0.23 [-3.86 – 4.15]	1.01	0.08 [-3.98 – 4.10]	1.00	-47247.40
	6400	Q	1.28 [1.25 – 1.32]	1.00	0.83 [0.63 – 1.03]	1.02	0.02 [-4.09 – 4.12]	0.99	0.00 [-4.06 – 4.02]	0.99	-47229.46
	10000	Q	1.28 [1.25 – 1.32]	0.97	0.84 [0.63 – 1.03]	1.00	0.14 [-3.90 – 4.20]	0.97	0.05 [-4.08 – 4.15]	1.01	-47226.26
	1000	L	1.28 [1.25 – 1.32]	1.01	0.84 [0.63 – 1.03]	1.00	0.21 [-3.80 – 4.22]	0.98			-47221.87
	10000	L	1.28 [1.25 – 1.32]	1.00	0.83 [0.64 – 1.03]	0.98	0.10 [-3.95 – 4.12]	1.00			-47168.34
	6400	L	1.29 [1.25 – 1.32]	1.03	0.84 [0.63 – 1.03]	1.02	0.15 [-3.94 – 4.27]	1.01			-47141.29
	3000	L	1.28 [1.25 – 1.32]	0.98	0.84 [0.64 – 1.03]	0.99	0.00 [-4.06 – 4.14]	1.02			-47128.64
	15000	Q	1.28 [1.25 – 1.32]	1.03	0.83 [0.63 – 1.03]	1.00	0.55 [-3.47 – 4.64]	0.98	-0.01 [-3.99 – 4.13]	1.01	-47042.58
	15000	L	1.29 [1.25 – 1.32]	1.01	0.83 [0.63 – 1.04]	1.01	0.60 [-3.49 – 4.58]	1.03			-46972.70
	20000	L	1.29 [1.25 – 1.32]	1.02	0.71 [0.45 – 0.96]	1.01	2.84 [-0.68 – 6.31]	1.00			-45042.10
	20000	Q	1.28 [1.25 – 1.32]	1.01	0.71 [0.44 – 0.96]	1.01	2.74 [-0.67 – 6.31]	1.00	0.53 [-3.58 – 4.54]	0.99	-44948.13
PBS	1000	L	1.29 [1.26 – 1.32]	1.01	0.41 [-0.03 – 0.84]	1.02	2.69 [0.22 – 5.39]	1.03			-46368.05
	3000	L	1.29 [1.25 – 1.32]	1.02	0.23 [-0.32 – 0.78]	0.99	2.75 [0.44 – 5.27]	0.99			-46269.55
	1000	Q	1.29 [1.25 – 1.32]	1.02	0.42 [-0.03 – 0.86]	1.00	2.22 [-0.58 – 5.11]	0.99	1.68 [-2.19 – 5.50]	1.00	-46157.66
	3000	Q	1.29 [1.25 – 1.32]	1.00	0.25 [-0.33 – 0.81]	1.00	2.11 [-0.69 – 5.08]	1.01	1.84 [-1.69 – 5.43]	1.01	-45646.01
	6400	L	1.28 [1.25 – 1.32]	1.03	0.08 [-0.55 – 0.67]	1.00	2.77 [0.73 – 5.19]	1.00			-44471.08
	6400	Q	1.28 [1.25 – 1.32]	0.99	0.12 [-0.57 – 0.75]	1.00	1.95 [-0.91 – 4.98]	0.99	2.04 [-1.26 – 5.40]	1.02	-43607.50
	20000	L	1.28 [1.25 – 1.32]	0.97	0.27 [-0.46 – 0.89]	0.99	1.48 [-0.06 – 3.42]	0.99			-43586.07
	10000	L	1.28 [1.25 – 1.32]	1.01	0.12 [-0.53 – 0.71]	1.00	2.39 [0.51 – 4.63]	1.00			-43566.21
	15000	L	1.29 [1.25 – 1.32]	0.99	0.21 [-0.44 – 0.79]	1.01	1.92 [0.24 – 3.96]	1.01			-43355.31
	10000	Q	1.29 [1.25 – 1.32]	0.99	0.22 [-0.46 – 0.88]	0.97	1.30 [-1.48 – 4.13]	0.98	2.04 [-0.99 – 5.29]	0.98	-42171.20
	15000	Q	1.28 [1.25 – 1.32]	1.00	0.35 [-0.35 – 1.04]	1.01	0.62 [-2.16 – 3.43]	1.03	2.14 [-0.65 – 5.08]	1.03	-41349.73
	20000	Q	1.28 [1.25 – 1.32]	0.98	0.47 [-0.34 – 1.28]	1.00	0.01 [-2.84 – 2.84]	1.01	2.01 [-0.54 – 4.69]	0.98	-40847.31
PSB	1000	L	1.29 [1.25 – 1.32]	0.99	0.33 [-0.16 – 0.81]	0.98	2.55 [0.35 – 5.10]	0.97			-46552.83
	3000	L	1.29 [1.25 – 1.32]	1.04	0.16 [-0.46 – 0.76]	1.02	2.70 [0.45 – 5.32]	1.04			-46338.64
	1000	Q	1.28 [1.25 – 1.32]	1.00	0.33 [-0.17 – 0.82]	1.02	1.92 [-0.85 – 4.85]	1.02	2.08 [-1.58 – 5.68]	1.01	-46327.82
	3000	Q	1.28 [1.25 – 1.32]	0.98	0.18 [-0.45 – 0.81]	1.02	1.95 [-0.99 – 4.91]	1.03	2.07 [-1.32 – 5.54]	1.02	-45604.97

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	6400	L	1.28 [1.25 – 1.32]	1.00	0.07 [-0.56 – 0.67]	1.02	2.76 [0.69 – 5.22]	1.02			-44616.52
	20000	L	1.29 [1.25 – 1.32]	0.99	0.29 [-0.42 – 0.93]	1.01	1.38 [-0.15 – 3.19]	1.00			-43712.52
	10000	L	1.28 [1.25 – 1.32]	0.99	0.12 [-0.52 – 0.73]	0.97	2.38 [0.45 – 4.64]	0.97			-43579.17
	6400	Q	1.28 [1.25 – 1.32]	1.00	0.12 [-0.56 – 0.79]	0.99	1.96 [-1.02 – 4.89]	1.00	1.99 [-1.28 – 5.40]	1.00	-43484.60
	15000	L	1.29 [1.26 – 1.32]	0.99	0.21 [-0.42 – 0.81]	1.01	1.86 [0.16 – 3.78]	1.01			-43476.93
	10000	Q	1.28 [1.25 – 1.32]	1.01	0.20 [-0.48 – 0.87]	1.01	1.33 [-1.47 – 4.17]	0.99	2.12 [-0.98 – 5.38]	0.99	-42282.83
	15000	Q	1.28 [1.25 – 1.32]	0.99	0.35 [-0.37 – 1.06]	1.00	0.59 [-2.17 – 3.33]	0.99	2.19 [-0.66 – 5.11]	0.97	-41342.69
	20000	Q	1.29 [1.25 – 1.32]	1.02	0.51 [-0.31 – 1.35]	0.99	-0.11 [-3.04 – 2.74]	0.99	1.98 [-0.64 – 4.71]	1.00	-41261.11
SBHT	1000	Q	1.29 [1.25 – 1.32]	1.01	0.32 [-0.22 – 0.83]	0.99	1.90 [-0.90 – 4.90]	1.00	1.89 [-1.61 – 5.53]	1.01	-47446.96
	1000	L	1.29 [1.25 – 1.32]	1.01	0.34 [-0.20 – 0.83]	1.01	2.40 [0.22 – 5.12]	1.02			-47355.92
	3000	L	1.29 [1.25 – 1.32]	1.00	0.08 [-0.63 – 0.73]	0.99	2.52 [0.44 – 5.09]	0.99			-47296.51
	3000	Q	1.28 [1.25 – 1.32]	1.02	0.03 [-0.68 – 0.75]	1.00	1.90 [-0.99 – 4.80]	1.00	2.06 [-1.15 – 5.63]	1.01	-46886.92
	6400	L	1.28 [1.25 – 1.32]	0.98	-0.05 [-0.81 – 0.65]	0.98	2.47 [0.60 – 4.82]	0.99			-45601.23
	20000	L	1.28 [1.25 – 1.32]	1.01	0.35 [-0.46 – 1.12]	1.02	0.97 [-0.51 – 2.57]	1.02			-45435.11
	10000	L	1.29 [1.25 – 1.32]	0.97	0.04 [-0.70 – 0.72]	1.00	1.99 [0.34 – 3.89]	0.99			-44872.47
	15000	L	1.28 [1.25 – 1.32]	0.97	0.18 [-0.52 – 0.87]	1.01	1.47 [-0.01 – 3.08]	1.01			-44770.79
	6400	Q	1.29 [1.25 – 1.32]	1.01	-0.03 [-0.82 – 0.76]	1.00	1.58 [-1.26 – 4.43]	0.99	2.00 [-1.08 – 5.22]	1.01	-44282.66
	10000	Q	1.29 [1.25 – 1.32]	1.01	0.18 [-0.60 – 0.96]	1.03	0.63 [-2.13 – 3.29]	1.02	2.10 [-0.74 – 5.05]	1.02	-43289.40
	15000	Q	1.29 [1.25 – 1.32]	1.02	0.41 [-0.37 – 1.24]	1.00	-0.31 [-2.98 – 2.36]	1.00	2.27 [-0.37 – 4.97]	0.99	-42300.74
	20000	Q	1.28 [1.25 – 1.32]	0.99	0.61 [-0.28 – 1.54]	1.02	-0.68 [-3.43 – 2.03]	1.00	1.90 [-0.56 – 4.44]	0.98	-42197.80
BD	1000	L	1.28 [1.25 – 1.32]	0.99	1.16 [0.51 – 1.82]	1.04	-1.56 [-4.70 – 1.47]	1.04			-45653.03
	1000	Q	1.29 [1.25 – 1.32]	1.00	1.19 [0.53 – 1.86]	1.00	-1.20 [-4.32 – 1.88]	1.00	-1.73 [-5.62 – 2.05]	1.01	-45199.36
	3000	L	1.29 [1.25 – 1.32]	1.00	1.19 [0.57 – 1.85]	0.98	-1.80 [-4.91 – 1.14]	0.98			-45034.25
	6400	L	1.29 [1.25 – 1.32]	1.00	1.17 [0.63 – 1.71]	1.01	-1.65 [-4.15 – 0.79]	1.00			-44271.61
	10000	L	1.28 [1.25 – 1.32]	1.00	1.19 [0.67 – 1.69]	0.99	-1.58 [-3.68 – 0.55]	0.98			-44163.42
	3000	Q	1.29 [1.25 – 1.32]	1.00	1.28 [0.62 – 1.93]	1.00	-1.50 [-4.64 – 1.59]	0.99	-2.09 [-5.99 – 1.87]	1.01	-43868.51
	10000	Q	1.29 [1.25 – 1.32]	1.00	1.20 [0.69 – 1.72]	0.98	-1.13 [-3.56 – 1.31]	0.97	-1.53 [-5.41 – 2.36]	0.98	-43772.49
	6400	Q	1.28 [1.25 – 1.32]	1.00	1.23 [0.67 – 1.76]	1.01	-1.23 [-3.83 – 1.38]	1.00	-1.91 [-5.81 – 1.86]	1.01	-43599.55

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	15000	L	1.28 [1.25 – 1.32]	0.98	1.40 [0.87 – 1.92]	0.98	-2.38 [-4.43 – -0.34]	0.97			-42179.05
	15000	Q	1.28 [1.25 – 1.32]	1.01	1.41 [0.89 – 1.94]	1.01	-1.85 [-4.25 – 0.46]	0.97	-1.69 [-5.42 – 2.17]	0.98	-41925.63
	20000	L	1.29 [1.25 – 1.32]	1.00	1.58 [1.04 – 2.09]	1.01	-2.87 [-4.79 – -0.96]	1.01			-40770.26
	20000	Q	1.29 [1.25 – 1.32]	0.99	1.58 [1.06 – 2.10]	0.97	-2.19 [-4.56 – 0.04]	0.99	-2.00 [-5.63 – 1.77]	1.00	-40667.40
BDR	20000	L	1.29 [1.25 – 1.32]	1.01	0.51 [-0.18 – 1.18]	1.00	0.94 [-0.91 – 2.79]	1.01			-48421.41
	20000	Q	1.29 [1.25 – 1.32]	1.00	0.52 [-0.16 – 1.20]	1.00	0.65 [-1.93 – 3.24]	1.00	0.60 [-2.85 – 4.10]	0.99	-48165.82
	15000	L	1.28 [1.25 – 1.32]	1.01	0.81 [0.13 – 1.52]	0.99	0.07 [-1.89 – 1.93]	1.00			-47390.29
	15000	Q	1.29 [1.25 – 1.32]	1.00	0.82 [0.13 – 1.51]	1.00	0.20 [-2.43 – 2.79]	1.00	-0.35 [-3.65 – 3.05]	0.99	-47387.34
	10000	L	1.29 [1.25 – 1.32]	1.01	1.23 [0.57 – 1.89]	0.99	-1.20 [-3.07 – 0.71]	0.99			-44940.14
	1000	L	1.28 [1.25 – 1.32]	1.00	1.30 [0.73 – 1.87]	1.01	-2.37 [-4.94 – 0.34]	1.01			-44631.50
	1000	Q	1.28 [1.25 – 1.32]	0.99	1.33 [0.76 – 1.88]	1.04	-2.05 [-4.81 – 0.85]	1.03	-1.22 [-4.94 – 2.50]	1.01	-44601.30
	3000	L	1.28 [1.25 – 1.32]	1.00	1.34 [0.74 – 1.92]	1.00	-2.15 [-4.42 – 0.24]	0.99			-44438.84
	10000	Q	1.29 [1.25 – 1.32]	1.02	1.21 [0.52 – 1.87]	1.00	-0.31 [-2.92 – 2.29]	0.99	-1.68 [-5.04 – 1.65]	1.00	-43972.88
	3000	Q	1.28 [1.25 – 1.32]	0.99	1.33 [0.74 – 1.93]	0.98	-1.48 [-4.17 – 1.25]	0.98	-1.72 [-5.28 – 1.90]	1.00	-43947.80
	6400	L	1.29 [1.25 – 1.32]	1.00	1.32 [0.70 – 1.92]	1.00	-1.74 [-3.66 – 0.34]	1.00			-43794.44
	6400	Q	1.29 [1.25 – 1.32]	1.02	1.28 [0.68 – 1.87]	1.00	-0.84 [-3.33 – 1.70]	1.00	-1.86 [-5.29 – 1.61]	1.01	-43333.34
GU	1000	L	1.28 [1.25 – 1.32]	1.02	1.23 [0.16 – 2.34]	1.00	-1.19 [-4.47 – 1.98]	1.00			-45874.36
	1000	Q	1.29 [1.25 – 1.32]	0.98	1.31 [0.21 – 2.42]	0.96	-0.80 [-4.07 – 2.48]	0.96	-1.58 [-5.35 – 2.18]	0.99	-45534.22
	3000	L	1.29 [1.25 – 1.32]	1.01	1.28 [0.28 – 2.33]	0.99	-1.32 [-4.38 – 1.56]	0.99			-45372.76
	6400	L	1.28 [1.25 – 1.32]	1.00	1.24 [0.47 – 2.05]	1.02	-1.39 [-4.08 – 1.20]	1.02			-44886.95
	10000	L	1.29 [1.25 – 1.32]	1.00	1.20 [0.53 – 1.86]	1.00	-1.39 [-3.74 – 1.00]	1.00			-44833.96
	6400	Q	1.28 [1.25 – 1.32]	1.02	1.27 [0.46 – 2.08]	0.97	-1.02 [-3.94 – 1.93]	0.97	-1.41 [-5.11 – 2.32]	0.97	-44675.67
	3000	Q	1.29 [1.25 – 1.32]	1.00	1.37 [0.35 – 2.44]	1.01	-0.98 [-4.15 – 2.19]	1.02	-1.64 [-5.30 – 2.10]	1.00	-44519.12
	10000	Q	1.28 [1.25 – 1.32]	0.97	1.18 [0.52 – 1.84]	0.98	-0.90 [-3.54 – 1.81]	0.97	-1.21 [-4.91 – 2.58]	1.00	-44340.94
	15000	L	1.28 [1.25 – 1.32]	0.99	1.40 [0.74 – 2.07]	0.99	-2.16 [-4.65 – 0.21]	0.99			-43467.18
	15000	Q	1.29 [1.25 – 1.32]	0.97	1.42 [0.75 – 2.10]	0.99	-1.78 [-4.50 – 0.92]	0.99	-1.48 [-5.24 – 2.32]	0.98	-42916.39
	20000	L	1.29 [1.25 – 1.32]	0.99	1.74 [1.02 – 2.46]	1.01	-3.16 [-5.60 – -0.68]	1.01			-41817.35
	20000	Q	1.29 [1.25 – 1.32]	1.01	1.74 [1.04 – 2.47]	0.98	-2.51 [-5.21 – 0.19]	0.99	-2.03 [-5.80 – 1.71]	1.02	-41260.53

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
GUR	20000	Q	1.28 [1.25 – 1.32]	1.00	0.68 [-0.02 – 1.36]	0.99	0.45 [-2.09 – 3.00]	0.97	-0.04 [-3.39 – 3.37]	0.98	-48002.20
	20000	L	1.28 [1.25 – 1.32]	1.00	0.66 [-0.01 – 1.34]	1.00	0.53 [-1.41 – 2.39]	1.01			-47971.47
	15000	L	1.28 [1.25 – 1.32]	1.02	1.03 [0.35 – 1.73]	1.01	-0.60 [-2.67 – 1.40]	1.01			-45984.53
	15000	Q	1.28 [1.25 – 1.32]	1.02	1.01 [0.30 – 1.71]	0.98	-0.09 [-2.72 – 2.57]	0.99	-1.15 [-4.58 – 2.29]	1.00	-45806.55
	10000	L	1.29 [1.25 – 1.32]	0.99	1.37 [0.74 – 1.94]	0.99	-1.70 [-3.40 – 0.20]	0.99			-43162.38
	1000	Q	1.28 [1.25 – 1.32]	1.02	1.40 [0.87 – 1.89]	1.00	-2.04 [-4.62 – 0.70]	0.98	-1.75 [-5.52 – 1.72]	0.97	-43094.07
	1000	L	1.29 [1.25 – 1.32]	1.03	1.42 [0.89 – 1.92]	1.03	-2.79 [-4.88 – -0.44]	1.02			-43080.22
	3000	L	1.28 [1.25 – 1.32]	0.98	1.43 [0.90 – 1.91]	0.98	-2.47 [-4.24 – -0.41]	0.98			-42625.53
	10000	Q	1.29 [1.25 – 1.32]	0.99	1.29 [0.67 – 1.86]	1.02	-0.41 [-2.99 – 2.16]	1.02	-2.19 [-5.46 – 1.14]	1.01	-42567.35
	6400	L	1.29 [1.25 – 1.32]	1.00	1.39 [0.82 – 1.91]	0.98	-2.01 [-3.71 – -0.11]	1.00			-42430.71
	3000	Q	1.28 [1.25 – 1.32]	0.99	1.38 [0.84 – 1.86]	1.00	-1.41 [-3.88 – 1.19]	1.00	-2.15 [-5.56 – 1.29]	1.02	-42146.84
	6400	Q	1.29 [1.25 – 1.32]	0.99	1.31 [0.76 – 1.83]	1.02	-0.71 [-3.27 – 1.84]	1.02	-2.30 [-5.67 – 1.05]	1.03	-42114.70
SL	1000	L	1.28 [1.25 – 1.32]	0.99	1.09 [-0.09 – 2.41]	0.99	-0.66 [-4.06 – 2.39]	0.99			-46379.82
	3000	L	1.28 [1.25 – 1.32]	0.99	1.14 [-0.03 – 2.43]	1.03	-0.76 [-3.99 – 2.12]	1.03			-46320.98
	1000	Q	1.29 [1.25 – 1.32]	0.98	1.23 [0.03 – 2.56]	1.02	-0.24 [-3.56 – 2.91]	1.02	-1.88 [-5.53 – 1.91]	1.00	-45808.29
	6400	L	1.29 [1.25 – 1.32]	1.00	1.33 [0.31 – 2.47]	1.01	-1.20 [-3.97 – 1.29]	1.02			-45273.00
	3000	Q	1.28 [1.25 – 1.32]	1.00	1.36 [0.13 – 2.70]	1.01	-0.28 [-3.58 – 2.87]	0.99	-2.41 [-6.05 – 1.41]	1.01	-44818.08
	10000	L	1.29 [1.25 – 1.32]	1.00	1.52 [0.56 – 2.51]	1.02	-1.62 [-3.88 – 0.60]	1.02			-44038.62
	6400	Q	1.28 [1.25 – 1.32]	1.01	1.44 [0.36 – 2.56]	0.99	-0.38 [-3.40 – 2.64]	1.01	-2.30 [-5.83 – 1.29]	1.01	-44025.28
	10000	Q	1.28 [1.25 – 1.32]	1.00	1.49 [0.52 – 2.46]	0.97	-0.48 [-3.34 – 2.36]	0.97	-2.08 [-5.45 – 1.31]	1.01	-43004.19
	15000	L	1.29 [1.25 – 1.32]	0.99	1.86 [0.98 – 2.72]	1.00	-2.37 [-4.32 – -0.41]	1.00			-41625.76
	15000	Q	1.29 [1.25 – 1.32]	1.00	1.73 [0.86 – 2.61]	1.01	-0.94 [-3.79 – 1.87]	1.02	-2.24 [-5.58 – 1.11]	1.03	-41174.02
	20000	L	1.28 [1.25 – 1.32]	1.00	1.96 [1.17 – 2.77]	1.00	-2.53 [-4.29 – -0.82]	0.99			-40469.89
	20000	Q	1.29 [1.25 – 1.32]	0.98	1.82 [1.03 – 2.62]	1.01	-1.03 [-3.78 – 1.67]	1.01	-2.22 [-5.40 – 1.02]	1.02	-40316.94
CTI	20000	Q	1.29 [1.25 – 1.32]	1.01	0.52 [-0.55 – 1.59]	1.02	0.48 [-2.49 – 3.51]	1.02	0.02 [-2.39 – 2.48]	1.03	-47373.86
	15000	L	1.29 [1.25 – 1.32]	1.00	0.50 [-0.42 – 1.37]	1.02	0.61 [-0.95 – 2.28]	1.02			-47302.12
	20000	L	1.29 [1.25 – 1.32]	1.01	0.57 [-0.37 – 1.44]	1.03	0.46 [-1.00 – 2.04]	1.03			-47282.16
	15000	Q	1.29 [1.25 – 1.32]	1.01	0.47 [-0.55 – 1.52]	1.02	0.58 [-2.39 – 3.53]	1.02	0.13 [-2.38 – 2.77]	1.03	-47109.06

			τ		Intercept		β		β^2		
Cov.	MW	Form	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	Mean [80% CI]	GR	DIC
	10000	L	1.29 [1.25 – 1.32]	1.00	0.39 [-0.53 – 1.24]	0.99	0.92 [-0.81 – 2.89]	0.99			-46820.24
	6400	L	1.29 [1.25 – 1.32]	0.99	0.27 [-0.70 – 1.15]	1.00	1.27 [-0.64 – 3.42]	1.00			-46801.35
	10000	Q	1.28 [1.25 – 1.32]	0.99	0.38 [-0.59 – 1.33]	0.97	0.85 [-2.07 – 3.79]	0.96	0.25 [-2.61 – 3.17]	0.95	-46529.41
	1000	L	1.28 [1.25 – 1.32]	0.97	0.40 [-0.39 – 1.17]	0.99	1.87 [-1.27 – 5.12]	0.99			-46338.69
	6400	Q	1.29 [1.25 – 1.32]	0.99	0.26 [-0.74 – 1.22]	0.98	1.04 [-1.86 – 3.95]	1.00	0.50 [-2.42 – 3.64]	1.03	-46317.58
	1000	Q	1.28 [1.25 – 1.32]	0.99	0.36 [-0.43 – 1.13]	0.97	1.77 [-1.55 – 5.13]	0.97	1.03 [-2.79 – 4.90]	0.98	-46049.87
	3000	L	1.29 [1.25 – 1.32]	0.98	0.13 [-0.84 – 1.03]	1.00	1.77 [-0.43 – 4.30]	1.01			-45850.82
	3000	Q	1.29 [1.26 – 1.32]	0.98	0.15 [-0.84 – 1.09]	0.98	1.30 [-1.72 – 4.29]	0.99	1.10 [-2.13 – 4.51]	1.03	-45479.26
S	20000	L	1.29 [1.25 – 1.32]	1.00	0.80 [0.21 – 1.38]	1.03	0.16 [-1.91 – 2.17]	1.02			-47248.54
	20000	Q	1.28 [1.25 – 1.32]	1.01	0.81 [0.22 – 1.40]	0.97	-0.05 [-2.44 – 2.32]	0.98	0.53 [-3.14 – 4.08]	1.00	-47245.97
	1000	L	1.29 [1.25 – 1.32]	0.99	0.90 [0.28 – 1.55]	1.01	-0.31 [-3.20 – 2.48]	1.01			-47219.03
	15000	Q	1.29 [1.25 – 1.32]	1.00	0.85 [0.25 – 1.46]	1.03	-0.14 [-2.55 – 2.25]	1.01	0.21 [-3.26 – 3.72]	0.99	-47186.32
	15000	L	1.29 [1.25 – 1.32]	1.01	0.86 [0.24 – 1.46]	0.99	-0.07 [-2.09 – 1.90]	0.99			-47172.76
	10000	L	1.29 [1.25 – 1.32]	0.97	0.91 [0.31 – 1.54]	1.01	-0.27 [-2.31 – 1.68]	1.00			-46929.89
	1000	Q	1.29 [1.25 – 1.32]	1.00	0.90 [0.29 – 1.55]	0.98	-0.36 [-3.30 – 2.46]	0.98	0.12 [-3.76 – 3.93]	0.98	-46902.53
	10000	Q	1.29 [1.25 – 1.32]	1.01	0.92 [0.31 – 1.55]	0.98	-0.28 [-2.77 – 2.09]	0.98	0.05 [-3.43 – 3.62]	0.98	-46882.88
	6400	L	1.28 [1.25 – 1.32]	1.02	0.99 [0.36 – 1.63]	1.03	-0.60 [-2.94 – 1.72]	1.02			-46712.93
	6400	Q	1.28 [1.25 – 1.32]	0.99	0.98 [0.34 – 1.63]	1.01	-0.53 [-3.13 – 2.06]	1.02	-0.02 [-3.77 – 3.60]	0.99	-46662.63
	3000	Q	1.29 [1.25 – 1.32]	0.98	1.01 [0.39 – 1.67]	1.00	-0.72 [-3.47 – 2.02]	1.00	-0.14 [-3.91 – 3.60]	0.99	-46578.46
	3000	L	1.28 [1.25 – 1.32]	1.01	1.01 [0.39 – 1.65]	0.99	-0.72 [-3.27 – 1.77]	0.98			-46382.21

APPENDIX XII

Table S12.1. Deviance information criterion (DIC) and ranking, deviance (Dbar), and penalty for increased complexity (Dhat) for all multivariable genetic connectivity models for the range-wide extent of Gunnison sage-grouse. See Table 3.1 in main text for the variable names corresponding to abbreviations.

Model	DIC	ΔDIC	Dbar	Dhat
Anthropogenic Change				
int + DOG + DLD + DAG + DP	-48476.15	0.00	11200.22	59676.38
int + DD + DAG	-48411.41	64.74	11200.49	59611.90
int + D12 + DAG	-48296.20	179.96	11200.39	59496.59
int + DOG + DLD + DAG	-48291.40	184.75	11200.14	59491.54
int + DOG + DAG + DP	-48290.14	186.01	11200.37	59490.51
int + DD + D12 + DOG + DAG + DP	-48260.18	215.97	11200.57	59460.75
int + DD + D12 + DAG + DP	-48248.60	227.55	11200.43	59449.04
int + D12 + DOG + DAG + DP	-48226.58	249.58	11200.40	59426.98
int + DD + DOG	-48209.90	266.28	15529.24	63739.14
int + DLD + DAG	-48189.18	286.98	11199.46	59388.63
int + D12 + DOG + DLD + DAG + DP	-48171.81	304.34	11200.01	59371.82
int + D12 + DLD + DAG	-48135.99	340.16	11199.41	59335.40
int + D12 + DOG + DAG	-48111.92	364.23	11200.33	59312.26
int + DOG + DAG	-48109.59	366.56	11200.45	59310.04
int + DD + D12 + DAG	-48086.79	389.37	11200.48	59287.26
int + D12 + DAG + DP	-48064.50	411.65	11200.34	59264.85
int + DD + DOG + DAG + DP	-48061.35	414.81	11200.47	59261.82
int + DD + DAG + DP	-48051.76	424.39	11200.50	59252.26
int + DD + DLD + DAG + DP	-47936.27	539.89	11200.54	59136.81
int + D12 + DOG + DLD + DAG	-47935.68	540.47	11200.09	59135.77
int + DD + D12 + DOG + DAG	-47930.03	546.12	11200.44	59130.47
int + DD + DOG + DAG	-47903.28	572.87	11200.55	59103.83

Model	DIC	ΔDIC	Dbar	Dhat
int + DD + D12 + DLD + DAG + DP	-47861.92	614.23	11199.36	59061.28
int + DD + DOG + DLD + DAG + DP	-47807.45	668.71	11200.11	59007.56
int + DD + D12 + DOG + DLD + DAG	-47771.66	704.50	11200.09	58971.75
int + DAG + DP	-47767.84	708.32	11200.44	58968.28
int + DD + DOG + DLD + DAG	-47734.24	741.91	11200.24	58934.48
int + DOG + DLD	-47689.48	786.68	11200.30	58889.77
int + DD + DLD + DAG	-47688.48	787.68	11199.38	58887.86
int + DD + D12 + DOG + DLD + DAG + DP	-47663.70	812.45	11200.03	58863.72
int + D12 + DOG + DLD	-47659.34	816.81	11200.20	58859.54
int + DOG + DLD + DP	-47649.43	826.72	11200.26	58849.69
int + D12 + DLD + DAG + DP	-47646.30	829.85	11200.51	58846.81
int + DLD + DP	-47635.15	841.01	11199.74	58834.88
int + D12 + DLD	-47567.41	908.75	11199.71	58767.11
int + DD + D12 + DLD + DP	-47552.89	923.26	11201.24	58754.14
int + D12 + DOG + DLD + DP	-47549.69	926.47	11200.18	58749.87
int + DD + DLD	-47496.08	980.08	11199.80	58695.87
int + DD + D12 + DLD + DAG	-47457.80	1018.35	11199.50	58657.30
int + DOG + DP	-47436.30	1039.85	11200.85	58637.15
int + DD + D12 + DOG + DLD	-47406.92	1069.23	11200.30	58607.23
int + DD + D12 + DOG	-47396.11	1080.05	11201.10	58597.20
int + DD + DOG + DP	-47360.14	1116.01	11201.10	58561.24
int + D12 + DLD + DP	-47359.97	1116.19	11199.76	58559.72
int + DD + DLD + DP	-47309.23	1166.92	11199.81	58509.04
int + DD + D12 + DOG + DLD + DP	-47307.68	1168.47	11200.22	58507.90
int + DD + D12 + DLD	-47277.23	1198.92	11199.62	58476.86
int + DD + D12 + DP	-47212.98	1263.17	11201.01	58413.99
int + D12 + DOG	-47212.91	1263.25	11200.95	58413.86
int + DD + D12	-47196.88	1279.28	11201.06	58397.94

Model	DIC	ΔDIC	Dbar	Dhat
int + DD + DAG + D14 + DP	-47174.32	1301.83	11199.61	58373.93
int + D12 + DOG + DAG + D14	-47154.15	1322.00	11199.62	58353.77
int + DD + DP	-47092.22	1383.93	11201.10	58293.32
int + DD + DOG + DLD + DP	-47054.81	1421.34	11200.23	58255.05
int + DAG + D14 + DP	-47052.37	1423.78	11199.64	58252.02
int + DD + D12 + DOG + DAG + D14	-47047.21	1428.94	11199.55	58246.76
int + DOG + DAG + D14 + DP	-47041.11	1435.04	11199.56	58240.67
int + D12 + DP	-47020.93	1455.22	11200.84	58221.78
int + DOG + DP	-46989.32	1486.84	11200.93	58190.24
int + D12 + DOG + DAG + D14 + DP	-46978.78	1497.37	11199.96	58178.74
int + D12 + DAG + D14 + DP	-46942.00	1534.15	11199.75	58141.75
int + D12 + DLD + DAG + D14	-46910.04	1566.11	11198.79	58108.83
int + DLD + DAG + D14	-46905.99	1570.17	11198.92	58104.90
int + DLD + DAG + D14 + DP	-46893.21	1582.95	11198.62	58091.83
int + DD + DOG + DAG + D14 + DP	-46847.86	1628.29	11200.04	58047.90
int + DD + DOG + DLD + DAG + D14 + DP	-46845.00	1631.15	11199.59	58044.59
int + DD + D12 + DOG + DP	-46791.03	1685.12	11201.02	57992.05
int + D12 + DOG + DLD + DAG + D14 + DP	-46788.60	1687.55	11199.60	57988.20
int + DD + DOG + DAG + D14	-46750.38	1725.77	11199.69	57950.06
int + DOG + DAG + D14	-46743.52	1732.64	11199.60	57943.12
int + DD + D12 + DAG + D14 + DP	-46710.47	1765.68	11199.65	57910.12
int + DD + DLD + DAG + D14 + DP	-46701.57	1774.58	11198.70	57900.28
int + DD + D12 + DLD + DAG + D14 + DP	-46698.19	1777.96	11198.91	57897.10
int + DOG + DLD + DAG + D14	-46692.76	1783.39	11199.40	57892.16
int + DD + D12 + DOG + DAG + D14 + DP	-46660.20	1815.95	11200.02	57860.22
int + DOG + DLD + DAG + D14 + DP	-46628.76	1847.39	11199.46	57828.22
int + DD + D12 + DAG + D14	-46608.14	1868.01	11199.65	57807.79
int + D12 + DOG + DLD + DAG + D14	-46583.71	1892.44	11199.49	57783.21

Model	DIC	ΔDIC	Dbar	Dhat
int + DD + D12 + DOG + DLD + DAG + D14	-46553.94	1922.21	11199.23	57753.18
int + D12 + DLD + DAG + D14 + DP	-46527.15	1949.00	11198.56	57725.72
int + DD + DLD + DAG + D14	-46499.01	1977.15	11198.74	57697.74
int + DD + D12 + DLD + DAG + D14	-46491.94	1984.21	11198.78	57690.72
int + DD + DOG + DLD + DAG + D14	-46483.94	1992.22	11199.38	57683.32
int + DLD + D14 + DP	-46439.99	2036.16	11198.83	57638.83
int + DD + D12 + DOG + DLD + DAG + D14 + DP	-46392.01	2084.14	11199.60	57591.61
int + DD + D12 + DLD + D14	-46387.93	2088.23	11200.42	57588.34
int + D12 + DLD + D14 + DP	-46339.66	2136.49	11198.81	57538.47
int + D12 + DOG + DLD + D14	-46319.38	2156.78	11199.62	57519.00
int + D12 + DLD + D14	-46278.05	2198.11	11198.89	57476.94
int + DOG + DLD + D14 + DP	-46259.09	2217.07	11199.82	57458.90
int + D12 + DOG + DLD + D14 + DP	-46248.80	2227.36	11199.58	57448.38
int + DOG + DLD + D14	-46227.37	2248.79	11199.58	57426.95
int + DLD + D14	-46211.02	2265.14	11198.90	57409.91
int + DD + D12 + DOG + DLD + D14	-46167.63	2308.52	11199.64	57367.27
int + DOG + D14 + DP	-46020.39	2455.76	11200.16	57220.55
int + DD + DOG + DLD + D14	-45969.50	2506.66	11199.58	57169.08
int + DD + D14 + DP	-45904.25	2571.90	11200.34	57104.59
int + DD + D12 + D14	-45886.49	2589.67	11200.36	57086.85
int + D12 + DOG + D14	-45846.62	2629.54	11200.25	57046.87
int + DD + DLD + D14 + DP	-45838.17	2637.98	11198.99	57037.17
int + DD + D12 + D14 + DP	-45836.36	2639.79	11200.34	57036.70
int + D12 + DOG + D14 + DP	-45828.17	2647.99	11200.21	57028.38
int + D14 + DP	-45816.18	2659.98	11200.23	57016.41
int + DD + DOG + DLD + D14 + DP	-45774.05	2702.10	11199.83	56973.88
int + DD + DOG + D14 + DP	-45766.87	2709.28	11200.41	56967.28
int + DD + D12 + DOG + D14 + DP	-45763.96	2712.19	11200.31	56964.27

Model	DIC	ΔDIC	Dbar	Dhat
int + DD + D12 + DOG + D14	-45733.36	2742.80	11200.24	56933.59
int + DD + D14	-45689.72	2786.43	11200.34	56890.06
int + D12 + D14	-45676.72	2799.43	11200.15	56876.87
int + DD + D12 + DOG + DLD + D14 + DP	-45674.63	2801.52	11199.70	56874.33
int + DOG + D14	-45647.60	2828.56	11200.23	56847.82
int + DD + D12 + DLD + D14 + DP	-45545.58	2930.57	11198.87	56744.46
int + DLD + DAG + DP	-44760.21	3715.94	15527.85	60288.06
int + DD + DAG + D14	-42638.13	6108.02	15526.13	57894.85
int + DD + DOG + DLD	-41938.21	6537.85	15529.33	57467.54
int + DD + DLD + D14	-39704.85	8771.30	15527.67	55232.52
int + DID + DIA	-47300.88	0.00	11201.59	58502.47
int + DID + DI12 + DIA	-47125.57	175.31	11200.59	58326.16
int + DID + DI12	-46939.38	361.50	11200.76	58140.13
int + DI12 + DIA	-46376.99	923.88	11200.40	57577.40
int + DID + DIP	-45213.99	2086.89	11199.63	56413.61
int + DIP + DIA	-45155.67	2145.21	11199.13	56354.80
int + DID + DIP + DIA	-45092.22	2208.66	11199.54	56291.76
int + DID + DIP + DI12	-44779.55	2521.33	11199.14	55978.69
int + DIP + DI12	-44756.64	2544.23	11198.69	55955.33
int + DID + DIP + DI12 + DIA	-44720.53	2580.34	11198.83	55919.36
int + DID + DIOG + DIA	-44694.62	2606.26	11197.42	55892.04
int + DIP + DI12 + DIA	-44684.70	2616.17	11198.67	55883.37
int + DID + DIOG + DI12 + DIA	-44578.42	2722.46	11197.15	55775.57
int + DID + DIOG + DI12	-44557.07	2743.81	11197.09	55754.16
int + DIOG + DI12	-44507.23	2793.65	11196.74	55703.96
int + DIOG + DIA	-44477.74	2823.13	11197.00	55674.75
int + DID + DIOG	-44467.02	2833.86	11197.49	55664.51
int + DID + DIP + DIOG + DIA	-44364.21	2936.67	11197.32	55561.53

Model	DIC	ΔDIC	Dbar	Dhat
int + DID + DIP + DIOG + DI12	-44320.68	2980.20	11197.09	55517.76
int + DID + DIP + DIOG	-44309.27	2991.60	11197.37	55506.65
int + DIOG + DI12 + DIA	-44306.02	2994.85	11196.75	55502.77
int + DIP + DIOG + DIA	-44179.92	3120.95	11196.98	55376.90
int + DIP + DIOG	-43979.52	3321.35	11196.98	55176.50
int + DID + DIP + DIOG + DI12 + DIA	-43946.98	3353.90	11197.05	55144.03
int + DIP + DIOG + DI12 + DIA	-43684.05	3616.83	11196.66	54880.71
int + DIP + DIOG + DI12	-42663.92	4636.95	11196.56	53860.49
Temperature-moisture Regime				
int +DRI + MAR	-48018.45		11200.88	58907.38
Phenology				
int + BDR + SL	-48008.10	0.00	11201.44	59209.54
int + BDR + GU + SL	-47751.27	256.84	11201.39	58952.65
int + BDR + GU + SL	-47580.10	428.00	11201.15	58781.25
int + GU + SL	-45508.37	2499.73	11200.48	56708.85
Terrain Morphology				
int + CTI	-47373.86		11201.80	58575.67
Habitat Composition and Configuration				
int + AS + CON	-47925.83	0.00	11200.65	59126.48
int + AS + CON + CC	-47879.54	46.29	11200.57	59080.11
int + AS + CON + CC + SBHT	-47817.64	108.19	11199.44	59017.08
int + AS + CC	-47738.32	187.51	11200.03	58938.35
int + AS + CON + SBHT	-47653.68	272.15	11199.39	58853.06
int + AS + CC + SBHT	-47583.07	342.75	11199.05	58782.12
int + AS + SBHT	-47517.54	408.29	11199.09	58716.63
int + CON + CC + SBHT	-47186.27	739.56	11199.84	58386.10
int + AS + LS + CON + CC	-47172.30	753.52	11200.07	58372.38
int + CON + SBHT	-47167.01	758.82	11199.92	58366.93

Model	DIC	ΔDIC	Dbar	Dhat
int + CC + SBHT	-47156.29	769.54	11199.13	58355.42
int + AS + LS + CON	-46997.28	928.55	11200.14	58197.41
int + AS + LS	-46947.23	978.60	11199.63	58146.87
int + AS + LS + CC	-46803.53	1122.30	11199.75	58003.28
int + LS + CC	-46783.10	1142.72	11201.45	57984.56
int + AS + LS + CON + SBHT	-46539.80	1386.03	11198.39	57738.19
int + LS + CON + CC	-46519.48	1406.34	11202.25	57721.73
int + AS + LS + CON + CC + SBHT	-46478.15	1447.68	11198.42	57676.57
int + CON + CC	-46373.36	1552.46	11201.63	57575.00
int + LS + CON	-46263.85	1661.98	11202.37	57466.22
int + AS + LS + CC + SBHT	-46075.27	1850.56	11198.25	57273.52
int + LS + CON + SBHT	-46026.00	1899.83	11199.11	57225.11
int + AS + LS + SBHT	-46022.02	1903.81	11198.26	57220.28
int + LS + CC + SBHT	-45864.73	2061.10	11198.46	57063.19
int + LS + SBHT	-45837.67	2088.16	11198.34	57036.01
int + LS + CON + CC + SBHT	-45687.45	2238.38	11198.87	56886.32

APPENDIX XIII

Table S13.1. Deviance information criterion (DIC) ranking, deviance (Dbar), and penalty for increased complexity (Dhat) for all multiple hypothesis genetic connectivity models for the range-wide extent of Gunnison sage-grouse. See Table 3.1 in main text for the variable names corresponding to abbreviations.

Model	DIC	ΔDIC	Dbar	Dhat
int + AS + BDR + CTI	-49265.71	0.00	11443.67	60709.39
int + DIA + DID + AS + BDR + CTI	-48799.38	466.34	11199.96	59999.34
int + AS + CTI	-48727.23	538.48	11200.98	59928.21
int + DIA + DID + CTI	-48700.89	564.82	11200.27	59901.17
int + DAG + DP + DLD + DOG + AS + BDR + CTI	-48538.68	727.04	11200.39	59739.06
int + DIA + DID + AS + CTI	-48341.79	923.92	11443.98	59785.77
int + DAG + DP + DLD + DOG + AS + CTI	-48309.58	956.13	11444.44	59754.03
int + DIA + DID + AS + BDR	-48306.38	959.33	11443.23	59749.61
int + DIA + DID + AS	-48239.13	1026.58	11200.20	59439.33
int + AS + BDR	-47990.13	1275.58	11200.74	59190.87
int + DAG + DP + DLD + DOG + AS + BDR	-47934.97	1330.75	11444.02	59378.99
int + DAG + DP + DLD + DOG + BDR	-47891.55	1374.16	11444.47	59336.02
int + DAG + DP + DLD + DOG + BDR + CTI	-47810.90	1454.82	11444.10	59255.00
int + DAG + DP + DLD + DOG + AS	-47810.33	1455.38	11443.49	59253.82
int + BDR + CTI	-47748.10	1517.61	11202.27	58950.37
int + DIA + DID + BDR + CTI	-47720.04	1545.68	11444.28	59164.32
int + DAG + DP + DLD + DOG + CTI	-47565.11	1700.60	11444.65	59009.76
int + DAG + DP + DLD + DOG + DIA + DID + AS + BDR + CTI	-47544.23	1721.48	11199.95	58744.18
int + DIA + DID + BDR	-47332.76	1932.95	11200.79	58533.56
int + DAG + DP + DLD + DOG + DIA + DID + AS + CTI	-47323.73	1941.98	11200.73	58524.46
int + DAG + DP + DLD + DOG + DIA + DID + AS + BDR	-47241.76	2023.96	11200.06	58441.81
int + DAG + DP + DLD + DOG + DIA + DID + CTI	-47217.24	2048.48	11201.16	58418.40
int + DAG + DP + DLD + DOG + DIA + DID + BDR + CTI	-47127.48	2138.24	11200.10	58327.58
int + DAG + DP + DLD + DOG + DIA + DID + BDR	-47006.76	2258.96	11443.78	58450.54
int + DAG + DP + DLD + DOG + DIA + DID + AS	-46967.06	2298.66	11443.70	58410.75
int + DAG + DP + DLD + DOG + DIA + DID	-46878.70	2387.01	11443.53	58322.24

APPENDIX XIV

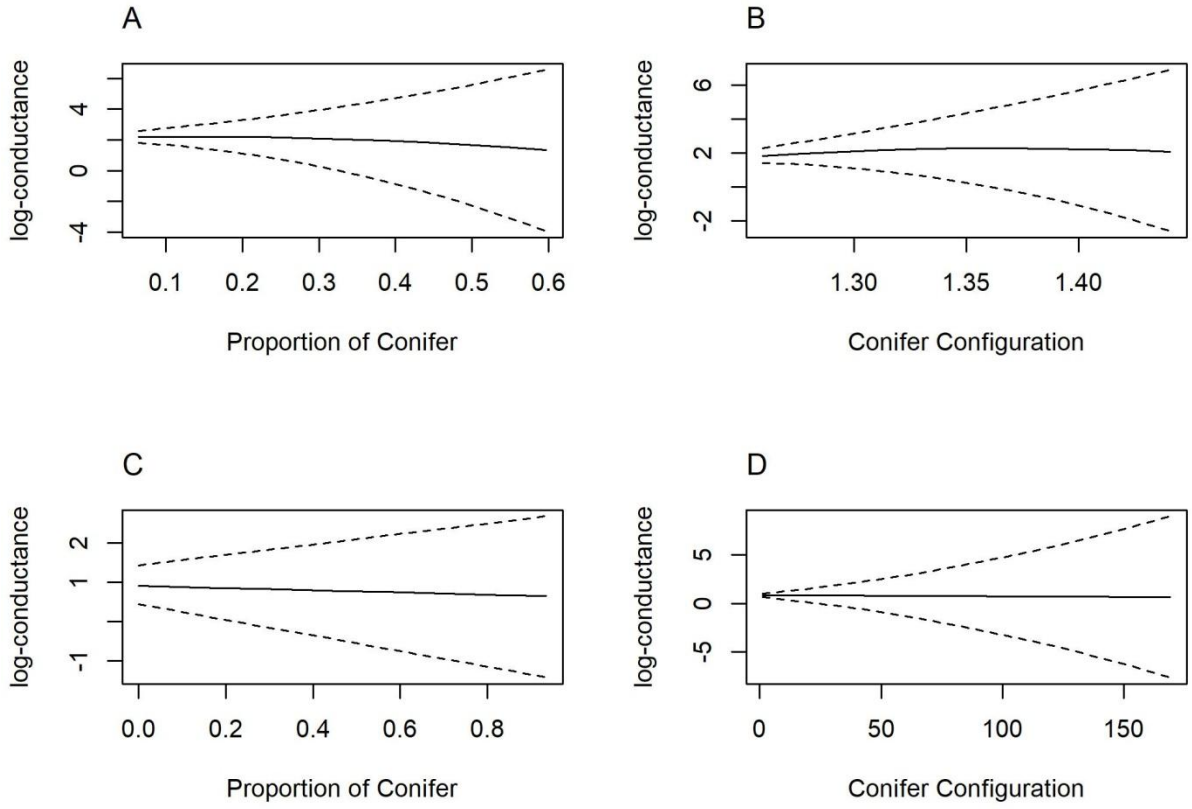

Figure S14.1.Univariable functional response for landscape genetic connectivity models for Gunnison sage-grouse including conifer cover (A), and conifer configuration (B) in the Gunnison Basin and conifer cover (C) and conifer configuration (D) range-wide.

APPENDIX XV

Table S15.1. F_{ST} (Weir and Cockerharm 1984) values for all lek comparisons. Upper and lower bounds for 95% confidence intervals are in the last two columns.

Lek Comparison	F_{ST}	lower	upper
Almont, vs. Antelope North Blinberry Gulch,	0.07	0.02	0.11
Almont, vs. Big Mesa,	0.09	0.04	0.15
Almont, vs. Campbell,	0.12	0.04	0.21
Almont, vs. Chance Gulch,	0.09	0.05	0.13
Almont, vs. Chance Gulch E,	0.10	0.05	0.16
Almont, vs. Flat Top Section 31,	0.08	0.03	0.12
Almont, vs. Hartman Gulch,	0.09	0.04	0.14
Almont, vs. Henkel Road,	0.07	0.02	0.13
Almont, vs. Kezar Basin North,	0.11	0.05	0.17
Almont, vs. Lost Canyon 2,	0.10	-0.02	0.22
Almont, vs. 7MB Lek,	0.10	0.06	0.15
Almont, vs. 7MB Eagle,	0.08	0.02	0.15
Almont, vs. 7MB Hupp,	0.08	0.01	0.16
Almont, vs. McCabe's Lane,	0.04	-0.07	0.16
Almont, vs. Miller Ranch,	0.08	0.03	0.13
Almont, vs. Razor Creek,	0.10	0.03	0.18
Almont, vs. Razor Creek Divide,	0.13	0.03	0.24
Almont, vs. Razor Dome 1 & 2,	0.09	0.04	0.14
Almont, vs. Ridgeline,	0.14	0.03	0.24
Almont, vs. Sapinero Corral,	0.10	0.00	0.19
Almont, vs. South Beaver Creek,	0.10	0.05	0.16
Almont, vs. Sugar Creek,	0.09	0.05	0.14
Almont, vs. Sewell Gulch,	0.13	0.04	0.22
Almont, vs. Signal Peak,	0.07	0.00	0.15
Almont, vs. South 6 Mile Meadow,	0.14	0.05	0.24
Almont, vs. Sapinero 10 Mile Spring,	0.12	0.05	0.18
Almont, vs. South 6 Mile Ridge,	0.14	0.07	0.21
Almont, vs. South Parlin 1,	0.08	0.04	0.13
Almont, vs. South Parlin 3,	0.11	0.05	0.17
Almont, vs. Sapinero Powerline,	0.11	0.06	0.16
Almont, vs. South Parlin Upper,	0.07	0.03	0.11
Almont, vs. Signal Peak West,	0.08	0.03	0.13
Almont, vs. Sapinero Ridge,	0.10	0.03	0.19
Almont, vs. Sapinero South,	0.11	0.06	0.18
Almont, vs. Scout,	0.16	0.10	0.21
Almont, vs. Steven's Creek East,	0.08	-0.04	0.18
Almont, vs. Taila's Lek,	0.10	0.03	0.18

Lek Comparison	F_{ST}	lower	upper
Almont, vs. Teachout 1 & 2,	0.09	0.04	0.15
Almont, vs. Teachout 3,5,6,	0.11	0.06	0.16
Almont, vs. Vito,	0.11	0.06	0.17
Almont, vs. Wood's Gulch,	0.15	0.09	0.21
Almont, vs. Waunita,	0.11	0.05	0.18
Almont, vs. Waunita NW,	0.17	0.11	0.24
Antelope North Blinberry Gulch, vs. Big Mesa,	0.01	-0.01	0.03
Antelope North Blinberry Gulch, vs. Campbell,	0.04	0.00	0.07
Antelope North Blinberry Gulch, vs. Chance Gulch,	0.02	0.00	0.03
Antelope North Blinberry Gulch, vs. Chance Gulch E,	0.00	-0.01	0.02
Antelope North Blinberry Gulch, vs. Flat Top Section 31,	0.00	-0.02	0.02
Antelope North Blinberry Gulch, vs. Hartman Gulch,	0.01	-0.01	0.03
Antelope North Blinberry Gulch, vs. Henkel Road,	0.02	0.01	0.04
Antelope North Blinberry Gulch, vs. Kezar Basin North,	0.02	0.00	0.05
Antelope North Blinberry Gulch, vs. Lost Canyon 2,	0.00	-0.06	0.06
Antelope North Blinberry Gulch, vs. 7MB Lek,	0.02	-0.01	0.05
Antelope North Blinberry Gulch, vs. 7MB Eagle,	-0.02	-0.06	0.03
Antelope North Blinberry Gulch, vs. 7MB Hupp,	0.00	-0.03	0.04
Antelope North Blinberry Gulch, vs. McCabe's Lane,	-0.02	-0.09	0.05
Antelope North Blinberry Gulch, vs. Miller Ranch,	0.01	-0.01	0.04
Antelope North Blinberry Gulch, vs. Razor Creek,	0.02	-0.01	0.06
Antelope North Blinberry Gulch, vs. Razor Creek Divide,	-0.04	-0.09	0.01
Antelope North Blinberry Gulch, vs. Razor Dome 1 & 2,	0.03	0.01	0.05
Antelope North Blinberry Gulch, vs. Ridgeline,	0.05	-0.01	0.12
Antelope North Blinberry Gulch, vs. Sapinero Corral,	0.02	-0.02	0.06
Antelope North Blinberry Gulch, vs. South Beaver Creek,	0.03	0.00	0.05
Antelope North Blinberry Gulch, vs. Sugar Creek,	0.02	-0.01	0.03
Antelope North Blinberry Gulch, vs. Sewell Gulch,	0.04	-0.03	0.12
Antelope North Blinberry Gulch, vs. Signal Peak,	0.01	-0.02	0.04
Antelope North Blinberry Gulch, vs. South 6 Mile Meadow,	0.09	0.03	0.16
Antelope North Blinberry Gulch, vs. Sapinero 10 Mile Spring,	0.03	0.01	0.06
Antelope North Blinberry Gulch, vs. South 6 Mile Ridge,	0.09	0.05	0.13
Antelope North Blinberry Gulch, vs. South Parlin 1,	0.02	0.00	0.04
Antelope North Blinberry Gulch, vs. South Parlin 3,	0.01	-0.01	0.04
Antelope North Blinberry Gulch, vs. Sapinero Powerline,	0.05	0.02	0.08
Antelope North Blinberry Gulch, vs. South Parlin Upper,	0.01	0.00	0.02
Antelope North Blinberry Gulch, vs. Signal Peak West,	0.03	0.00	0.06
Antelope North Blinberry Gulch, vs. Sapinero Ridge,	0.03	-0.01	0.10
Antelope North Blinberry Gulch, vs. Sapinero South,	0.02	0.00	0.05
Antelope North Blinberry Gulch, vs. Scout,	0.06	0.04	0.09
Antelope North Blinberry Gulch, vs. Steven's Creek East,	0.04	-0.03	0.12
Antelope North Blinberry Gulch, vs. Taila's Lek,	0.02	-0.01	0.05

Lek Comparison	F_{ST}	lower	upper
Antelope North Blinberry Gulch, vs. Teachout 1 & 2,	0.00	-0.02	0.02
Antelope North Blinberry Gulch, vs. Teachout 3,5,6,	0.04	0.01	0.07
Antelope North Blinberry Gulch, vs. Vito,	0.05	0.02	0.09
Antelope North Blinberry Gulch, vs. Wood's Gulch,	0.05	0.02	0.09
Antelope North Blinberry Gulch, vs. Waunita,	0.08	0.03	0.14
Antelope North Blinberry Gulch, vs. Waunita NW,	0.10	0.03	0.17
Big Mesa, vs. Campbell,	0.00	-0.04	0.03
Big Mesa, vs. Chance Gulch,	0.04	0.00	0.08
Big Mesa, vs. Chance Gulch E,	0.03	-0.01	0.07
Big Mesa, vs. Flat Top Section 31,	-0.01	-0.04	0.03
Big Mesa, vs. Hartman Gulch,	0.01	0.00	0.03
Big Mesa, vs. Henkel Road,	0.03	-0.01	0.08
Big Mesa, vs. Kezar Basin North,	0.02	-0.01	0.05
Big Mesa, vs. Lost Canyon 2,	-0.02	-0.10	0.06
Big Mesa, vs. 7MB Lek,	0.02	-0.01	0.06
Big Mesa, vs. 7MB Eagle,	-0.02	-0.06	0.02
Big Mesa, vs. 7MB Hupp,	0.01	-0.03	0.06
Big Mesa, vs. McCabe's Lane,	-0.01	-0.07	0.06
Big Mesa, vs. Miller Ranch,	0.02	-0.01	0.05
Big Mesa, vs. Razor Creek,	0.03	-0.02	0.08
Big Mesa, vs. Razor Creek Divide,	-0.03	-0.11	0.05
Big Mesa, vs. Razor Dome 1 & 2,	0.02	0.00	0.05
Big Mesa, vs. Ridgeline,	0.03	-0.03	0.08
Big Mesa, vs. Sapinero Corral,	0.00	-0.06	0.06
Big Mesa, vs. South Beaver Creek,	0.01	-0.01	0.04
Big Mesa, vs. Sugar Creek,	0.02	-0.01	0.04
Big Mesa, vs. Sewell Gulch,	0.02	-0.08	0.11
Big Mesa, vs. Signal Peak,	-0.02	-0.07	0.03
Big Mesa, vs. South 6 Mile Meadow,	0.03	-0.02	0.10
Big Mesa, vs. Sapinero 10 Mile Spring,	0.00	-0.01	0.02
Big Mesa, vs. South 6 Mile Ridge,	0.05	0.00	0.10
Big Mesa, vs. South Parlin 1,	0.04	0.00	0.08
Big Mesa, vs. South Parlin 3,	0.04	0.00	0.09
Big Mesa, vs. Sapinero Powerline,	0.02	-0.01	0.05
Big Mesa, vs. South Parlin Upper,	0.03	-0.01	0.07
Big Mesa, vs. Signal Peak West,	0.06	0.01	0.10
Big Mesa, vs. Sapinero Ridge,	0.03	0.00	0.06
Big Mesa, vs. Sapinero South,	0.03	0.01	0.05
Big Mesa, vs. Scout,	0.07	0.03	0.11
Big Mesa, vs. Steven's Creek East,	0.00	-0.06	0.04
Big Mesa, vs. Taila's Lek,	0.04	0.01	0.08
Big Mesa, vs. Teachout 1 & 2,	0.03	0.01	0.06

Lek Comparison	F_{ST}	lower	upper
Big Mesa, vs. Teachout 3,5,6,	0.04	0.00	0.08
Big Mesa, vs. Vito,	0.04	0.01	0.09
Big Mesa, vs. Wood's Gulch,	0.03	0.00	0.07
Big Mesa, vs. Waunita,	0.06	0.02	0.10
Big Mesa, vs. Waunita NW,	0.09	0.03	0.15
Campbell, vs. Chance Gulch,	0.05	0.02	0.09
Campbell, vs. Chance Gulch E,	0.03	0.00	0.06
Campbell, vs. Flat Top Section 31,	0.03	-0.02	0.10
Campbell, vs. Hartman Gulch,	0.02	-0.01	0.05
Campbell, vs. Henkel Road,	0.03	0.00	0.06
Campbell, vs. Kezar Basin North,	0.04	0.01	0.07
Campbell, vs. Lost Canyon 2,	-0.04	-0.09	0.02
Campbell, vs. 7MB Lek,	0.01	-0.01	0.04
Campbell, vs. 7MB Eagle,	-0.01	-0.06	0.05
Campbell, vs. 7MB Hupp,	0.00	-0.05	0.05
Campbell, vs. McCabe's Lane,	-0.07	-0.14	0.02
Campbell, vs. Miller Ranch,	0.02	-0.01	0.04
Campbell, vs. Razor Creek,	-0.01	-0.04	0.02
Campbell, vs. Razor Creek Divide,	-0.05	-0.14	0.05
Campbell, vs. Razor Dome 1 & 2,	0.02	0.00	0.06
Campbell, vs. Ridgeline,	0.05	-0.04	0.14
Campbell, vs. Sapinero Corral,	0.00	-0.06	0.08
Campbell, vs. South Beaver Creek,	0.05	0.01	0.10
Campbell, vs. Sugar Creek,	0.05	0.01	0.10
Campbell, vs. Sewell Gulch,	-0.06	-0.15	0.04
Campbell, vs. Signal Peak,	0.01	-0.05	0.06
Campbell, vs. South 6 Mile Meadow,	0.05	0.00	0.09
Campbell, vs. Sapinero 10 Mile Spring,	0.04	0.00	0.07
Campbell, vs. South 6 Mile Ridge,	0.07	0.03	0.11
Campbell, vs. South Parlin 1,	0.05	0.02	0.08
Campbell, vs. South Parlin 3,	0.06	0.02	0.11
Campbell, vs. Sapinero Powerline,	0.05	0.00	0.10
Campbell, vs. South Parlin Upper,	0.04	0.02	0.07
Campbell, vs. Signal Peak West,	0.06	0.01	0.12
Campbell, vs. Sapinero Ridge,	0.07	0.02	0.12
Campbell, vs. Sapinero South,	0.04	0.01	0.08
Campbell, vs. Scout,	0.06	0.02	0.09
Campbell, vs. Steven's Creek East,	0.00	-0.08	0.09
Campbell, vs. Taila's Lek,	0.03	0.00	0.07
Campbell, vs. Teachout 1 & 2,	0.02	-0.01	0.05
Campbell, vs. Teachout 3,5,6,	0.05	0.01	0.09
Campbell, vs. Vito,	0.03	0.00	0.06

Lek Comparison	F_{ST}	lower	upper
Campbell, vs. Wood's Gulch,	0.03	0.00	0.07
Campbell, vs. Waunita,	0.04	-0.01	0.10
Campbell, vs. Waunita NW,	0.07	0.01	0.13
Chance Gulch, vs. Chance Gulch E,	0.02	0.00	0.03
Chance Gulch, vs. Flat Top Section 31,	0.02	0.00	0.04
Chance Gulch, vs. Hartman Gulch,	0.02	0.01	0.03
Chance Gulch, vs. Henkel Road,	0.00	-0.01	0.01
Chance Gulch, vs. Kezar Basin North,	0.02	0.01	0.03
Chance Gulch, vs. Lost Canyon 2,	0.06	0.00	0.13
Chance Gulch, vs. 7MB Lek,	0.05	0.01	0.08
Chance Gulch, vs. 7MB Eagle,	0.02	-0.02	0.07
Chance Gulch, vs. 7MB Hupp,	0.02	-0.02	0.07
Chance Gulch, vs. McCabe's Lane,	0.02	-0.02	0.07
Chance Gulch, vs. Miller Ranch,	0.03	0.02	0.05
Chance Gulch, vs. Razor Creek,	0.01	-0.01	0.03
Chance Gulch, vs. Razor Creek Divide,	0.00	-0.04	0.05
Chance Gulch, vs. Razor Dome 1 & 2,	0.02	0.01	0.04
Chance Gulch, vs. Ridgeline,	0.07	0.01	0.13
Chance Gulch, vs. Sapinero Corral,	0.03	0.00	0.06
Chance Gulch, vs. South Beaver Creek,	0.02	0.00	0.03
Chance Gulch, vs. Sugar Creek,	0.03	0.01	0.04
Chance Gulch, vs. Sewell Gulch,	0.04	-0.02	0.13
Chance Gulch, vs. Signal Peak,	0.03	-0.03	0.09
Chance Gulch, vs. South 6 Mile Meadow,	0.08	0.02	0.14
Chance Gulch, vs. Sapinero 10 Mile Spring,	0.04	0.02	0.06
Chance Gulch, vs. South 6 Mile Ridge,	0.06	0.03	0.10
Chance Gulch, vs. South Parlin 1,	0.01	0.00	0.02
Chance Gulch, vs. South Parlin 3,	0.01	0.00	0.03
Chance Gulch, vs. Sapinero Powerline,	0.05	0.02	0.08
Chance Gulch, vs. South Parlin Upper,	0.01	0.00	0.03
Chance Gulch, vs. Signal Peak West,	0.04	0.01	0.06
Chance Gulch, vs. Sapinero Ridge,	0.04	0.02	0.07
Chance Gulch, vs. Sapinero South,	0.03	0.02	0.05
Chance Gulch, vs. Scout,	0.08	0.05	0.11
Chance Gulch, vs. Steven's Creek East,	0.08	0.00	0.16
Chance Gulch, vs. Taila's Lek,	0.02	0.00	0.05
Chance Gulch, vs. Teachout 1 & 2,	0.02	0.01	0.03
Chance Gulch, vs. Teachout 3,5,6,	0.07	0.05	0.09
Chance Gulch, vs. Vito,	0.06	0.03	0.08
Chance Gulch, vs. Wood's Gulch,	0.06	0.03	0.10
Chance Gulch, vs. Waunita,	0.08	0.04	0.13
Chance Gulch, vs. Waunita NW,	0.07	0.03	0.13

Lek Comparison	F_{ST}	lower	upper
Chance Gulch E, vs. Flat Top Section 31,	0.01	-0.02	0.05
Chance Gulch E, vs. Hartman Gulch,	0.01	0.00	0.03
Chance Gulch E, vs. Henkel Road,	0.02	0.00	0.04
Chance Gulch E, vs. Kezar Basin North,	0.01	0.00	0.02
Chance Gulch E, vs. Lost Canyon 2,	0.03	-0.04	0.11
Chance Gulch E, vs. 7MB Lek,	0.02	0.00	0.04
Chance Gulch E, vs. 7MB Eagle,	-0.01	-0.05	0.04
Chance Gulch E, vs. 7MB Hupp,	0.03	-0.03	0.09
Chance Gulch E, vs. McCabe's Lane,	-0.05	-0.13	0.01
Chance Gulch E, vs. Miller Ranch,	0.01	0.00	0.03
Chance Gulch E, vs. Razor Creek,	0.01	-0.03	0.05
Chance Gulch E, vs. Razor Creek Divide,	-0.07	-0.14	-0.01
Chance Gulch E, vs. Razor Dome 1 & 2,	0.02	0.00	0.04
Chance Gulch E, vs. Ridgeline,	0.05	-0.01	0.10
Chance Gulch E, vs. Sapinero Corral,	-0.02	-0.07	0.03
Chance Gulch E, vs. South Beaver Creek,	0.03	0.01	0.05
Chance Gulch E, vs. Sugar Creek,	0.03	0.02	0.05
Chance Gulch E, vs. Sewell Gulch,	0.03	-0.02	0.08
Chance Gulch E, vs. Signal Peak,	0.01	-0.02	0.06
Chance Gulch E, vs. South 6 Mile Meadow,	0.07	0.02	0.13
Chance Gulch E, vs. Sapinero 10 Mile Spring,	0.04	0.02	0.06
Chance Gulch E, vs. South 6 Mile Ridge,	0.07	0.03	0.12
Chance Gulch E, vs. South Parlin 1,	0.01	0.00	0.02
Chance Gulch E, vs. South Parlin 3,	0.01	-0.01	0.02
Chance Gulch E, vs. Sapinero Powerline,	0.05	0.02	0.08
Chance Gulch E, vs. South Parlin Upper,	0.01	0.00	0.02
Chance Gulch E, vs. Signal Peak West,	0.03	0.00	0.05
Chance Gulch E, vs. Sapinero Ridge,	0.05	0.02	0.09
Chance Gulch E, vs. Sapinero South,	0.03	0.02	0.05
Chance Gulch E, vs. Scout,	0.06	0.03	0.09
Chance Gulch E, vs. Steven's Creek East,	0.04	-0.04	0.11
Chance Gulch E, vs. Taila's Lek,	0.02	-0.01	0.04
Chance Gulch E, vs. Teachout 1 & 2,	0.01	-0.01	0.02
Chance Gulch E, vs. Teachout 3,5,6,	0.04	0.01	0.07
Chance Gulch E, vs. Vito,	0.04	0.02	0.07
Chance Gulch E, vs. Wood's Gulch,	0.05	0.03	0.08
Chance Gulch E, vs. Waunita,	0.05	0.02	0.09
Chance Gulch E, vs. Waunita NW,	0.06	0.01	0.11
Flat Top Section 31, vs. Hartman Gulch,	0.01	-0.01	0.03
Flat Top Section 31, vs. Henkel Road,	0.02	-0.01	0.05
Flat Top Section 31, vs. Kezar Basin North,	0.02	-0.01	0.05
Flat Top Section 31, vs. Lost Canyon 2,	0.03	-0.03	0.09

Lek Comparison	F_{ST}	lower	upper
Flat Top Section 31, vs. 7MB Lek,	0.05	0.00	0.12
Flat Top Section 31, vs. 7MB Eagle,	0.00	-0.07	0.08
Flat Top Section 31, vs. 7MB Hupp,	0.03	-0.04	0.11
Flat Top Section 31, vs. McCabe's Lane,	0.02	-0.04	0.09
Flat Top Section 31, vs. Miller Ranch,	-0.01	-0.03	0.02
Flat Top Section 31, vs. Razor Creek,	0.04	-0.02	0.09
Flat Top Section 31, vs. Razor Creek Divide,	-0.01	-0.07	0.08
Flat Top Section 31, vs. Razor Dome 1 & 2,	0.03	-0.01	0.08
Flat Top Section 31, vs. Ridgeline,	0.07	-0.02	0.15
Flat Top Section 31, vs. Sapinero Corral,	-0.04	-0.07	0.00
Flat Top Section 31, vs. South Beaver Creek,	0.01	-0.01	0.03
Flat Top Section 31, vs. Sugar Creek,	0.01	-0.01	0.03
Flat Top Section 31, vs. Sewell Gulch,	0.07	-0.05	0.22
Flat Top Section 31, vs. Signal Peak,	0.01	-0.04	0.07
Flat Top Section 31, vs. South 6 Mile Meadow,	0.08	0.00	0.20
Flat Top Section 31, vs. Sapinero 10 Mile Spring,	0.01	-0.01	0.03
Flat Top Section 31, vs. South 6 Mile Ridge,	0.07	0.03	0.11
Flat Top Section 31, vs. South Parlin 1,	0.02	0.00	0.05
Flat Top Section 31, vs. South Parlin 3,	0.02	-0.01	0.04
Flat Top Section 31, vs. Sapinero Powerline,	0.02	0.00	0.05
Flat Top Section 31, vs. South Parlin Upper,	0.02	-0.01	0.05
Flat Top Section 31, vs. Signal Peak West,	0.03	-0.01	0.06
Flat Top Section 31, vs. Sapinero Ridge,	0.03	0.01	0.07
Flat Top Section 31, vs. Sapinero South,	0.02	0.00	0.04
Flat Top Section 31, vs. Scout,	0.06	0.02	0.11
Flat Top Section 31, vs. Steven's Creek East,	0.04	-0.03	0.12
Flat Top Section 31, vs. Taila's Lek,	0.01	-0.02	0.04
Flat Top Section 31, vs. Teachout 1 & 2,	0.01	-0.02	0.06
Flat Top Section 31, vs. Teachout 3,5,6,	0.03	0.00	0.05
Flat Top Section 31, vs. Vito,	0.03	0.00	0.06
Flat Top Section 31, vs. Wood's Gulch,	0.03	0.01	0.05
Flat Top Section 31, vs. Waunita,	0.06	0.00	0.15
Flat Top Section 31, vs. Waunita NW,	0.11	0.03	0.20
Hartman Gulch, vs. Henkel Road,	0.01	0.00	0.02
Hartman Gulch, vs. Kezar Basin North,	0.01	0.01	0.02
Hartman Gulch, vs. Lost Canyon 2,	0.03	-0.03	0.09
Hartman Gulch, vs. 7MB Lek,	0.02	0.00	0.05
Hartman Gulch, vs. 7MB Eagle,	-0.01	-0.04	0.02
Hartman Gulch, vs. 7MB Hupp,	0.02	-0.03	0.07
Hartman Gulch, vs. McCabe's Lane,	0.00	-0.05	0.04
Hartman Gulch, vs. Miller Ranch,	0.01	0.00	0.02
Hartman Gulch, vs. Razor Creek,	0.02	-0.01	0.04

Lek Comparison	F_{ST}	lower	upper
Hartman Gulch, vs. Razor Creek Divide,	-0.03	-0.08	0.02
Hartman Gulch, vs. Razor Dome 1 & 2,	0.01	0.00	0.02
Hartman Gulch, vs. Ridgeline,	0.03	-0.02	0.07
Hartman Gulch, vs. Sapinero Corral,	0.01	-0.03	0.05
Hartman Gulch, vs. South Beaver Creek,	0.02	0.01	0.04
Hartman Gulch, vs. Sugar Creek,	0.02	0.01	0.03
Hartman Gulch, vs. Sewell Gulch,	0.02	-0.03	0.09
Hartman Gulch, vs. Signal Peak,	0.00	-0.03	0.04
Hartman Gulch, vs. South 6 Mile Meadow,	0.07	0.02	0.12
Hartman Gulch, vs. Sapinero 10 Mile Spring,	0.02	0.00	0.03
Hartman Gulch, vs. South 6 Mile Ridge,	0.05	0.03	0.07
Hartman Gulch, vs. South Parlin 1,	0.02	0.01	0.04
Hartman Gulch, vs. South Parlin 3,	0.01	-0.01	0.02
Hartman Gulch, vs. Sapinero Powerline,	0.02	0.00	0.04
Hartman Gulch, vs. South Parlin Upper,	0.02	0.01	0.03
Hartman Gulch, vs. Signal Peak West,	0.03	0.01	0.06
Hartman Gulch, vs. Sapinero Ridge,	0.02	0.01	0.04
Hartman Gulch, vs. Sapinero South,	0.01	0.01	0.02
Hartman Gulch, vs. Scout,	0.05	0.03	0.07
Hartman Gulch, vs. Steven's Creek East,	0.04	-0.01	0.10
Hartman Gulch, vs. Taila's Lek,	0.01	0.00	0.03
Hartman Gulch, vs. Teachout 1 & 2,	0.00	0.00	0.01
Hartman Gulch, vs. Teachout 3,5,6,	0.04	0.02	0.06
Hartman Gulch, vs. Vito,	0.03	0.01	0.06
Hartman Gulch, vs. Wood's Gulch,	0.04	0.02	0.08
Hartman Gulch, vs. Waunita,	0.06	0.02	0.10
Hartman Gulch, vs. Waunita NW,	0.07	0.03	0.13
Henkel Road, vs. Kezar Basin North,	0.01	0.00	0.03
Henkel Road, vs. Lost Canyon 2,	0.02	-0.04	0.10
Henkel Road, vs. 7MB Lek,	0.01	-0.01	0.04
Henkel Road, vs. 7MB Eagle,	-0.01	-0.04	0.03
Henkel Road, vs. 7MB Hupp,	-0.01	-0.06	0.04
Henkel Road, vs. McCabe's Lane,	-0.02	-0.07	0.03
Henkel Road, vs. Miller Ranch,	0.01	-0.01	0.03
Henkel Road, vs. Razor Creek,	0.00	-0.03	0.03
Henkel Road, vs. Razor Creek Divide,	0.01	-0.08	0.11
Henkel Road, vs. Razor Dome 1 & 2,	0.01	0.00	0.02
Henkel Road, vs. Ridgeline,	0.07	0.01	0.14
Henkel Road, vs. Sapinero Corral,	0.02	-0.04	0.08
Henkel Road, vs. South Beaver Creek,	0.01	-0.01	0.04
Henkel Road, vs. Sugar Creek,	0.03	0.02	0.06
Henkel Road, vs. Sewell Gulch,	0.04	-0.03	0.11

Lek Comparison	F_{ST}	lower	upper
Henkel Road, vs. Signal Peak,	0.00	-0.05	0.05
Henkel Road, vs. South 6 Mile Meadow,	0.07	0.02	0.14
Henkel Road, vs. Sapinero 10 Mile Spring,	0.02	0.00	0.05
Henkel Road, vs. South 6 Mile Ridge,	0.04	0.01	0.07
Henkel Road, vs. South Parlin 1,	0.01	-0.01	0.02
Henkel Road, vs. South Parlin 3,	0.00	-0.02	0.02
Henkel Road, vs. Sapinero Powerline,	0.03	0.00	0.07
Henkel Road, vs. South Parlin Upper,	0.00	-0.01	0.01
Henkel Road, vs. Signal Peak West,	0.02	-0.01	0.05
Henkel Road, vs. Sapinero Ridge,	0.04	0.02	0.07
Henkel Road, vs. Sapinero South,	0.02	0.00	0.03
Henkel Road, vs. Scout,	0.06	0.03	0.08
Henkel Road, vs. Steven's Creek East,	0.05	-0.03	0.13
Henkel Road, vs. Taila's Lek,	0.01	0.00	0.04
Henkel Road, vs. Teachout 1 & 2,	0.01	-0.01	0.02
Henkel Road, vs. Teachout 3,5,6,	0.05	0.02	0.07
Henkel Road, vs. Vito,	0.04	0.02	0.06
Henkel Road, vs. Wood's Gulch,	0.06	0.02	0.12
Henkel Road, vs. Waunita,	0.04	0.02	0.07
Henkel Road, vs. Waunita NW,	0.06	0.02	0.09
Kezar Basin North, vs. Lost Canyon 2,	0.04	-0.02	0.11
Kezar Basin North, vs. 7MB Lek,	0.03	0.01	0.06
Kezar Basin North, vs. 7MB Eagle,	0.00	-0.03	0.04
Kezar Basin North, vs. 7MB Hupp,	0.02	-0.02	0.07
Kezar Basin North, vs. McCabe's Lane,	0.00	-0.05	0.06
Kezar Basin North, vs. Miller Ranch,	0.01	0.00	0.03
Kezar Basin North, vs. Razor Creek,	0.02	-0.01	0.05
Kezar Basin North, vs. Razor Creek Divide,	-0.01	-0.06	0.04
Kezar Basin North, vs. Razor Dome 1 & 2,	0.02	0.01	0.04
Kezar Basin North, vs. Ridgeline,	0.04	-0.01	0.08
Kezar Basin North, vs. Sapinero Corral,	0.01	-0.03	0.05
Kezar Basin North, vs. South Beaver Creek,	0.01	0.00	0.02
Kezar Basin North, vs. Sugar Creek,	0.02	0.01	0.03
Kezar Basin North, vs. Sewell Gulch,	0.04	-0.01	0.11
Kezar Basin North, vs. Signal Peak,	0.00	-0.03	0.04
Kezar Basin North, vs. South 6 Mile Meadow,	0.09	0.05	0.14
Kezar Basin North, vs. Sapinero 10 Mile Spring,	0.01	0.00	0.02
Kezar Basin North, vs. South 6 Mile Ridge,	0.05	0.03	0.08
Kezar Basin North, vs. South Parlin 1,	0.02	0.01	0.03
Kezar Basin North, vs. South Parlin 3,	0.01	-0.01	0.03
Kezar Basin North, vs. Sapinero Powerline,	0.02	0.00	0.05
Kezar Basin North, vs. South Parlin Upper,	0.02	0.01	0.03

Lek Comparison	F_{ST}	lower	upper
Kezar Basin North, vs. Signal Peak West,	0.03	0.01	0.05
Kezar Basin North, vs. Sapinero Ridge,	0.03	0.01	0.04
Kezar Basin North, vs. Sapinero South,	0.01	0.01	0.02
Kezar Basin North, vs. Scout,	0.05	0.03	0.07
Kezar Basin North, vs. Steven's Creek East,	0.05	-0.03	0.14
Kezar Basin North, vs. Taila's Lek,	0.02	0.00	0.03
Kezar Basin North, vs. Teachout 1 & 2,	0.01	0.00	0.02
Kezar Basin North, vs. Teachout 3,5,6,	0.05	0.02	0.08
Kezar Basin North, vs. Vito,	0.04	0.02	0.07
Kezar Basin North, vs. Wood's Gulch,	0.05	0.03	0.07
Kezar Basin North, vs. Waunita,	0.07	0.02	0.12
Kezar Basin North, vs. Waunita NW,	0.08	0.03	0.13
Lost Canyon 2, vs. 7MB Lek,	-0.04	-0.10	0.03
Lost Canyon 2, vs. 7MB Eagle,	-0.01	-0.08	0.06
Lost Canyon 2, vs. 7MB Hupp,	-0.06	-0.14	0.02
Lost Canyon 2, vs. McCabe's Lane,	-0.16	-0.32	0.00
Lost Canyon 2, vs. Miller Ranch,	0.01	-0.04	0.07
Lost Canyon 2, vs. Razor Creek,	0.02	-0.04	0.07
Lost Canyon 2, vs. Razor Creek Divide,	-0.05	-0.21	0.09
Lost Canyon 2, vs. Razor Dome 1 & 2,	0.00	-0.04	0.05
Lost Canyon 2, vs. Ridgeline,	0.10	0.00	0.20
Lost Canyon 2, vs. Sapinero Corral,	-0.04	-0.13	0.05
Lost Canyon 2, vs. South Beaver Creek,	0.04	-0.01	0.12
Lost Canyon 2, vs. Sugar Creek,	0.03	-0.01	0.07
Lost Canyon 2, vs. Sewell Gulch,	-0.13	-0.24	-0.01
Lost Canyon 2, vs. Signal Peak,	-0.01	-0.08	0.08
Lost Canyon 2, vs. South 6 Mile Meadow,	0.00	-0.07	0.09
Lost Canyon 2, vs. Sapinero 10 Mile Spring,	0.03	-0.01	0.08
Lost Canyon 2, vs. South 6 Mile Ridge,	0.09	0.01	0.17
Lost Canyon 2, vs. South Parlin 1,	0.05	0.00	0.11
Lost Canyon 2, vs. South Parlin 3,	0.06	-0.01	0.15
Lost Canyon 2, vs. Sapinero Powerline,	0.07	0.01	0.15
Lost Canyon 2, vs. South Parlin Upper,	0.02	-0.04	0.10
Lost Canyon 2, vs. Signal Peak West,	0.07	0.00	0.13
Lost Canyon 2, vs. Sapinero Ridge,	0.06	0.02	0.11
Lost Canyon 2, vs. Sapinero South,	0.05	0.01	0.09
Lost Canyon 2, vs. Scout,	0.08	0.01	0.14
Lost Canyon 2, vs. Steven's Creek East,	-0.06	-0.23	0.08
Lost Canyon 2, vs. Taila's Lek,	0.07	-0.02	0.14
Lost Canyon 2, vs. Teachout 1 & 2,	0.03	-0.02	0.08
Lost Canyon 2, vs. Teachout 3,5,6,	0.02	-0.04	0.09
Lost Canyon 2, vs. Vito,	0.03	-0.03	0.10

Lek Comparison	F_{ST}	lower	upper
Lost Canyon 2, vs. Wood's Gulch,	0.03	-0.03	0.09
Lost Canyon 2, vs. Waunita,	0.05	-0.02	0.14
Lost Canyon 2, vs. Waunita NW,	0.12	0.05	0.20
7MB Lek, vs. 7MB Eagle,	-0.05	-0.07	-0.03
7MB Lek, vs. 7MB Hupp,	-0.03	-0.05	0.00
7MB Lek, vs. McCabe's Lane,	-0.06	-0.12	0.00
7MB Lek, vs. Miller Ranch,	0.02	-0.01	0.06
7MB Lek, vs. Razor Creek,	0.01	-0.01	0.04
7MB Lek, vs. Razor Creek Divide,	-0.05	-0.10	0.01
7MB Lek, vs. Razor Dome 1 & 2,	0.02	0.00	0.04
7MB Lek, vs. Ridgeline,	0.08	0.00	0.15
7MB Lek, vs. Sapinero Corral,	0.02	-0.03	0.08
7MB Lek, vs. South Beaver Creek,	0.04	0.01	0.08
7MB Lek, vs. Sugar Creek,	0.04	0.01	0.09
7MB Lek, vs. Sewell Gulch,	-0.06	-0.12	0.00
7MB Lek, vs. Signal Peak,	0.00	-0.03	0.04
7MB Lek, vs. South 6 Mile Meadow,	0.04	0.00	0.08
7MB Lek, vs. Sapinero 10 Mile Spring,	0.03	0.01	0.07
7MB Lek, vs. South 6 Mile Ridge,	0.05	0.02	0.08
7MB Lek, vs. South Parlin 1,	0.03	0.01	0.05
7MB Lek, vs. South Parlin 3,	0.04	0.00	0.09
7MB Lek, vs. Sapinero Powerline,	0.04	0.00	0.10
7MB Lek, vs. South Parlin Upper,	0.02	0.00	0.05
7MB Lek, vs. Signal Peak West,	0.04	-0.01	0.09
7MB Lek, vs. Sapinero Ridge,	0.05	0.03	0.09
7MB Lek, vs. Sapinero South,	0.04	0.02	0.07
7MB Lek, vs. Scout,	0.04	0.02	0.07
7MB Lek, vs. Steven's Creek East,	0.01	-0.07	0.08
7MB Lek, vs. Taila's Lek,	0.05	0.02	0.08
7MB Lek, vs. Teachout 1 & 2,	0.01	-0.01	0.03
7MB Lek, vs. Teachout 3,5,6,	0.03	0.02	0.05
7MB Lek, vs. Vito,	0.03	0.01	0.05
7MB Lek, vs. Wood's Gulch,	0.05	0.02	0.10
7MB Lek, vs. Waunita,	0.04	0.00	0.07
7MB Lek, vs. Waunita NW,	0.07	0.02	0.12
7MB Eagle, vs. 7MB Hupp,	-0.02	-0.07	0.02
7MB Eagle, vs. McCabe's Lane,	-0.02	-0.09	0.06
7MB Eagle, vs. Miller Ranch,	-0.03	-0.06	-0.01
7MB Eagle, vs. Razor Creek,	0.01	-0.04	0.06
7MB Eagle, vs. Razor Creek Divide,	-0.07	-0.16	0.01
7MB Eagle, vs. Razor Dome 1 & 2,	-0.01	-0.05	0.02
7MB Eagle, vs. Ridgeline,	0.06	-0.04	0.15

Lek Comparison	F_{ST}	lower	upper
7MB Eagle, vs. Sapinero Corral,	-0.04	-0.10	0.02
7MB Eagle, vs. South Beaver Creek,	0.03	-0.01	0.06
7MB Eagle, vs. Sugar Creek,	0.02	-0.02	0.06
7MB Eagle, vs. Sewell Gulch,	-0.08	-0.14	-0.01
7MB Eagle, vs. Signal Peak,	-0.05	-0.10	-0.01
7MB Eagle, vs. South 6 Mile Meadow,	0.05	0.01	0.10
7MB Eagle, vs. Sapinero 10 Mile Spring,	-0.01	-0.04	0.03
7MB Eagle, vs. South 6 Mile Ridge,	0.04	-0.01	0.09
7MB Eagle, vs. South Parlin 1,	0.01	-0.02	0.04
7MB Eagle, vs. South Parlin 3,	0.03	-0.03	0.08
7MB Eagle, vs. Sapinero Powerline,	0.01	-0.04	0.06
7MB Eagle, vs. South Parlin Upper,	0.00	-0.03	0.03
7MB Eagle, vs. Signal Peak West,	0.01	-0.03	0.06
7MB Eagle, vs. Sapinero Ridge,	0.00	-0.03	0.04
7MB Eagle, vs. Sapinero South,	-0.01	-0.04	0.01
7MB Eagle, vs. Scout,	0.01	-0.04	0.06
7MB Eagle, vs. Steven's Creek East,	-0.02	-0.13	0.07
7MB Eagle, vs. Taila's Lek,	0.00	-0.04	0.04
7MB Eagle, vs. Teachout 1 & 2,	-0.03	-0.06	-0.01
7MB Eagle, vs. Teachout 3,5,6,	-0.01	-0.04	0.02
7MB Eagle, vs. Vito,	0.00	-0.02	0.02
7MB Eagle, vs. Wood's Gulch,	0.04	0.00	0.08
7MB Eagle, vs. Waunita,	0.03	-0.01	0.07
7MB Eagle, vs. Waunita NW,	0.09	0.02	0.16
7MB Hupp, vs. McCabe's Lane,	-0.11	-0.23	0.00
7MB Hupp, vs. Miller Ranch,	0.03	-0.04	0.10
7MB Hupp, vs. Razor Creek,	-0.02	-0.06	0.03
7MB Hupp, vs. Razor Creek Divide,	-0.03	-0.12	0.06
7MB Hupp, vs. Razor Dome 1 & 2,	-0.01	-0.06	0.05
7MB Hupp, vs. Ridgeline,	0.08	0.00	0.16
7MB Hupp, vs. Sapinero Corral,	0.03	-0.09	0.12
7MB Hupp, vs. South Beaver Creek,	0.02	-0.03	0.07
7MB Hupp, vs. Sugar Creek,	0.01	-0.04	0.06
7MB Hupp, vs. Sewell Gulch,	-0.04	-0.11	0.04
7MB Hupp, vs. Signal Peak,	0.01	-0.08	0.08
7MB Hupp, vs. South 6 Mile Meadow,	-0.01	-0.07	0.04
7MB Hupp, vs. Sapinero 10 Mile Spring,	0.02	-0.03	0.08
7MB Hupp, vs. South 6 Mile Ridge,	0.06	0.01	0.11
7MB Hupp, vs. South Parlin 1,	0.01	-0.03	0.04
7MB Hupp, vs. South Parlin 3,	0.05	-0.01	0.11
7MB Hupp, vs. Sapinero Powerline,	0.06	0.01	0.12
7MB Hupp, vs. South Parlin Upper,	0.02	-0.02	0.06

Lek Comparison	F_{ST}	lower	upper
7MB Hupp, vs. Signal Peak West,	0.04	-0.01	0.09
7MB Hupp, vs. Sapinero Ridge,	0.05	0.00	0.10
7MB Hupp, vs. Sapinero South,	0.03	-0.02	0.08
7MB Hupp, vs. Scout,	0.06	0.02	0.11
7MB Hupp, vs. Steven's Creek East,	-0.04	-0.17	0.08
7MB Hupp, vs. Taila's Lek,	0.03	-0.02	0.09
7MB Hupp, vs. Teachout 1 & 2,	0.00	-0.04	0.06
7MB Hupp, vs. Teachout 3,5,6,	0.05	0.01	0.09
7MB Hupp, vs. Vito,	0.04	0.00	0.08
7MB Hupp, vs. Wood's Gulch,	0.06	0.01	0.12
7MB Hupp, vs. Waunita,	0.06	0.00	0.10
7MB Hupp, vs. Waunita NW,	0.09	0.04	0.14
McCabe's Lane, vs. Miller Ranch,	0.01	-0.04	0.06
McCabe's Lane, vs. Razor Creek,	-0.04	-0.11	0.03
McCabe's Lane, vs. Razor Creek Divide,	-0.03	-0.11	0.05
McCabe's Lane, vs. Razor Dome 1 & 2,	0.00	-0.06	0.05
McCabe's Lane, vs. Ridgeline,	0.06	-0.03	0.14
McCabe's Lane, vs. Sapinero Corral,	-0.03	-0.14	0.08
McCabe's Lane, vs. South Beaver Creek,	0.02	-0.03	0.08
McCabe's Lane, vs. Sugar Creek,	0.02	-0.05	0.08
McCabe's Lane, vs. Sewell Gulch,	-0.09	-0.14	-0.04
McCabe's Lane, vs. Signal Peak,	0.00	-0.07	0.07
McCabe's Lane, vs. South 6 Mile Meadow,	0.03	-0.05	0.11
McCabe's Lane, vs. Sapinero 10 Mile Spring,	0.02	-0.04	0.08
McCabe's Lane, vs. South 6 Mile Ridge,	0.08	0.01	0.15
McCabe's Lane, vs. South Parlin 1,	-0.02	-0.07	0.05
McCabe's Lane, vs. South Parlin 3,	0.02	-0.02	0.06
McCabe's Lane, vs. Sapinero Powerline,	0.05	-0.01	0.11
McCabe's Lane, vs. South Parlin Upper,	-0.01	-0.06	0.04
McCabe's Lane, vs. Signal Peak West,	-0.02	-0.10	0.05
McCabe's Lane, vs. Sapinero Ridge,	0.06	-0.01	0.13
McCabe's Lane, vs. Sapinero South,	0.02	-0.03	0.09
McCabe's Lane, vs. Scout,	0.06	-0.01	0.12
McCabe's Lane, vs. Steven's Creek East,	-0.07	-0.14	0.00
McCabe's Lane, vs. Taila's Lek,	0.03	-0.05	0.10
McCabe's Lane, vs. Teachout 1 & 2,	-0.01	-0.08	0.06
McCabe's Lane, vs. Teachout 3,5,6,	0.00	-0.07	0.07
McCabe's Lane, vs. Vito,	0.00	-0.08	0.08
McCabe's Lane, vs. Wood's Gulch,	0.04	-0.04	0.10
McCabe's Lane, vs. Waunita,	0.02	-0.05	0.10
McCabe's Lane, vs. Waunita NW,	0.10	0.02	0.19
Miller Ranch, vs. Razor Creek,	0.02	-0.02	0.05

Lek Comparison	F_{ST}	lower	upper
Miller Ranch, vs. Razor Creek Divide,	-0.03	-0.09	0.04
Miller Ranch, vs. Razor Dome 1 & 2,	0.01	0.00	0.02
Miller Ranch, vs. Ridgeline,	0.03	-0.02	0.09
Miller Ranch, vs. Sapinero Corral,	-0.02	-0.06	0.02
Miller Ranch, vs. South Beaver Creek,	0.01	0.00	0.03
Miller Ranch, vs. Sugar Creek,	0.02	0.01	0.04
Miller Ranch, vs. Sewell Gulch,	0.00	-0.05	0.07
Miller Ranch, vs. Signal Peak,	0.00	-0.04	0.03
Miller Ranch, vs. South 6 Mile Meadow,	0.07	0.03	0.12
Miller Ranch, vs. Sapinero 10 Mile Spring,	0.02	0.01	0.03
Miller Ranch, vs. South 6 Mile Ridge,	0.05	0.02	0.08
Miller Ranch, vs. South Parlin 1,	0.03	0.01	0.05
Miller Ranch, vs. South Parlin 3,	0.01	-0.01	0.03
Miller Ranch, vs. Sapinero Powerline,	0.03	0.00	0.05
Miller Ranch, vs. South Parlin Upper,	0.01	0.00	0.03
Miller Ranch, vs. Signal Peak West,	0.02	-0.01	0.06
Miller Ranch, vs. Sapinero Ridge,	0.03	0.02	0.05
Miller Ranch, vs. Sapinero South,	0.02	0.01	0.03
Miller Ranch, vs. Scout,	0.03	0.02	0.05
Miller Ranch, vs. Steven's Creek East,	0.04	-0.02	0.09
Miller Ranch, vs. Taila's Lek,	0.00	-0.01	0.02
Miller Ranch, vs. Teachout 1 & 2,	0.00	-0.01	0.01
Miller Ranch, vs. Teachout 3,5,6,	0.02	0.00	0.04
Miller Ranch, vs. Vito,	0.02	0.00	0.05
Miller Ranch, vs. Wood's Gulch,	0.03	0.02	0.05
Miller Ranch, vs. Waunita,	0.04	0.01	0.08
Miller Ranch, vs. Waunita NW,	0.07	0.02	0.12
Razor Creek, vs. Razor Creek Divide,	-0.02	-0.09	0.06
Razor Creek, vs. Razor Dome 1 & 2,	0.01	-0.02	0.04
Razor Creek, vs. Ridgeline,	0.07	-0.01	0.14
Razor Creek, vs. Sapinero Corral,	0.03	-0.04	0.09
Razor Creek, vs. South Beaver Creek,	0.03	0.00	0.06
Razor Creek, vs. Sugar Creek,	0.02	-0.01	0.04
Razor Creek, vs. Sewell Gulch,	0.00	-0.05	0.06
Razor Creek, vs. Signal Peak,	0.05	-0.01	0.11
Razor Creek, vs. South 6 Mile Meadow,	0.07	0.03	0.10
Razor Creek, vs. Sapinero 10 Mile Spring,	0.03	0.00	0.06
Razor Creek, vs. South 6 Mile Ridge,	0.06	0.01	0.10
Razor Creek, vs. South Parlin 1,	0.01	-0.02	0.03
Razor Creek, vs. South Parlin 3,	0.03	0.00	0.06
Razor Creek, vs. Sapinero Powerline,	0.05	0.01	0.09
Razor Creek, vs. South Parlin Upper,	0.01	-0.02	0.03

Lek Comparison	F_{ST}	lower	upper
Razor Creek, vs. Signal Peak West,	0.04	0.00	0.08
Razor Creek, vs. Sapinero Ridge,	0.05	0.01	0.09
Razor Creek, vs. Sapinero South,	0.03	0.00	0.05
Razor Creek, vs. Scout,	0.05	0.02	0.09
Razor Creek, vs. Steven's Creek East,	0.05	-0.02	0.12
Razor Creek, vs. Taila's Lek,	0.01	-0.01	0.03
Razor Creek, vs. Teachout 1 & 2,	0.02	-0.01	0.05
Razor Creek, vs. Teachout 3,5,6,	0.04	0.00	0.08
Razor Creek, vs. Vito,	0.01	-0.02	0.04
Razor Creek, vs. Wood's Gulch,	0.03	0.01	0.06
Razor Creek, vs. Waunita,	0.05	0.00	0.09
Razor Creek, vs. Waunita NW,	0.05	0.01	0.11
Razor Creek Divide, vs. Razor Dome 1 & 2,	-0.01	-0.07	0.05
Razor Creek Divide, vs. Ridgeline,	0.10	-0.04	0.21
Razor Creek Divide, vs. Sapinero Corral,	-0.09	-0.22	0.03
Razor Creek Divide, vs. South Beaver Creek,	0.00	-0.05	0.07
Razor Creek Divide, vs. Sugar Creek,	0.00	-0.03	0.04
Razor Creek Divide, vs. Sewell Gulch,	-0.06	-0.18	0.04
Razor Creek Divide, vs. Signal Peak,	-0.03	-0.11	0.05
Razor Creek Divide, vs. South 6 Mile Meadow,	0.03	-0.05	0.10
Razor Creek Divide, vs. Sapinero 10 Mile Spring,	0.01	-0.04	0.07
Razor Creek Divide, vs. South 6 Mile Ridge,	0.06	-0.02	0.15
Razor Creek Divide, vs. South Parlin 1,	-0.01	-0.05	0.05
Razor Creek Divide, vs. South Parlin 3,	0.03	-0.05	0.12
Razor Creek Divide, vs. Sapinero Powerline,	0.03	-0.03	0.10
Razor Creek Divide, vs. South Parlin Upper,	0.01	-0.06	0.09
Razor Creek Divide, vs. Signal Peak West,	0.03	-0.05	0.12
Razor Creek Divide, vs. Sapinero Ridge,	0.03	-0.04	0.10
Razor Creek Divide, vs. Sapinero South,	0.01	-0.04	0.06
Razor Creek Divide, vs. Scout,	0.06	-0.01	0.14
Razor Creek Divide, vs. Steven's Creek East,	0.08	-0.05	0.20
Razor Creek Divide, vs. Taila's Lek,	0.00	-0.07	0.08
Razor Creek Divide, vs. Teachout 1 & 2,	-0.02	-0.08	0.04
Razor Creek Divide, vs. Teachout 3,5,6,	-0.01	-0.08	0.07
Razor Creek Divide, vs. Vito,	0.01	-0.06	0.08
Razor Creek Divide, vs. Wood's Gulch,	0.02	-0.03	0.07
Razor Creek Divide, vs. Waunita,	-0.01	-0.09	0.07
Razor Creek Divide, vs. Waunita NW,	0.06	-0.01	0.12
Razor Dome 1 & 2, vs. Ridgeline,	0.05	-0.01	0.09
Razor Dome 1 & 2, vs. Sapinero Corral,	0.01	-0.02	0.04
Razor Dome 1 & 2, vs. South Beaver Creek,	0.02	0.01	0.04
Razor Dome 1 & 2, vs. Sugar Creek,	0.02	0.01	0.05

Lek Comparison	F_{ST}	lower	upper
Razor Dome 1 & 2, vs. Sewell Gulch,	0.01	-0.02	0.05
Razor Dome 1 & 2, vs. Signal Peak,	0.00	-0.03	0.04
Razor Dome 1 & 2, vs. South 6 Mile Meadow,	0.05	0.01	0.10
Razor Dome 1 & 2, vs. Sapinero 10 Mile Spring,	0.02	0.01	0.04
Razor Dome 1 & 2, vs. South 6 Mile Ridge,	0.04	0.02	0.06
Razor Dome 1 & 2, vs. South Parlin 1,	0.02	0.01	0.03
Razor Dome 1 & 2, vs. South Parlin 3,	0.01	0.00	0.03
Razor Dome 1 & 2, vs. Sapinero Powerline,	0.04	0.01	0.07
Razor Dome 1 & 2, vs. South Parlin Upper,	0.02	0.01	0.03
Razor Dome 1 & 2, vs. Signal Peak West,	0.04	0.01	0.07
Razor Dome 1 & 2, vs. Sapinero Ridge,	0.04	0.02	0.06
Razor Dome 1 & 2, vs. Sapinero South,	0.02	0.01	0.03
Razor Dome 1 & 2, vs. Scout,	0.05	0.03	0.07
Razor Dome 1 & 2, vs. Steven's Creek East,	0.03	-0.03	0.10
Razor Dome 1 & 2, vs. Taila's Lek,	0.02	0.00	0.04
Razor Dome 1 & 2, vs. Teachout 1 & 2,	0.01	0.00	0.02
Razor Dome 1 & 2, vs. Teachout 3,5,6,	0.06	0.04	0.08
Razor Dome 1 & 2, vs. Vito,	0.05	0.02	0.08
Razor Dome 1 & 2, vs. Wood's Gulch,	0.06	0.03	0.09
Razor Dome 1 & 2, vs. Waunita,	0.06	0.03	0.09
Razor Dome 1 & 2, vs. Waunita NW,	0.06	0.03	0.10
Ridgeline, vs. Sapinero Corral,	0.07	-0.02	0.16
Ridgeline, vs. South Beaver Creek,	0.09	0.04	0.14
Ridgeline, vs. Sugar Creek,	0.04	-0.01	0.08
Ridgeline, vs. Sewell Gulch,	0.07	-0.09	0.24
Ridgeline, vs. Signal Peak,	0.08	-0.01	0.17
Ridgeline, vs. South 6 Mile Meadow,	0.18	0.09	0.29
Ridgeline, vs. Sapinero 10 Mile Spring,	0.03	-0.04	0.10
Ridgeline, vs. South 6 Mile Ridge,	0.13	0.06	0.21
Ridgeline, vs. South Parlin 1,	0.07	0.01	0.13
Ridgeline, vs. South Parlin 3,	0.07	0.01	0.14
Ridgeline, vs. Sapinero Powerline,	0.04	-0.02	0.11
Ridgeline, vs. South Parlin Upper,	0.06	0.01	0.12
Ridgeline, vs. Signal Peak West,	0.06	-0.02	0.15
Ridgeline, vs. Sapinero Ridge,	0.02	-0.03	0.06
Ridgeline, vs. Sapinero South,	0.04	-0.01	0.09
Ridgeline, vs. Scout,	0.13	0.04	0.21
Ridgeline, vs. Steven's Creek East,	-0.01	-0.13	0.13
Ridgeline, vs. Taila's Lek,	0.05	-0.01	0.11
Ridgeline, vs. Teachout 1 & 2,	0.06	0.00	0.11
Ridgeline, vs. Teachout 3,5,6,	0.06	-0.01	0.12
Ridgeline, vs. Vito,	0.05	-0.01	0.12

Lek Comparison	F_{ST}	lower	upper
Ridgeline, vs. Wood's Gulch,	0.11	0.03	0.18
Ridgeline, vs. Waunita,	0.10	0.02	0.18
Ridgeline, vs. Waunita NW,	0.16	0.07	0.25
Sapinero Corral, vs. South Beaver Creek,	0.03	-0.01	0.08
Sapinero Corral, vs. Sugar Creek,	0.03	-0.01	0.07
Sapinero Corral, vs. Sewell Gulch,	0.01	-0.10	0.12
Sapinero Corral, vs. Signal Peak,	-0.02	-0.08	0.03
Sapinero Corral, vs. South 6 Mile Meadow,	0.07	-0.01	0.16
Sapinero Corral, vs. Sapinero 10 Mile Spring,	-0.01	-0.05	0.02
Sapinero Corral, vs. South 6 Mile Ridge,	0.07	0.02	0.12
Sapinero Corral, vs. South Parlin 1,	0.01	-0.02	0.04
Sapinero Corral, vs. South Parlin 3,	0.01	-0.04	0.06
Sapinero Corral, vs. Sapinero Powerline,	0.02	-0.02	0.07
Sapinero Corral, vs. South Parlin Upper,	0.01	-0.03	0.05
Sapinero Corral, vs. Signal Peak West,	0.00	-0.05	0.06
Sapinero Corral, vs. Sapinero Ridge,	0.01	-0.03	0.06
Sapinero Corral, vs. Sapinero South,	0.00	-0.03	0.02
Sapinero Corral, vs. Scout,	0.06	0.00	0.11
Sapinero Corral, vs. Steven's Creek East,	0.04	-0.06	0.14
Sapinero Corral, vs. Taila's Lek,	0.02	-0.03	0.07
Sapinero Corral, vs. Teachout 1 & 2,	0.00	-0.04	0.04
Sapinero Corral, vs. Teachout 3,5,6,	0.01	-0.03	0.05
Sapinero Corral, vs. Vito,	0.01	-0.04	0.07
Sapinero Corral, vs. Wood's Gulch,	0.03	-0.01	0.07
Sapinero Corral, vs. Waunita,	0.03	-0.03	0.10
Sapinero Corral, vs. Waunita NW,	0.08	0.01	0.15
South Beaver Creek, vs. Sugar Creek,	0.02	0.00	0.03
South Beaver Creek, vs. Sewell Gulch,	0.06	-0.01	0.15
South Beaver Creek, vs. Signal Peak,	0.01	-0.04	0.05
South Beaver Creek, vs. South 6 Mile Meadow,	0.07	0.03	0.13
South Beaver Creek, vs. Sapinero 10 Mile Spring,	0.02	0.00	0.03
South Beaver Creek, vs. South 6 Mile Ridge,	0.05	0.02	0.07
South Beaver Creek, vs. South Parlin 1,	0.02	0.01	0.04
South Beaver Creek, vs. South Parlin 3,	0.01	-0.01	0.03
South Beaver Creek, vs. Sapinero Powerline,	0.04	0.01	0.07
South Beaver Creek, vs. South Parlin Upper,	0.02	0.00	0.04
South Beaver Creek, vs. Signal Peak West,	0.03	0.01	0.05
South Beaver Creek, vs. Sapinero Ridge,	0.05	0.03	0.07
South Beaver Creek, vs. Sapinero South,	0.03	0.02	0.05
South Beaver Creek, vs. Scout,	0.06	0.03	0.08
South Beaver Creek, vs. Steven's Creek East,	0.08	0.00	0.16
South Beaver Creek, vs. Taila's Lek,	0.02	0.00	0.04

Lek Comparison	F_{ST}	lower	upper
South Beaver Creek, vs. Teachout 1 & 2,	0.02	0.01	0.04
South Beaver Creek, vs. Teachout 3,5,6,	0.06	0.02	0.09
South Beaver Creek, vs. Vito,	0.05	0.03	0.09
South Beaver Creek, vs. Wood's Gulch,	0.04	0.03	0.07
South Beaver Creek, vs. Waunita,	0.08	0.03	0.14
South Beaver Creek, vs. Waunita NW,	0.11	0.06	0.17
Sugar Creek, vs. Sewell Gulch,	0.05	-0.01	0.16
Sugar Creek, vs. Signal Peak,	0.01	-0.02	0.05
Sugar Creek, vs. South 6 Mile Meadow,	0.08	0.02	0.16
Sugar Creek, vs. Sapinero 10 Mile Spring,	0.01	0.00	0.03
Sugar Creek, vs. South 6 Mile Ridge,	0.05	0.03	0.08
Sugar Creek, vs. South Parlin 1,	0.02	0.01	0.04
Sugar Creek, vs. South Parlin 3,	0.03	0.01	0.06
Sugar Creek, vs. Sapinero Powerline,	0.04	0.01	0.06
Sugar Creek, vs. South Parlin Upper,	0.03	0.01	0.05
Sugar Creek, vs. Signal Peak West,	0.04	0.02	0.06
Sugar Creek, vs. Sapinero Ridge,	0.03	0.01	0.06
Sugar Creek, vs. Sapinero South,	0.02	0.01	0.03
Sugar Creek, vs. Scout,	0.06	0.04	0.09
Sugar Creek, vs. Steven's Creek East,	0.03	-0.03	0.10
Sugar Creek, vs. Taila's Lek,	0.02	0.01	0.04
Sugar Creek, vs. Teachout 1 & 2,	0.02	0.00	0.04
Sugar Creek, vs. Teachout 3,5,6,	0.05	0.03	0.07
Sugar Creek, vs. Vito,	0.04	0.02	0.06
Sugar Creek, vs. Wood's Gulch,	0.04	0.03	0.06
Sugar Creek, vs. Waunita,	0.08	0.03	0.14
Sugar Creek, vs. Waunita NW,	0.10	0.04	0.17
Sewell Gulch, vs. Signal Peak,	-0.02	-0.11	0.06
Sewell Gulch, vs. South 6 Mile Meadow,	0.03	-0.03	0.09
Sewell Gulch, vs. Sapinero 10 Mile Spring,	0.05	-0.01	0.13
Sewell Gulch, vs. South 6 Mile Ridge,	0.11	0.04	0.18
Sewell Gulch, vs. South Parlin 1,	0.04	-0.01	0.10
Sewell Gulch, vs. South Parlin 3,	0.09	0.01	0.19
Sewell Gulch, vs. Sapinero Powerline,	0.07	-0.02	0.18
Sewell Gulch, vs. South Parlin Upper,	0.03	-0.02	0.10
Sewell Gulch, vs. Signal Peak West,	0.03	-0.07	0.14
Sewell Gulch, vs. Sapinero Ridge,	0.05	-0.01	0.13
Sewell Gulch, vs. Sapinero South,	0.03	-0.02	0.11
Sewell Gulch, vs. Scout,	0.06	-0.01	0.14
Sewell Gulch, vs. Steven's Creek East,	-0.04	-0.11	0.09
Sewell Gulch, vs. Taila's Lek,	0.06	-0.02	0.16
Sewell Gulch, vs. Teachout 1 & 2,	0.02	-0.03	0.07

Lek Comparison	F_{ST}	lower	upper
Sewell Gulch, vs. Teachout 3,5,6,	0.01	-0.05	0.08
Sewell Gulch, vs. Vito,	0.00	-0.07	0.07
Sewell Gulch, vs. Wood's Gulch,	0.05	-0.04	0.16
Sewell Gulch, vs. Waunita,	0.00	-0.08	0.08
Sewell Gulch, vs. Waunita NW,	0.06	-0.02	0.14
Signal Peak, vs. South 6 Mile Meadow,	0.03	-0.03	0.10
Signal Peak, vs. Sapinero 10 Mile Spring,	-0.01	-0.05	0.02
Signal Peak, vs. South 6 Mile Ridge,	0.02	-0.03	0.07
Signal Peak, vs. South Parlin 1,	0.01	-0.03	0.05
Signal Peak, vs. South Parlin 3,	0.03	-0.02	0.08
Signal Peak, vs. Sapinero Powerline,	0.03	-0.03	0.08
Signal Peak, vs. South Parlin Upper,	-0.01	-0.04	0.03
Signal Peak, vs. Signal Peak West,	0.04	-0.02	0.10
Signal Peak, vs. Sapinero Ridge,	0.02	-0.02	0.07
Signal Peak, vs. Sapinero South,	0.00	-0.03	0.03
Signal Peak, vs. Scout,	0.05	0.00	0.08
Signal Peak, vs. Steven's Creek East,	0.06	-0.03	0.16
Signal Peak, vs. Taila's Lek,	0.02	-0.04	0.09
Signal Peak, vs. Teachout 1 & 2,	0.00	-0.02	0.03
Signal Peak, vs. Teachout 3,5,6,	0.03	-0.01	0.06
Signal Peak, vs. Vito,	0.03	0.00	0.06
Signal Peak, vs. Wood's Gulch,	0.03	-0.01	0.06
Signal Peak, vs. Waunita,	0.02	-0.02	0.06
Signal Peak, vs. Waunita NW,	0.08	0.01	0.17
South 6 Mile Meadow, vs. Sapinero 10 Mile Spring,	0.09	0.04	0.16
South 6 Mile Meadow, vs. South 6 Mile Ridge,	0.08	0.04	0.13
South 6 Mile Meadow, vs. South Parlin 1,	0.07	0.03	0.13
South 6 Mile Meadow, vs. South Parlin 3,	0.11	0.04	0.20
South 6 Mile Meadow, vs. Sapinero Powerline,	0.11	0.05	0.19
South 6 Mile Meadow, vs. South Parlin Upper,	0.08	0.02	0.13
South 6 Mile Meadow, vs. Signal Peak West,	0.13	0.07	0.20
South 6 Mile Meadow, vs. Sapinero Ridge,	0.11	0.04	0.18
South 6 Mile Meadow, vs. Sapinero South,	0.10	0.05	0.17
South 6 Mile Meadow, vs. Scout,	0.10	0.06	0.13
South 6 Mile Meadow, vs. Steven's Creek East,	0.09	0.02	0.19
South 6 Mile Meadow, vs. Taila's Lek,	0.11	0.06	0.17
South 6 Mile Meadow, vs. Teachout 1 & 2,	0.08	0.03	0.13
South 6 Mile Meadow, vs. Teachout 3,5,6,	0.10	0.05	0.14
South 6 Mile Meadow, vs. Vito,	0.10	0.05	0.14
South 6 Mile Meadow, vs. Wood's Gulch,	0.08	0.04	0.15
South 6 Mile Meadow, vs. Waunita,	0.09	0.04	0.14
South 6 Mile Meadow, vs. Waunita NW,	0.12	0.07	0.18

Lek Comparison	F_{ST}	lower	upper
Sapinero 10 Mile Spring, vs. South 6 Mile Ridge,	0.04	0.02	0.07
Sapinero 10 Mile Spring, vs. South Parlin 1,	0.03	0.02	0.05
Sapinero 10 Mile Spring, vs. South Parlin 3,	0.02	-0.01	0.05
Sapinero 10 Mile Spring, vs. Sapinero Powerline,	0.00	-0.01	0.01
Sapinero 10 Mile Spring, vs. South Parlin Upper,	0.03	0.01	0.05
Sapinero 10 Mile Spring, vs. Signal Peak West,	0.03	0.01	0.06
Sapinero 10 Mile Spring, vs. Sapinero Ridge,	0.02	0.00	0.04
Sapinero 10 Mile Spring, vs. Sapinero South,	0.00	-0.01	0.00
Sapinero 10 Mile Spring, vs. Scout,	0.05	0.03	0.07
Sapinero 10 Mile Spring, vs. Steven's Creek East,	0.03	-0.04	0.12
Sapinero 10 Mile Spring, vs. Taila's Lek,	0.03	0.01	0.05
Sapinero 10 Mile Spring, vs. Teachout 1 & 2,	0.01	0.00	0.03
Sapinero 10 Mile Spring, vs. Teachout 3,5,6,	0.05	0.03	0.09
Sapinero 10 Mile Spring, vs. Vito,	0.04	0.01	0.08
Sapinero 10 Mile Spring, vs. Wood's Gulch,	0.04	0.02	0.05
Sapinero 10 Mile Spring, vs. Waunita,	0.08	0.03	0.13
Sapinero 10 Mile Spring, vs. Waunita NW,	0.10	0.05	0.16
South 6 Mile Ridge, vs. South Parlin 1,	0.06	0.03	0.08
South 6 Mile Ridge, vs. South Parlin 3,	0.07	0.04	0.10
South 6 Mile Ridge, vs. Sapinero Powerline,	0.05	0.03	0.08
South 6 Mile Ridge, vs. South Parlin Upper,	0.05	0.02	0.08
South 6 Mile Ridge, vs. Signal Peak West,	0.10	0.06	0.13
South 6 Mile Ridge, vs. Sapinero Ridge,	0.07	0.05	0.09
South 6 Mile Ridge, vs. Sapinero South,	0.06	0.03	0.09
South 6 Mile Ridge, vs. Scout,	0.07	0.04	0.10
South 6 Mile Ridge, vs. Steven's Creek East,	0.11	0.01	0.21
South 6 Mile Ridge, vs. Taila's Lek,	0.05	0.03	0.07
South 6 Mile Ridge, vs. Teachout 1 & 2,	0.06	0.03	0.09
South 6 Mile Ridge, vs. Teachout 3,5,6,	0.06	0.04	0.09
South 6 Mile Ridge, vs. Vito,	0.06	0.04	0.08
South 6 Mile Ridge, vs. Wood's Gulch,	0.08	0.04	0.11
South 6 Mile Ridge, vs. Waunita,	0.10	0.06	0.14
South 6 Mile Ridge, vs. Waunita NW,	0.13	0.06	0.19
South Parlin 1, vs. South Parlin 3,	0.02	0.00	0.04
South Parlin 1, vs. Sapinero Powerline,	0.05	0.02	0.09
South Parlin 1, vs. South Parlin Upper,	0.01	0.00	0.02
South Parlin 1, vs. Signal Peak West,	0.02	0.00	0.04
South Parlin 1, vs. Sapinero Ridge,	0.04	0.01	0.08
South Parlin 1, vs. Sapinero South,	0.03	0.02	0.04
South Parlin 1, vs. Scout,	0.07	0.04	0.10
South Parlin 1, vs. Steven's Creek East,	0.05	-0.02	0.12
South Parlin 1, vs. Taila's Lek,	0.02	0.01	0.05

Lek Comparison	F_{ST}	lower	upper
South Parlin 1, vs. Teachout 1 & 2,	0.02	0.01	0.03
South Parlin 1, vs. Teachout 3,5,6,	0.06	0.04	0.09
South Parlin 1, vs. Vito,	0.05	0.03	0.08
South Parlin 1, vs. Wood's Gulch,	0.06	0.03	0.09
South Parlin 1, vs. Waunita,	0.06	0.04	0.10
South Parlin 1, vs. Waunita NW,	0.06	0.04	0.09
South Parlin 3, vs. Sapinero Powerline,	0.02	0.00	0.04
South Parlin 3, vs. South Parlin Upper,	0.00	-0.01	0.01
South Parlin 3, vs. Signal Peak West,	0.03	0.01	0.06
South Parlin 3, vs. Sapinero Ridge,	0.04	0.02	0.06
South Parlin 3, vs. Sapinero South,	0.02	0.00	0.03
South Parlin 3, vs. Scout,	0.05	0.03	0.08
South Parlin 3, vs. Steven's Creek East,	0.05	-0.03	0.15
South Parlin 3, vs. Taila's Lek,	0.01	-0.01	0.03
South Parlin 3, vs. Teachout 1 & 2,	0.01	-0.01	0.03
South Parlin 3, vs. Teachout 3,5,6,	0.05	0.02	0.08
South Parlin 3, vs. Vito,	0.04	0.02	0.07
South Parlin 3, vs. Wood's Gulch,	0.05	0.01	0.11
South Parlin 3, vs. Waunita,	0.07	0.03	0.13
South Parlin 3, vs. Waunita NW,	0.10	0.04	0.17
Sapinero Powerline, vs. South Parlin Upper,	0.03	0.02	0.06
Sapinero Powerline, vs. Signal Peak West,	0.06	0.02	0.09
Sapinero Powerline, vs. Sapinero Ridge,	0.03	0.00	0.05
Sapinero Powerline, vs. Sapinero South,	0.02	0.01	0.04
Sapinero Powerline, vs. Scout,	0.06	0.03	0.09
Sapinero Powerline, vs. Steven's Creek East,	0.04	-0.03	0.11
Sapinero Powerline, vs. Taila's Lek,	0.05	0.02	0.08
Sapinero Powerline, vs. Teachout 1 & 2,	0.04	0.00	0.07
Sapinero Powerline, vs. Teachout 3,5,6,	0.06	0.02	0.09
Sapinero Powerline, vs. Vito,	0.04	0.01	0.07
Sapinero Powerline, vs. Wood's Gulch,	0.05	0.01	0.09
Sapinero Powerline, vs. Waunita,	0.08	0.03	0.14
Sapinero Powerline, vs. Waunita NW,	0.11	0.04	0.19
South Parlin Upper, vs. Signal Peak West,	0.02	0.00	0.03
South Parlin Upper, vs. Sapinero Ridge,	0.04	0.02	0.07
South Parlin Upper, vs. Sapinero South,	0.03	0.01	0.04
South Parlin Upper, vs. Scout,	0.05	0.03	0.07
South Parlin Upper, vs. Steven's Creek East,	0.02	-0.04	0.10
South Parlin Upper, vs. Taila's Lek,	0.02	0.00	0.03
South Parlin Upper, vs. Teachout 1 & 2,	0.01	0.00	0.02
South Parlin Upper, vs. Teachout 3,5,6,	0.04	0.02	0.06
South Parlin Upper, vs. Vito,	0.03	0.01	0.05

Lek Comparison	F_{ST}	lower	upper
South Parlin Upper, vs. Wood's Gulch,	0.05	0.02	0.10
South Parlin Upper, vs. Waunita,	0.05	0.02	0.08
South Parlin Upper, vs. Waunita NW,	0.07	0.04	0.11
Signal Peak West, vs. Sapinero Ridge,	0.04	0.01	0.07
Signal Peak West, vs. Sapinero South,	0.03	0.01	0.06
Signal Peak West, vs. Scout,	0.04	0.01	0.08
Signal Peak West, vs. Steven's Creek East,	0.02	-0.05	0.09
Signal Peak West, vs. Taila's Lek,	0.02	0.00	0.05
Signal Peak West, vs. Teachout 1 & 2,	0.03	0.00	0.05
Signal Peak West, vs. Teachout 3,5,6,	0.04	0.00	0.08
Signal Peak West, vs. Vito,	0.04	0.00	0.08
Signal Peak West, vs. Wood's Gulch,	0.07	0.02	0.10
Signal Peak West, vs. Waunita,	0.05	-0.01	0.12
Signal Peak West, vs. Waunita NW,	0.11	0.04	0.17
Sapinero Ridge, vs. Sapinero South,	0.01	0.00	0.02
Sapinero Ridge, vs. Scout,	0.08	0.05	0.11
Sapinero Ridge, vs. Steven's Creek East,	0.05	-0.02	0.12
Sapinero Ridge, vs. Taila's Lek,	0.04	0.02	0.07
Sapinero Ridge, vs. Teachout 1 & 2,	0.03	0.01	0.04
Sapinero Ridge, vs. Teachout 3,5,6,	0.04	0.02	0.06
Sapinero Ridge, vs. Vito,	0.04	0.02	0.06
Sapinero Ridge, vs. Wood's Gulch,	0.07	0.04	0.11
Sapinero Ridge, vs. Waunita,	0.07	0.03	0.13
Sapinero Ridge, vs. Waunita NW,	0.10	0.05	0.16
Sapinero South, vs. Scout,	0.06	0.04	0.08
Sapinero South, vs. Steven's Creek East,	0.05	-0.01	0.14
Sapinero South, vs. Taila's Lek,	0.03	0.01	0.05
Sapinero South, vs. Teachout 1 & 2,	0.01	0.00	0.02
Sapinero South, vs. Teachout 3,5,6,	0.05	0.03	0.07
Sapinero South, vs. Vito,	0.04	0.02	0.07
Sapinero South, vs. Wood's Gulch,	0.05	0.04	0.08
Sapinero South, vs. Waunita,	0.06	0.03	0.10
Sapinero South, vs. Waunita NW,	0.08	0.04	0.12
Scout, vs. Steven's Creek East,	0.05	0.00	0.08
Scout, vs. Taila's Lek,	0.04	0.02	0.06
Scout, vs. Teachout 1 & 2,	0.05	0.02	0.07
Scout, vs. Teachout 3,5,6,	0.06	0.03	0.09
Scout, vs. Vito,	0.05	0.02	0.07
Scout, vs. Wood's Gulch,	0.06	0.04	0.09
Scout, vs. Waunita,	0.08	0.04	0.13
Scout, vs. Waunita NW,	0.12	0.06	0.20
Steven's Creek East, vs. Taila's Lek,	0.06	-0.02	0.13

Lek Comparison	F_{ST}	lower	upper
Steven's Creek East, vs. Teachout 1 & 2,	0.05	-0.03	0.13
Steven's Creek East, vs. Teachout 3,5,6,	0.02	-0.04	0.07
Steven's Creek East, vs. Vito,	0.01	-0.05	0.07
Steven's Creek East, vs. Wood's Gulch,	0.11	0.01	0.20
Steven's Creek East, vs. Waunita,	0.04	-0.01	0.08
Steven's Creek East, vs. Waunita NW,	0.16	0.08	0.23
Taila's Lek, vs. Teachout 1 & 2,	0.00	-0.01	0.01
Taila's Lek, vs. Teachout 3,5,6,	0.04	0.01	0.07
Taila's Lek, vs. Vito,	0.02	0.00	0.05
Taila's Lek, vs. Wood's Gulch,	0.05	0.02	0.10
Taila's Lek, vs. Waunita,	0.06	0.01	0.11
Taila's Lek, vs. Waunita NW,	0.09	0.04	0.14
Teachout 1 & 2, vs. Teachout 3,5,6,	0.03	0.01	0.05
Teachout 1 & 2, vs. Vito,	0.02	0.01	0.05
Teachout 1 & 2, vs. Wood's Gulch,	0.05	0.03	0.08
Teachout 1 & 2, vs. Waunita,	0.05	0.01	0.08
Teachout 1 & 2, vs. Waunita NW,	0.08	0.04	0.12
Teachout 3,5,6, vs. Vito,	0.00	-0.01	0.02
Teachout 3,5,6, vs. Wood's Gulch,	0.07	0.03	0.10
Teachout 3,5,6, vs. Waunita,	0.03	0.00	0.07
Teachout 3,5,6, vs. Waunita NW,	0.10	0.05	0.15
Vito, vs. Wood's Gulch,	0.05	0.02	0.08
Vito, vs. Waunita,	0.02	0.00	0.06
Vito, vs. Waunita NW,	0.09	0.05	0.14
Wood's Gulch, vs. Waunita,	0.09	0.05	0.16
Wood's Gulch, vs. Waunita NW,	0.10	0.03	0.18
Waunita, vs. Waunita NW,	0.02	-0.01	0.06

Table S15.2. F_{ST} (Weir and Cockerharm 1984) values for all population comparisons. Upper and lower bounds for 95% confidence intervals are in the last two columns.

Population Comparison	F_{ST}	lower	upper
Cimarron, vs. Crawford,	0.12	0.10	0.24
Cimarron, vs. Dove Creek,	0.18	0.16	0.29
Cimarron, vs. Gunnison Basin,	0.12	0.10	0.22
Cimarron, vs. Piñon Mesa,	0.29	0.28	0.40
Cimarron, vs. San Miguel,	0.15	0.13	0.24
Crawford, vs. Dove Creek,	0.18	0.16	0.22
Crawford, vs. Gunnison Basin,	0.09	0.08	0.12
Crawford, vs. Piñon Mesa,	0.29	0.28	0.35
Crawford, vs. San Miguel,	0.14	0.12	0.19
Dove Creek, vs. Gunnison Basin,	0.17	0.16	0.19
Dove Creek, vs. Piñon Mesa,	0.27	0.26	0.31
Dove Creek, vs. San Miguel,	0.14	0.13	0.18
Gunnison Basin, vs. Piñon Mesa,	0.24	0.24	0.27
Gunnison Basin, vs. San Miguel,	0.14	0.13	0.17
Piñon Mesa, vs. San Miguel,	0.23	0.22	0.27

APPENDIX XVI

I calculated a dryness index (DRI) and growing degree days (GDD) from Daymet (Thornton et al. 2017) data (see below for calculations). Individual tiles covering the study area (tiles 11376, 11377, 11556, 11557, 11558) were obtained for the time period 1997 to 2005 in the form of a NETcdf file. NETcdf files were converted to raster format and joined into a single surface (Python scripts available at https://daymet.ornl.gov/tools.html). GDD was calculated in ArcGIS10.1 by finding the average temperature, and counting the number of days in each year between 1 March and 31 August with temperatures greater than 5°C. The final GDD raster layer is an average across 9 years (1977 – 2005) to represent contemporary conditions. DRI was calculated by dividing GDD by the cumulative precipitation between 1 March and 31 August for each year. The final DRI raster layer is an average of 9 years. My habitat variables were obtained from 30-m resolution Landfire data and processed in ArcGIS 10.1. I broke the cover types up into all sagebrush cover, low sagebrush cover, big sagebrush cover, and conifer cover, reclassifying a binary raster for each variable with the target variable given a 1 and everything else a 0. At the original 30-m resolution, cover type is presence/absence based. I was also interested in the configuration of conifer cover. To assess configuration I first had to convert the 30-m presence/absence conifer cover raster to point data. Next I applied a nearest neighbor analysis using the "near" tool in the analysis tools of arcMap. The output was then converted back to a raster and the nearest neighbor index was calculated by dividing the raster output by the mean distance (0.5*sqrt(total area/# of points in the distribution). Values less than 1 are considered clustered, while values greater than one are considered dispersed. The phenology tool (Talbert et al., 2013) was used to vegetation index values at different points on the phenology curve from MODIS normalized difference vegetation index (NDVI) data: green-up (beginning of

growing season), brown-down (end of growing season), green-up rate (left derivative of the phenology curve), brown-down rate (right derivative of the phenology curve), and season length. Values for the years 2000 to 2010 were averaged for season 1 (the onset of growth). All spatial analyses were performed in ArcGIS10.1 unless stated otherwise. I obtained 30-year normals for annual and monthly rainfall, maximum temperature, minimum temperature, mean temperature, average dewpoint (the temperature below which water droplets begin to form; giving a sense of the amount of moisture in the air), minimum and maximum vapor pressure (the atmospheric pressure which is exerted by water vapor; a measure of humidity) at a resolution of 800 m from PRISM Climate Group (http://prism.oregonstate.edu). The monthly estimates were averaged into spring (average of April, May, and June), summer (average of July, August, September), fall (average of October, November, December) and winter (average of January, February, March) seasons according to the Farmer's Almanac (https://www.farmersalmanac.com/the-seasons). I also averaged across nesting/leking (March, April, May), brood rearing (June, July, August, September), and winter (October, November, December, January, February, March) seasons of habitat use. Values were extracted from rasters with a 1-km radius for each lek. Values for leks were averaged across populations.

Table S16.1. Covariates included in tests for outlier loci.

Covariate	Spatial Source	Derived
Elevation	DEM	
Dominant Shrub	Listing Decision	
Brown-Down	phenology tool	NDVI from MODIS
Brown-Down Rate	phenology tool	NDVI from MODIS
Green-Up	phenology tool	NDVI from MODIS
Green-Up Rate	phenology tool	NDVI from MODIS
Season Length	phenology tool	NDVI from MODIS
Low Sage	Landfire	
Conifer	Landfire	

Covariate	Spatial Source	Derived
Big Sage	Landfire	
All Sage	Landfire	
Growing Degree Days	Daymet	
Dryness Index	Daymet	
Conifer Configuration	Landfire	nearest neighbor index
Precipitation		
Annual	PRISM	
Spring	PRISM	ave. of Apr, May, Jun
Summer	PRISM	ave. of Jul, Aug, Sep
Fall	PRISM	ave. of Oct, Nov, Dec
Winter	PRISM	ave. of Jan, Feb, Mar
Life Stage Precipitation		
Nesting	PRISM	ave. Mar, Apr, May
Brood Rearing	PRISM	ave. Jun, Jul, Aug, Sep
Winter	PRISM	ave. Oct, Nov, Dec, Jan, Feb
Maximum Temperature		
Annual	PRISM	
Spring	PRISM	ave. of Apr, May, Jun
Summer	PRISM	ave. of Jul, Aug, Sep
Fall	PRISM	ave. of Oct, Nov, Dec
Winter	PRISM	ave. of Jan, Feb, Mar
Life Stage Maximum Temperature		
Nesting	PRISM	ave. Mar, Apr, May
Brood Rearing	PRISM	ave. Jun, Jul, Aug, Sep
Winter	PRISM	ave. Oct, Nov, Dec, Jan, Feb
Dew Point		
Annual	PRISM	
Spring	PRISM	ave. of Apr, May, Jun
Summer	PRISM	ave. of Jul, Aug, Sep
Fall	PRISM	ave. of Oct, Nov, Dec
Winter	PRISM	ave. of Jan, Feb, Mar
Life Stage Dew Point		
Nesting	PRISM	ave. Mar, Apr, May
Brood Rearing	PRISM	ave. Jun, Jul, Aug, Sep
Winter	PRISM	ave. Oct, Nov, Dec, Jan, Feb
Mean Temperature		
Annual	PRISM	
Spring	PRISM	ave. of Apr, May, Jun

Covariate	Spatial Source	Derived
Summer	PRISM	ave. of Jul, Aug, Sep
Fall	PRISM	ave. of Oct, Nov, Dec
Winter	PRISM	ave. of Jan, Feb, Mar
Life Stage Mean Temperature		
Nesting	PRISM	ave. Mar, Apr, May
Brood Rearing	PRISM	ave. Jun, Jul, Aug, Sep
Winter	PRISM	ave. Oct, Nov, Dec, Jan, Feb
Minimum Temperature		
Annual	PRISM	
Spring	PRISM	ave. of Apr, May, Jun
Summer	PRISM	ave. of Jul, Aug, Sep
Fall	PRISM	ave. of Oct, Nov, Dec
Winter	PRISM	ave. of Jan, Feb, Mar
Life Stage Minimum Temperature		
Nesting	PRISM	ave. Mar, Apr, May
Brood Rearing	PRISM	ave. Jun, Jul, Aug, Sep
Winter	PRISM	ave. Oct, Nov, Dec, Jan, Feb
Maximum Vapor Pressure		
Annual	PRISM	
Spring	PRISM	ave. of Apr, May, Jun
Summer	PRISM	ave. of Jul, Aug, Sep
Fall	PRISM	ave. of Oct, Nov, Dec
Winter	PRISM	ave. of Jan, Feb, Mar
Life Stage Maximum Vapor Pressure		
Nesting	PRISM	ave. Mar, Apr, May
Brood Rearing	PRISM	ave. Jun, Jul, Aug, Sep
Winter	PRISM	ave. Oct, Nov, Dec, Jan, Feb
Minimum Vapor Pressure		
Annual	PRISM	
Spring	PRISM	ave. of Apr, May, Jun
Summer	PRISM	ave. of Jul, Aug, Sep
Fall	PRISM	ave. of Oct, Nov, Dec
Winter	PRISM	ave. of Jan, Feb, Mar
Life Stage Minimum Vapor Pressure		
Nesting	PRISM	ave. Mar, Apr, May
Brood Rearing	PRISM	ave. Jun, Jul, Aug, Sep
Winter	PRISM	ave. Oct, Nov, Dec, Jan, Feb

Table S16.2. Correlation coefficients for uncorrelated variables included as covariates in tests for outlier loci.

	spring_ppt	fall_ppt	spring_tmax	winter_vpdmax	cti	gur	bs	dri
spring_ppt	1.00							
fall_ppt	0.52	1.00						
spring_tmax	-0.35	0.23	1.00					
winter_vpdmax	0.68	0.63	0.41	1.00				
cti	-0.39	0.19	0.61	0.23	1.00			
gur	0.31	0.47	-0.64	-0.23	-0.29	1.00		
bs	0.09	0.11	0.69	0.56	-0.01	-0.65	1.00	
dri	-0.62	-0.28	0.39	-0.47	-0.09	-0.30	0.14	1.00

Table S16.3. Loadings of uncorrelated variables onto principle components.

Covariate	PC1	PC2	PC3
spring_ppt	-0.13	0.53	-0.12
fall_ppt	-0.03	0.34	0.29
spring_tmax	0.53	-0.05	0.25
winter_vpdmax	0.28	0.54	0.15
cti	0.19	-0.07	0.76
gur	-0.53	0.15	0.11
bs	0.54	0.21	-0.48
dri	0.13	-0.50	-0.06

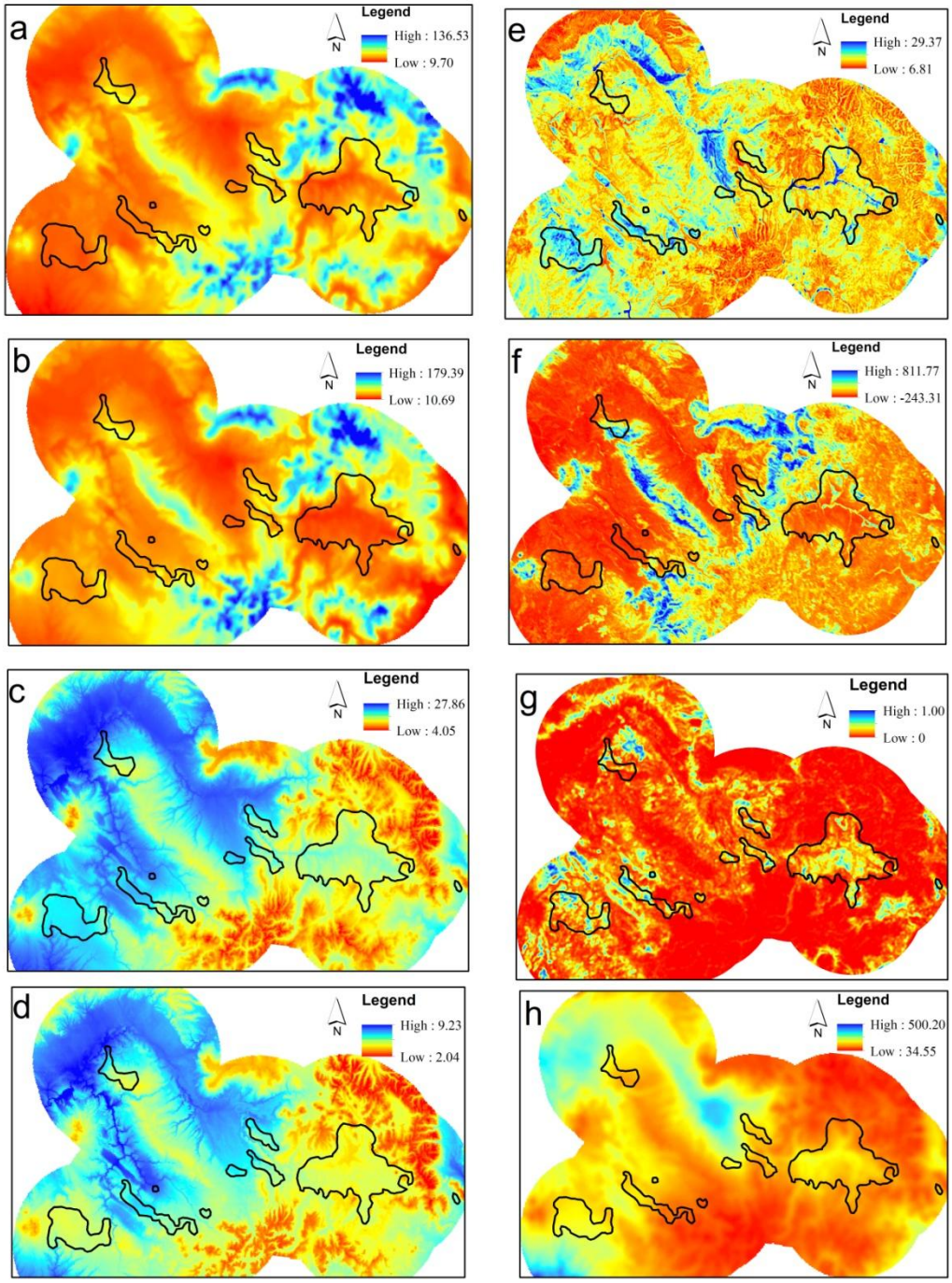

Figure S16.1. Covariate maps of the eight uncorrelated covariates used in the association analyses: a = spring precipitation (cm), b = fall precipitation (cm), c = spring maximum temperature (°C), d = winter maximum vapor pressure deficit (hPa), e = compound topographic index, f = green-up rate, g = big sagebrush cover (proportion of pixels with sagebrush cover), h = dryness index (# days with average temperature > 5 °C in growing season per cm of total spring precipitation). Pixel resolution = 1 km^2.

APPENDIX XVII

Table S17.1. Counts of SNPs in common identified in pairs of outlier and environmental association analyses.

	core	spring_ppt	fall_ppt	spring_tmax	cti	gur	bs	dri	pc1	pc2	pc3
core											
spring_ppt	16										
fall_ppt	6	12									
spring_tmax	1	5	1								
cti	30	55	14	5							
gur	40	320	184	18	396						
bs	12	46	15	6	49	168					
dri	37	87	31	7	45	412	65				
pc1	3	4	0	19	2	67	67	7			
pc2	2	51	4	0	4	41	9	15	1		
pc3	23	3	17	1	252	99	30	18	3	6	
rda	45	63	25	7	77	282	79	57	21	10	29

APPENDIX XIII

Table S18.1. List of gene code cited in the main text and the associated full gene names from outlier analyses of Gunnison sage-grouse populations.

Code	Gene Name
ACSL1	acyl-CoA synthetase long-chain family member 1
ACTR2	ARP2 actin-related protein 2 homolog (yeast)
ADAMTS20	ADAM metallopeptidase with thrombospondin type 1 motif, 20
ADCK1	aarF domain containing kinase 1
AFTPH	aftiphilin
AGPAT9	1-acylglycerol-3-phosphate O-acyltransferase 9
ALDH1A2	aldehyde dehydrogenase 1 family, member A2
ANO4	anoctamin 4
ARGAHP36	Rho GTPase activating protein 36
ARHGAP20	Rho GTPase activating protein 20
ARL3	ADP-ribosylation factor-like 3
ARV1	ARV1 homolog, fatty acid homeostasis modulator
ASMTL	acetylserotonin O-methyltransferase-like
ATXN10	ataxin 10
BDKRB1	bradykinin receptor B1
BIRC6	baculoviral IAP repeat containing 6
BMPER	BMP binding endothelial regulator
BRIP1	BRCA1 interacting protein C-terminal helicase 1
C16ORF45	chromosome 14 open reading frame, human C16orf45
C5	complement component 5
CACNG4	calcium channel, voltage-dependent, gamma subunit 4
CD36	CD36 molecule
CDH6	cadherin 6, type 2, K-cadherin (fetal kidney)
CENPW	centromere protein W
CHAF1B	chromatin assembly factor 1 subunit B
CNOT4	CCR4-NOT transcription complex subunit 4
CNTRL	centriolin
CPAMD8	C3 and PZP like, alpha-2-macroglobulin domain containing 8
CRB2	crumbs family member 2
CRYAA	crystallin, alpha A
CTBP1	C-terminal binding protein 1
CYB5R4	cytochrome b5 reductase 4
CYP2C23b	cytochrome P450, family 2, subfamily C, polypeptide 23b
CYP2R1	cytochrome P450 family 2 subfamily R member 1
CYP4B1	cytochrome P450, family 4, subfamily B, polypeptide 1
DDB2	damage specific DNA binding protein 2
DDX1	DEAD (Asp-Glu-Ala-Asp) box helicase 1
DDX60	DEAD (Asp-Glu-Ala-Asp) box polypeptide 60

Code	Gene Name
DENND5A	DENN/MADD domain containing 5A
DGKZ	diacylglycerol kinase, zeta
DMD	dystrophin
DNAH8	dynein, axonemal, heavy chain 8
DNAJC6	DnaJ (Hsp40) homolog, subfamily C, member 6
DOCK2	dedicator of cytokinesis 2
DYNC1LI1	dynein, cytoplasmic 1, light intermediate chain 1
EHD3	EH-domain containing 3
EHF	ETS homologous factor
EPHX1L	epoxide hydrolase 1-like
ERLIN2	ER lipid raft associated 2
FAM101A	family with sequence similarity 101 member A
FEZ2	fasciculation and elongation protein zeta 2
FGF20	fibroblast growth factor 20
FLT4	fms-related tyrosine kinase 4
GABRA4	gamma-aminobutyric acid (GABA) A receptor, alpha 4
GABRB3	gamma-aminobutyric acid (GABA) A receptor, beta 3
GART	phosphoribosylglycinamide formyltransferase, phosphoribosylglycinamide synthetase, phosphoribosylaminoimidazole synthetase
GLDN	gliomedin
GMPR	guanosine monophosphate reductase
GOPC	golgi-associated PDZ and coiled-coil motif containing
GPI	glucose-6-phosphate isomerase
GPM6A	glycoprotein M6A
GRIP1	helicase (DNA) B
GRXCR1	glutaredoxin and cysteine rich domain containing 1
HELB	glutamate receptor interacting protein 1
HTR2C	5-hydroxytryptamine (serotonin) receptor 2C, G protein-coupled
IAPP	islet amyloid polypeptide
INPP5E	inositol polyphosphate-5-phosphatase E
IQCA1	IQ motif containing with AAA domain 1
IRAK4	interleukin 1 receptor associated kinase 4
ITGAV	integrin, alpha V
JAG2	jagged 2
JARID2	jumonji and AT-rich interaction domain containing 2
KANSL1L	KAT8 regulatory NSL complex subunit 1-like
KCNH1	potassium voltage-gated channel, subfamily H (eag-related), member 1
KIF13A	kinesin family member 13A
KIF2C	kinesin family member 2C
LCP2	lymphocyte cytosolic protein 2 (SH2 domain containing leukocyte protein of 76kDa)
LOC100857837	ethanolaminephosphotransferase 1-like
LOC423347	acyl-CoA synthetase short-chain family member 1-like

Code	Gene Name
LOC770996	L-gulonolactone oxidase-like
LRP8	low density lipoprotein receptor-related protein 8, apolipoprotein e receptor
LYVE1	lymphatic vessel endothelial hyaluronan receptor 1
MAP2	microtubule-associated protein 2
MAP3K15	mitogen-activated protein kinase kinase kinase 15
MAP3K7	mitogen-activated protein kinase kinase kinase 7
MARCH8	membrane-associated ring finger (C3HC4) 8, E3 ubiquitin protein ligase
MAT1A	methionine adenosyltransferase I, alpha
MCF2L	MCF.2 cell line derived transforming sequence-like
MICU1	mitochondrial calcium uptake 1
MOCOS	molybdenum cofactor sulfurase
MTR	5-methyltetrahydrofolate-homocysteine methyltransferase
MYLIP	myosin regulatory light chain interacting protein
MYO1B	myosin IB
MYO1H	myosin IH
MYO3A	myosin IIIA
MYRFL	myelin regulatory factor-like
NAB1	NGFI-A binding protein 1 (EGR1 binding protein 1)
NARFL	nuclear prelamin A recognition factor-like
NCAPD3	non-SMC condensin II complex subunit D3
NCKAP1	NCK-associated protein 1
NDUFS6	NADH:ubiquinone oxidoreductase subunit S6
NETO2	neuropilin (NRP) and tolloid (TLL)-like 2
NMBR	neuromedin B receptor
NUS1	NUS1 dehydrodolichyl diphosphate synthase subunit
OMA1	OMA1 zinc metallopeptidase
ORC1	origin recognition complex subunit 1
ORC3	origin recognition complex subunit 3
OSBPL2	oxysterol binding protein-like 2
OTUD7A	OTU domain containing 7A
OVSTL	ovostatin-like
PARVA	parvin, alpha
PASK	PAS domain containing serine/threonine kinase
PDCD5	programmed cell death 5
PDPR	pyruvate dehydrogenase phosphatase regulatory subunit
PDZD8	PDZ domain containing 8
PHACTR1	phosphatase and actin regulator 1
PHC3	polyhomeotic homolog 3
PIK3C2A	phosphatidylinositol-4-phosphate 3-kinase, catalytic subunit type 2 alpha
PIK3C2G	phosphatidylinositol-4-phosphate 3-kinase, catalytic subunit type 2 gamma
PIK3CA	phosphatidylinositol-4,5-bisphosphate 3-kinase, catalytic subunit alpha
PITPNM3	PITPNM family member 3

Code	Gene Name
PKNOX1	PBX/knotted 1 homeobox 1
PKP2	plakophilin 2
PLEKHA5	pleckstrin homology domain containing A5
POLR3B	polymerase (RNA) III (DNA directed) polypeptide B
PRKCD	protein kinase C, delta
PSME4	proteasome activator subunit 4
PTDSS1	phosphatidylserine synthase 1
RAB2A	RAB2A, member RAS oncogene family
RANBP2	RAN binding protein 2
RAPGEF1	Rap guanine nucleotide exchange factor 1
RDX	radixin
RELN	reelin
RNF8	ring finger protein 8
RPS13	ribosomal protein S13
RPS6KC1	ribosomal protein S6 kinase, 52kDa, polypeptide 1
RTTN	rotatin
SCCPDH	saccharopine dehydrogenase (putative)
SCN9A	sodium channel, voltage-gated, type IX, alpha subunit
SDCBP	syndecan binding protein (syntenin)
SDK1	sidekick cell adhesion molecule 1
SEPN1	selenoprotein N, 1
SERPINB12	serpin peptidase inhibitor, clade B (ovalbumin), member 12
SESTD1	SEC14 and spectrin domain containing 1
SETX	senataxin
SIPA1L1	signal-induced proliferation-associated 1 like 1
SLC22A15	solute carrier family 22, member 15
SLC22A23	solute carrier family 22 member 23
SLC9A6	solute carrier family 9, subfamily A (NHE6, cation proton antiporter 6), member 6
SMPD4	sphingomyelin phosphodiesterase 4
SMURF1	SMAD specific E3 ubiquitin protein ligase 1
SNAP47	synaptosomal-associated protein, 47kDa
SRPX2	sushi-repeat containing protein, X-linked 2
SRRL	serine racemase-like
SSH2	slingshot protein phosphatase 2
ST6GAL2	ST6 beta-galactosamide alpha-2,6-sialyltranferase 2
STARD10	StAR-related lipid transfer (START) domain containing 10
STXBP5	syntaxin binding protein 5 (tomosyn)
STYK1	serine/threonine/tyrosine kinase 1
SYNE3	spectrin repeat containing, nuclear envelope family member 3
TBC1D9	TBC1 domain family, member 9 (with GRAM domain)
TBC1D9B	TBC1 domain family, member 9B (with GRAM domain)
TBXAS1	thromboxane A synthase 1

Code	Gene Name
TFAP2D	transcription factor AP-2 delta (activating enhancer binding protein 2 delta)
TGFB2	transforming growth factor, beta 2
TGFBRAP1	transforming growth factor beta receptor associated protein 1
TJAP1	tight junction associated protein 1
TMEM59	transmembrane protein 59
TRPC1	transient receptor potential cation channel, subfamily C, member 1
TRPV6	transient receptor potential cation channel, subfamily V, member 6
TSC1	tuberous sclerosis 1
TYRO3	TYRO3 protein tyrosine kinase
UGGT2	UDP-glucose glycoprotein glucosyltransferase 2
UST	uronyl 2-sulfotransferase
UXS1	UDP-glucuronate decarboxylase 1
VCL	vinculin
WNT7B	wingless-type MMTV integration site family, member 7B
WWTR1	WW domain containing transcription regulator 1
XRCC2	X-ray repair complementing defective repair in Chinese hamster cells 2
ZNF341	zinc finger protein 341
ZRSR2	zinc finger (CCCH type), RNA-binding motif and serine/arginine rich 2

APPENDIX XIX

Table S19.1. Summary of the outlier loci from Gunnison sage-grouse populations in each identified gene region. Findings from the core model ("Core"), the auxiliary model including principal component 1 ("pc1"), principal component 2 ("pc2"), principal component 3 ("pc3"), spring precipitation ("spring_ppt"), fall precipitation ("fall_ppt"), spring maximum temperature ("spring_tmax"), CTI ("cti"), big sagebrush cover ("bs"), dryness index ("dri"), and RDA with associated predictor variable ("rda.spring_ppt", "rda.fall_ppt", "rda.cti"). The name of the gene code is listed in the left-hand column ("Gene"; see Table S3.1 for a list of the corresponding full gene names) followed by the name of the pseudo-chromosome where it is located ("Chromosome"), the number of total number of SNPs identified as outliers in each gene region ("# SNPs"), indication of significance at *FDR* 0.05 (*) and *FDR* 0.01 (**) for BayPass in each model, and *FDR* 0.01 in Gowinda is shaded. Impact of each SNP as predicted by SnpEff is indicated in the by counts of SNPs in gene region in the corresponding "Effect" columns.

			Model													Effect				
Gene	Chromosome	# SNPs	core	pc1	pc2	pc3	spring_ppt	fall_ppt	spring_tmax	cti	bs	dri	rda.spring_ppt	rda.fall_ppt	rda.cti	Low	Moderate	Modifier	Downstream	Intron	Missense	Synonymous	Upstream
ADAMTS20	1	1	*															1		1			
ANO4	1	2												*				2		2			
ARHGAP20	1	1								*								1		1			
ASMTL	1	1								**								1		1			
ATXN10	1	3					**			*								3		3			
CD36	1	2									*							2		2			
CENPW	1	4					**			*			*					3		3			
CHAF1B	1	1					*											1		1			
CNOT4	1	1								**								1		1			
CRYAA	1	2						**						*				1		1			
DMD	1	2												*				2		2			
GABRB3	1	1											*					1		1			
GART	1	3				*				**	**							3		3			
GRIP1	1	1								**								1		1			

Gene	Chromosome	# SNPs	core	pc1	pc2	pc3	spring_ppt	fall_ppt	spring_tmax	cti	bs	dri	rda.spring_ppt	rda.fall_ppt	rda.cti	Low	Moderate	Modifier	Downstream	Intron	Missense	Synonymous	Upstream
HELB	1	1								**								1		1			
IAPP	1	1								*								1		1			
IRAK4	1	3					**						*					3	1	2			
MAP3K15	1	9										**						9		9			
MCF2L	1	2								*								2		2			
MYRFL	1	1								*					*	1		1				1	1
OVSTL	1	1								**								1		1			
PIK3C2G	1	1								*								1		1			
PKNOX1	1	1								*								1		1			
PKP2	1	3								**	**							3		3			
PLEKHA5	1	1								*								1		1			
POLR3B	1	1								**								1		1			
RAB2A	1	1								*								1		1			
RANBP2	1	1								**						1						1	
RDX	1	1								*								1		1			
RELN	1	1					*											1		1			
SDCBP	1	4					**											4		4			
SLC22A15	1	1								*								1		1			
ST6GAL2	1	1								**								1		1			
STYK1	1	1								*								1		1			
TBXAS1	1	1										*						1		1			
TGFBRAP1	1	2					*			*			*					2		2			
TRPV6	1	1								*								1		1			
UGGT2	1	2							*									2		2			
unknown	1	2								*								1		1			

Gene	Chromosome	# SNPs	core	pc1	pc2	pc3	spring_ppt	fall_ppt	spring_tmax	cti	bs	dri	rda.spring_ppt	rda.fall_ppt	rda.cti	Low	Moderate	Modifier	Downstream	Intron	Missense	Synonymous	Upstream
unknown	1	1						*										1		1			
UXS1	1	1	*															1		1			
WNT7B	1	1								**								3		3			
ZRSR2	1	1								*								1		1			
BMPER	2	1								**								1		1			
CDH6	2	2									**							2		2			
GMPR	2	8								**								8		8			
IQCA1	2	1								**								1		1			
ITGAV	2	1									*							1		1			
JARID2	2	2				*				*								2		2			
KANSL1L	2	1								*								1		1			
LOC100857837	2	1											*					1		1			
MAP2	2	1													*			1		1			
MOCOS	2	1								*								1		1			
MYLIP	2	1													*			1		1			
MYO1B	2	1													*			1		1			
MYO3A	2	1								*								1		1			
NAB1	2	3											*		*			3		3			
NCKAP1	2	5					*			*			*					5		5			
NDUFS6	2	1								*								1		1			
PDZD8	2	1								*								1		1			
PHACTR1	2	1												*				1		1			
PTDSS1	2	4									*	*		*				4		4			
RTTN	2	3					*											3		3			
SERPINB12	2	1								*								1		1			

Gene	Chromosome	# SNPs	core	pc1	pc2	pc3	spring_ppt	fall_ppt	spring_tmax	cti	bs	dri	rda.spring_ppt	rda.fall_ppt	rda.cti	Low	Moderate	Modifier	Downstream	Intron	Missense	Synonymous	Upstream
SESTD1	2	1						*										1		1			
SLC22A23	2	1								**								1		1			
SNAP47	2	6						**		**								6		6			
unknown	2	1				*				*	*					1						1	
unknown	2	1								*								1		1			
XRCC2	2	2											*					2		2			
ACTR2	3	2												*				2		2			
AFTPH	3	1								*								1		1			
ARV1	3	1								*								1		1			
BDKRB1	3	2				*				*								2		2			
BIRC6	3	2						*										2		2			
CYB5R4	3	2										*					1	1		1	1		
DDB2	3	1								*								1		1			
DGKZ	3	1					*											1		1			
DNAH8	3	1								*								1		1			
EHD3	3	1					*											1		1			
EHF	3	1								*								1		1			
EPHX1L	3	1								*								1		1			
FEZ2	3	2								*								2		2			
GOPC	3	1					*											1		1			
KCNH1	3	1						*										1		1			
KIF13A	3	2								**								2		2			
LOC770996	3	1										**						1		1			
MAP3K7	3	1									*							1		1			
MTR	3	5				**				*								1		1			

Gene	Chromosome	# SNPs	core	pc1	pc2	pc3	spring_ppt	fall_ppt	spring_tmax	cti	bs	dri	rda.spring_ppt	rda.fall_ppt	rda.cti	Low	Moderate	Modifier	Downstream	Intron	Missense	Synonymous	Upstream
NMBR	3	1								*								1		1			
NUS1	3	2									*							2		2			
ORC3	3	1								*								1		1			
PSME4	3	1						*								1						1	
RNF8	3	2		*														2		2			
RPS6KC1	3	2											*					2		2			
SCCPDH	3	1								*								1		1			
SIPA1L1	3	1						*										1		1			
STXBP5	3	1								*								1		1			
SYNE3	3	2				**				*								2		2			
TFAP2D	3	1								*								1		1			
TGFB2	3	1									**							1		1			
TJAP1	3	1											*					1		1			
TYRO3	3	1													*			1		1			
unknown	3	1								*								1		1			
unknown	3	4												*				1		1			
unknown	3	1					*											2		2			
UST	3	1								*								1		1			
ACSL1	4	1											*					1		1			
AGPAT9	4	2	*			*				**		**						2		2			
ARGAHP36	4	2								*								2		2			
CTBP1	4	2											*					2		2			
DDX1	4	1		*														1		1			
DDX60	4	6				*				**	**						1	4		4	1		
FGF20	4	1									**							1		1			

Gene	Chromosome	# SNPs	core	pc1	pc2	pc3	spring_ppt	fall_ppt	spring_tmax	cti	bs	dri	rda.spring_ppt	rda.fall_ppt	rda.cti	Low	Moderate	Modifier	Downstream	Intron	Missense	Synonymous	Upstream
GABRA4	4	1													*			1		1			
GPM6A	4	1												*				1		1			
GRXCR1	4	1				*												1		1			
HTR2C	4	1								*								1		1			
SLC9A6	4	1								*								1		1			
SRPX2	4	1												*				1		1			
TBC1D9	4	2	*							**								2		2			
unknown	4	1								*								1		1			
ADCK1	5	1								*								1		1			
CYP2R1	5	3	*							**		**						3		3			
DENND5A	5	5			*	*				*		**						5		5			
DYNC1LI1	5	1								*								1		1			
JAG2	5	4				*				**	**				*			4		4			
LOC423347	5	1								*								1		1			
LYVE1	5	1								*								1		1			
PARVA	5	1					*											1		1			
PIK3C2A	5	1				*				**								1		1			
RPS13	5	1								*								1		1			
unknown	5	1								*								1		1			
MARCH8	6	2												*				2		2			
ARL3	6	1									*							1		1			
CYP2C23b	6	2												*				2		2			
MAT1A	6	1				*				**								1		1			
MICU1	6	1			*			*										1		1			
SRRL	6	3	*			*				**								3		3			

Gene	Chromosome	# SNPs	core	pc1	pc2	pc3	spring_ppt	fall_ppt	spring_tmax	cti	bs	dri	rda.spring_ppt	rda.fall_ppt	rda.cti	Low	Moderate	Modifier	Downstream	Intron	Missense	Synonymous	Upstream
VCL	6	1									**							1		1			
SCN9A	7	1						*										1		1			
CYP4B1	8	1											*					1		1			
DNAJC6	8	1								*								1		1			
KIF2C	8	1								*								1		1			
LRP8	8	1					*											1		1			
OMA1	8	3										*						3	1	2			
ORC1	8	1		*														1		1			
TMEM59	8	2		*		*					**				*			2		2			
PASK	9	1		*							*							1		1			
PHC3	9	1								*								1		1			
PIK3CA	9	1					*					*						1		1			
TRPC1	9	1					*											1		1			
WWTR1	9	3				**				**						1		2		2		1	
ALDH1A2	10	3				*				**								2		2			
GLDN	10	1													*			1		1			
OTUD7A	10	1								*								1		1			
GPI	11	1										*						1		1			
NETO2	11	1					*											1		1			
PDCD5	11	1						*										1		1			
PDPR	11	1								**								1		1			
PRKCD	12	2				*	*			**								2		2			
DOCK2	13	2				*				*								2		2			
FLT4	13	2					**											2		2			
LCP2	13	3				*				**	*							3		3			

Gene	Chromosome	# SNPs	core	pc1	pc2	pc3	spring_ppt	fall_ppt	spring_tmax	cti	bs	dri	rda.spring_ppt	rda.fall_ppt	rda.cti	Low	Moderate	Modifier	Downstream	Intron	Missense	Synonymous	Upstream
STARD10	13	1								*					*			1		1			
TBC1D9B	13	1								*								1		1			
C16ORF45	14	1								*								1		1			
NARFL	14	3						*		*								3		3			
SDK1	14	1								*					*			1		1			
SMURF1	14	1													*			1		1			
FAM101A	15	3						**										3		3			
MYO1H	15	1	*															1		1			
SMPD4	15	1								*					*			1		1			
C5	17	1					**											1		1			
CNTRL	17	1					*											1		1			
CRB2	17	1					**											1		1			
INPP5E	17	1				*				**							1				1		
RAPGEF1	17	1					*											1		1			
SETX	17	2													*		2				2		
TSC1	17	1												*				1		1			
CACNG4	18	1								**								1		1			
unknown	18	1													*			4		4			
BRIP1	19	1								*								1		1			
PITPNM3	19	1								*						1						1	
SSH2	19	1								*								1		1			
OSBPL2	20	1								*								1		1			
ZNF341	20	1	*															1		1			
unknown	21	1													*			1		1			
ERLIN2	22	1								*								1		1			

Gene	Chromosome	# SNPs	core	pc1	pc2	pc3	spring_ppt	fall_ppt	spring_tmax	cti	bs	dri	rda.spring_ppt	rda.fall_ppt	rda.cti	Low	Moderate	Modifier	Downstream	Intron	Missense	Synonymous	Upstream
SEPN1	23	1								*								1		1			
NCAPD3	24	1								**								1		1			
CPAMD8	28	1						*										1		1			

APPENDIX XX

Table S20.1 GO analyses 192 putative divergent genes in Gunnison sage-grouse. The analysis was performed with DAVID (Huang *et al.*, 2009).

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
Biological Process (GOTERM_BP_FAT)								
GO:1902589~single-organism organelle organization	33	18.23	0.00	2.09	0.15	0.15	0.10	Q90828, E1C5S5, F1NWB1, Q5ZHM8, E1BR42, F1NTJ5, F1NS98, R4GGA5, E1BR21, E1BRS7, F1NRM5, E1C6D1, E1C7A6, F1P3H8, F1P2D7, O42391, E1BQZ3, F1NB03, E1BXI3, F1NGM0, E1C8I6, F1P4R5, A3FMM9, E1BZC1, E1C066, E1C2V3, Q9PU45, E1BQN0, E1C6G9, F1NFN4, F1NX76, F1P5V9, F1P3I1
GO:0007010~cytoskeleton organization	24	13.26	0.00	2.25	0.60	0.37	0.58	A3FMM9, E1BZC1, R4GJL4, E1C5S5, E1C2V3, F1NWB1, E1C066, Q5ZHM8, E1BR42, F1NTJ5, F1NS97, F1NNP2, Q9PU45, R4GGA5, E1BR21, F1NRM5, E1C6D1, E1C6G9, E1BQZ3, O42391, F1NB03, F1P5V9, F1P3I1, E1C8I6
GO:0030029~actin filament-based process	17	9.39	0.00	2.79	0.63	0.28	0.62	A3FMM9, E1C5S5, E1C2V3, F1NWB1, E1C066, Q5ZHM8, E1BR42, F1NTJ5, F1NNP2, Q9PU45, E1BR21, F1NRM5, E1C6G9, E1BQZ3, O42391, F1P5V9, F1P3I1
GO:0044802~single-organism membrane organization	17	9.39	0.00	2.67	0.79	0.32	0.98	F1NE63, F1P4R5, E1C2V3, E1C5S5, E1BR42, F1NNP2, Q9PU45, Q5ZLJ8, E1C7A6, F1NBS7, F1NFN4, F1NRD3, E1BXI3, F1NX76, F1NGM0, E1C8I6, F1NVE6
GO:0061024~membrane organization	18	9.94	0.00	2.50	0.88	0.35	1.34	F1NE63, F1P4R5, E1C2V3, E1C5S5, E1BR42, F1NNP2, Q9PU45, Q5ZLJ8, E1C7A6, F1NBS7, F1NFN4, F1NER9, F1NRD3, F1NX76, E1BXI3, F1NGM0, E1C8I6, F1NVE6

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0030036~actin cytoskeleton organization	15	8.29	0.00	2.81	0.91	0.33	1.48	A3FMM9, F1NWB1, E1C066, E1C5S5, Q5ZHM8, E1BR42, F1NTJ5, Q9PU45, E1BR21, F1NRM5, E1C6G9, E1BQZ3, O42391, F1P5V9, F1P3I1
GO:1902580~single-organism cellular localization	19	10.50	0.00	2.31	0.97	0.40	2.25	F1NE63, E1C5S5, F1NA05, E1C2V3, E1C066, E1BR42, F1NNP2, Q9PU45, F1P140, Q5ZLJ8, F1NRM5, F1N8Y0, F1NER9, O42391, F1NRD3, F1NX76, E1BXI3, F1NGM0, E1C8I6
GO:0034113~heterotypic cell-cell adhesion	4	2.21	0.00	12.85	1.00	0.70	5.88	F1NBS7, E1C2V3, P26008, F1P5V9
GO:0016337~single organismal cell-cell adhesion	14	7.73	0.00	2.52	1.00	0.67	6.04	F1NMD6, E1BYI1, E1C2V3, E1C066, E1C5S5, E1BR42, F1NLR2, P26008, Q9PU45, F1NX90, E1BS61, F1NBS7, F1NYY0, F1P5V9
GO:0007015~actin filament organization	10	5.52	0.00	3.08	1.00	0.76	8.52	A3FMM9, E1C066, E1C5S5, F1NWB1, E1C6G9, O42391, F1NTJ5, Q9PU45, E1BR21, F1NRM5
GO:0006928~movement of cell or subcellular component	26	14.36	0.01	1.76	1.00	0.75	9.22	F1NE63, Q90828, F1NWB1, E1C5S5, Q5ZHM8, P26008, F1NTJ5, E1BRS7, F1NRM5, E1C1A7, O42391, F1NB03, F1NYY0, F1N871, E1BZC1, E1C2V3, Q643S1, F1NLR2, Q9PU45, F1NNP2, E1C1G0, F1NX90, F1P140, Q5EES3, E1C0E9, F1P5V9
GO:0098609~cell-cell adhesion	16	8.84	0.01	2.19	1.00	0.75	9.86	F1NMD6, E1BYI1, E1C5S5, E1C2V3, E1C066, E1BR42, F1NLR2, P26008, Q9PU45, F1NX90, Q90762, E1BS61, F1NBS7, Q8AV58, F1NYY0, F1P5V9
GO:0034109~homotypic cell-cell adhesion	5	2.76	0.01	6.78	1.00	0.73	10.18	E1C5S5, E1C2V3, F1NYY0, F1NLR2, Q9PU45
GO:0051128~regulation of cellular component organization	32	17.68	0.01	1.59	1.00	0.79	12.71	Q5ZIZ6, F1NE63, Q90828, E1C5S5, Q5ZHM8, E1BR42, Q5F363, P26008, F1NRM5, F1NI67, Q5ZLJ8, E1C7A6, E1C6V5, F1NMI2, E1BQZ3, F1NER9, E1BXI3, F1NGM0, E1C8I6, A3FMM9, E1C2K7, E1BZC1, R4GJL4, E1C066, E1BYW1, Q9PU45, F1NNP2, F1NX90, E1BS61, E1C6G9, F1NFN4, F1P3I1

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0098602~single organism cell adhesion	14	7.73	0.01	2.27	1.00	0.79	13.68	F1NMD6, E1BYI1, E1C2V3, E1C066, E1C5S5, E1BR42, F1NLR2, P26008, Q9PU45, F1NX90, E1BS61, F1NBS7, F1NYY0, F1P5V9
GO:0048468~cell development	29	16.02	0.01	1.63	1.00	0.78	13.97	F1NE63, F1P3S9, Q5ZHM8, F1NHU1, P26008, R4GGA5, E1BR21, E1C6D1, F1NBS7, O42391, E1BQZ3, F1NYY0, Q3L254, P19019, A3FMM9, Q5ZM68, E1BZC1, F1ND07, E1BYW1, F1NLR2, Q9PU45, F1NNP2, F1NIE7, Q5EES3, E1BS61, F1NFN4, F1NCB2, F1P5V9, F1P3I1
GO:0006869~lipid transport	8	4.42	0.01	3.39	1.00	0.78	14.98	F1N8Y0, Q5ZLC4, Q5F420, E1C5S5, F1NER9, F1NRD3, P26008, F1NHY3
GO:0051049~regulation of transport	23	12.71	0.01	1.77	1.00	0.76	15.11	F1NE63, A3FMM9, F1P3S9, E1C2K7, E1C5S5, Q5ZHM8, E1BR42, P26008, F1NNP2, Q9PU45, F1N989, F1NI67, Q6DMS2, E1BRS7, F1N8Y0, F1NMI2, R4GIQ1, F1NER9, E1BXI3, F1NGM0, F1N9K6, E1C3U0, E1BYZ2
GO:0016192~vesicle-mediated transport	19	10.50	0.01	1.91	1.00	0.75	15.44	Q90965, F1P4R5, E1C2K7, Q5ZHM8, F1NS31, E1BR42, F1NTJ5, F1NLR2, P26008, Q9PU45, E1C1G0, F1P140, F1NI67, F1NMI2, F1NAK6, F1NER9, F1NX76, F1NGM0, E1C3U0
GO:0007399~nervous system development	29	16.02	0.01	1.62	1.00	0.74	15.80	F1NE63, F1NMD6, E1BZC1, E1C066, F1NS31, E1BYW1, F1NHU1, F1NLR2, F1NNP2, Q5F429, R4GGA5, F1NX90, E1C890, E1C6D1, Q8QG58, F1NIE7, E1C135, E1BS61, Q5EES3, F1NBS7, Q8AV58, F1NFN4, E1BQZ3, O42391, F1NYY0, Q3L254, F1NCB2, F1P3I1, P19019
GO:0051641~cellular localization	32	17.68	0.01	1.56	1.00	0.74	16.22	F1NE63, F1P3S9, E1C5S5, E1BR42, F1NI67, Q5ZLJ8, Q6DMS2, F1NRM5, F1NAK6, E1BRT1, O42391, F1NER9, F1NB03, F1NYY0, E1BXI3, F1NGM0, E1C8I6, F1P4R5, A3FMM9, E1C2K7, F1NA05, E1C066, E1C2V3, F1NV49, Q9PU45, F1NNP2, F1P140, F1N989, F1N8Y0, F1NFN4, F1NRD3, F1NX76

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0043112~receptor metabolic process	6	3.31	0.01	4.21	1.00	0.83	21.66	F1NFN4, Q5ZHM8, F1NER9, P26008, F1NGM0, Q5F429
GO:0051649~establishment of localization in cell	25	13.81	0.01	1.65	1.00	0.82	22.29	F1P3S9, E1C5S5, F1NI67, Q6DMS2, F1NRM5, F1NAK6, E1BRT1, F1NER9, O42391, F1NB03, E1BXI3, F1NGM0, A3FMM9, F1P4R5, E1C2K7, E1C066, F1NA05, Q9PU45, F1NNP2, F1P140, F1N989, F1N8Y0, F1NFN4, F1NRD3, F1NX76
GO:0032409~regulation of transporter activity	6	3.31	0.01	4.16	1.00	0.82	22.56	F1NE63, F1P3S9, R4GIQ1, E1C5S5, F1NGM0, E1BYZ2
GO:0043523~regulation of neuron apoptotic process	6	3.31	0.01	4.11	1.00	0.82	23.47	E1C135, O42391, F1NLR2, F1NNP2, R4GGA5, P19019
GO:1900449~regulation of glutamate receptor signaling pathway	3	1.66	0.02	15.25	1.00	0.82	24.53	F1NE63, R4GIQ1, E1BYZ2
GO:0007009~plasma membrane organization	8	4.42	0.02	3.01	1.00	0.83	25.71	E1C5S5, E1C2V3, F1NRD3, Q9PU45, F1NNP2, F1NGM0, Q5ZLJ8, F1NVE6
GO:0010876~lipid localization	8	4.42	0.02	3.01	1.00	0.83	25.71	F1N8Y0, Q5ZLC4, Q5F420, E1C5S5, F1NER9, F1NRD3, P26008, F1NHY3
GO:0030030~cell projection organization	20	11.05	0.02	1.76	1.00	0.82	25.91	F1NE63, E1C5S5, E1C066, F1NHU1, F1NNP2, Q9PU45, F1NRM5, E1C6D1, E1BS61, Q5EES3, F1P3H8, F1NBS7, E1C6G9, F1NFN4, E1BQZ3, O42391, F1NYY0, F1NGM0, F1NCB2, F1P3I1
GO:0048870~cell motility	20	11.05	0.02	1.76	1.00	0.82	25.91	F1NE63, E1BZC1, E1C5S5, Q643S1, F1NWB1, Q5ZHM8, F1NLR2, P26008, F1NNP2, Q9PU45, E1C1G0, F1NX90, E1BRS7, Q5EES3, E1C1A7, O42391, F1NYY0, E1C0E9, F1P5V9, F1N871
GO:0051674~localization of cell	20	11.05	0.02	1.76	1.00	0.81	26.22	F1NE63, E1BZC1, E1C5S5, Q643S1, F1NWB1, Q5ZHM8, F1NLR2, P26008, F1NNP2, Q9PU45, E1C1G0, F1NX90, E1BRS7, Q5EES3, E1C1A7, O42391, F1NYY0, E1C0E9, F1P5V9, F1N871
GO:0070588~calcium ion transmembrane transport	6	3.31	0.02	3.98	1.00	0.80	26.31	F1P3S9, R4GIQ1, E1BWC6, F1NGM0, Q6DMS2, F1N989

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0099601~regulation of neurotransmitter receptor activity	3	1.66	0.02	14.08	1.00	0.82	28.08	F1NE63, R4GIQ1, E1BYZ2
GO:0031401~positive regulation of protein modification process	17	9.39	0.02	1.87	1.00	0.81	28.33	F1NE63, Q5ZIZ6, A3FMM9, Q5F420, E1C5S5, Q643S1, Q5ZHM8, Q5F363, E1C063, F1NNP2, F1N989, Q9DG07, F1NFN4, F1NER9, O42391, F1NKW3, F1N871
GO:0007155~cell adhesion	20	11.05	0.02	1.74	1.00	0.80	28.79	F1NE63, F1NMD6, E1BYI1, E1C5S5, E1C2V3, E1C066, E1BR42, F1NLR2, P26008, F1NNP2, Q9PU45, F1NX90, Q90762, E1BS61, F1NBS7, Q8AV58, F1NER9, F1NYY0, F1P5V9, E1C9I1
GO:0007163~establishment or maintenance of cell polarity	6	3.31	0.02	3.85	1.00	0.80	29.29	O42391, F1NB03, E1BYW1, E1BR42, F1P5V9, F1NRM5
GO:0022610~biological adhesion	20	11.05	0.02	1.73	1.00	0.80	29.78	F1NE63, F1NMD6, E1BYI1, E1C5S5, E1C2V3, E1C066, E1BR42, F1NLR2, P26008, F1NNP2, Q9PU45, F1NX90, Q90762, E1BS61, F1NBS7, Q8AV58, F1NER9, F1NYY0, F1P5V9, E1C9I1
GO:0060627~regulation of vesicle-mediated transport	9	4.97	0.02	2.65	1.00	0.79	29.89	F1NMI2, E1C2K7, Q5ZHM8, F1NER9, E1BR42, P26008, Q9PU45, E1C3U0, F1NI67
GO:0033043~regulation of organelle organization	18	9.94	0.02	1.79	1.00	0.80	31.47	Q5ZIZ6, Q90828, E1C2K7, E1BZC1, E1C5S5, E1C066, Q5ZHM8, Q5F363, F1NNP2, Q9PU45, F1NI67, F1NRM5, E1C7A6, E1C6V5, E1C6G9, E1BXI3, F1NGM0, F1P3I1
GO:0000902~cell morphogenesis	20	11.05	0.02	1.72	1.00	0.79	31.48	F1NE63, A3FMM9, Q5ZHM8, E1BYW1, F1NLR2, P26008, F1NNP2, Q9PU45, F1NRM5, E1C6D1, Q5EES3, F1NFN4, E1BQZ3, O42391, F1NYY0, F1NGM0, F1NCB2, F1P5V9, F1P3I1, E1C8I6
GO:0097035~regulation of membrane lipid distribution	3	1.66	0.02	13.07	1.00	0.79	31.68	E1C5S5, F1NRD3, F1NVE6
GO:0022411~cellular component disassembly	9	4.97	0.02	2.61	1.00	0.78	31.87	F1NMI2, E1BZC1, F1P2D7, F1NFN4, O42391, F1NB03, Q9PU45, F1NNP2, E1BRS7

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0032989~cellular component morphogenesis	21	11.60	0.02	1.67	1.00	0.80	34.14	F1NE63, A3FMM9, Q5ZHM8, E1BYW1, F1NLR2, P26008, F1NNP2, Q9PU45, F1NRM5, E1C6D1, Q5EES3, E1BQN0, F1NFN4, E1BQZ3, O42391, F1NYY0, F1NGM0, F1NCB2, F1P5V9, F1P3I1, E1C8I6
GO:0051402~neuron apoptotic process	6	3.31	0.02	3.66	1.00	0.80	34.52	E1C135, O42391, F1NLR2, F1NNP2, R4GGA5, P19019
GO:0003016~respiratory system process	3	1.66	0.02	12.20	1.00	0.80	35.32	F1NMD6, F1P3S9, F1N871
GO:0006796~phosphate-containing compound metabolic process	34	18.78	0.02	1.44	1.00	0.79	35.37	E1C7H7, F1NE63, E1C5S5, Q5ZHM8, F1NIJ6, P26008, F1NRX7, O42391, F1NER9, R4GLI2, F1N871, F1P5J6, A3FMM9, A0A547, Q5F420, F1NA05, E1C066, Q643S1, E1C085, F1NQ69, F1NLR2, E1C063, Q5ZLL8, F1NNP2, Q5ZM65, F1NX90, F1N989, E1BS61, E1BQN0, Q9DG07, F1NNJ1, E1C0E9, F1N9K6, F1NKW3
GO:0006793~phosphorus metabolic process	34	18.78	0.02	1.43	1.00	0.80	36.42	E1C7H7, F1NE63, E1C5S5, Q5ZHM8, F1NIJ6, P26008, F1NRX7, O42391, F1NER9, R4GLI2, F1N871, F1P5J6, A3FMM9, A0A547, Q5F420, F1NA05, E1C066, Q643S1, E1C085, F1NQ69, F1NLR2, E1C063, Q5ZLL8, F1NNP2, Q5ZM65, F1NX90, F1N989, E1BS61, E1BQN0, Q9DG07, F1NNJ1, E1C0E9, F1N9K6, F1NKW3
GO:1902582~single-organism intracellular transport	11	6.08	0.03	2.22	1.00	0.80	36.94	F1N8Y0, E1C066, E1C5S5, F1NA05, O42391, F1NER9, F1NRD3, E1BXI3, F1NNP2, F1NGM0, F1P140
GO:0016477~cell migration	18	9.94	0.03	1.75	1.00	0.79	37.27	F1NE63, E1BZC1, E1C5S5, Q643S1, Q5ZHM8, F1NLR2, P26008, F1NNP2, Q9PU45, E1C1G0, F1NX90, E1BRS7, Q5EES3, E1C1A7, O42391, E1C0E9, F1P5V9, F1N871

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0051247~positive regulation of protein metabolic process	20	11.05	0.03	1.68	1.00	0.79	37.60	F1NE63, Q5ZIZ6, A3FMM9, Q5F420, E1C5S5, Q643S1, Q5ZHM8, Q5F363, E1C063, F1NNP2, Q9PU45, Q5F429, F1N989, Q9DG07, F1NFN4, F1NER9, O42391, E1BXI3, F1N871, F1NKW3
GO:0010639~negative regulation of organelle organization	8	4.42	0.03	2.74	1.00	0.78	37.67	Q5ZIZ6, E1C6V5, Q90828, E1BZC1, E1C5S5, Q5F363, Q9PU45, E1C7A6
GO:0034762~regulation of transmembrane transport	7	3.87	0.03	3.05	1.00	0.78	38.25	F1NE63, F1P3S9, R4GIQ1, E1BXI3, F1NGM0, Q6DMS2, E1BYZ2
GO:0032270~positive regulation of cellular protein metabolic process	19	10.50	0.03	1.70	1.00	0.79	39.69	F1NE63, Q5ZIZ6, A3FMM9, Q5F420, E1C5S5, Q643S1, Q5ZHM8, Q5F363, E1C063, F1NNP2, Q9PU45, F1N989, Q9DG07, F1NFN4, F1NER9, O42391, E1BXI3, F1N871, F1NKW3
GO:1901214~regulation of neuron death	6	3.31	0.03	3.49	1.00	0.79	39.99	E1C135, O42391, F1NLR2, F1NNP2, R4GGA5, P19019
GO:0046907~intracellular transport	20	11.05	0.03	1.66	1.00	0.79	40.25	F1P4R5, A3FMM9, E1C2K7, E1C5S5, F1NA05, E1C066, F1NNP2, Q9PU45, F1P140, F1NI67, F1NRM5, F1N8Y0, F1NAK6, F1NFN4, E1BRT1, F1NER9, O42391, F1NRD3, E1BXI3, F1NGM0
GO:0016310~phosphorylation	25	13.81	0.03	1.54	1.00	0.79	41.31	F1NE63, E1C7H7, E1C5S5, Q5ZHM8, F1NIJ6, P26008, O42391, F1NER9, F1N871, A3FMM9, E1C066, Q643S1, F1NA05, Q5F420, F1NLR2, E1C063, F1NNP2, F1N989, E1BS61, E1BQN0, Q9DG07, F1NNJ1, E1C0E9, F1N9K6, F1NKW3
GO:0043524~negative regulation of neuron apoptotic process	5	2.76	0.03	4.24	1.00	0.79	41.52	E1C135, O42391, F1NLR2, R4GGA5, P19019
GO:0040011~locomotion	21	11.60	0.03	1.62	1.00	0.79	42.50	F1NE63, E1BZC1, E1C5S5, Q643S1, F1NWB1, Q5ZHM8, E1BR42, F1NLR2, P26008, F1NNP2, Q9PU45, E1C1G0, F1NX90, E1BRS7, Q5EES3, E1C1A7, O42391, F1NYY0, E1C0E9, F1P5V9, F1N871

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0001934~positive regulation of protein phosphorylation	14	7.73	0.03	1.89	1.00	0.81	45.13	F1NE63, A3FMM9, Q5F420, Q643S1, E1C5S5, Q5ZHM8, E1C063, F1NNP2, F1N989, Q9DG07, F1NER9, O42391, F1NKW3, F1N871
GO:0033036~macromolecule localization	31	17.13	0.03	1.43	1.00	0.81	45.58	Q90965, F1NE63, E1C5S5, F1NHU1, P26008, F1NI67, Q5ZLJ8, E1BRS7, F1NER9, F1NYY0, E1BXI3, F1NGM0, E1C8I6, F1P4R5, Q5ZLC4, Q5ZM68, E1C2K7, Q5F420, F1NA05, E1C066, E1C2V3, F1NV49, Q9PU45, F1NNP2, F1P140, F1NHY3, F1N8Y0, Q9DG07, F1NFN4, F1NRD3, E1C3U0
GO:0008347~glial cell migration	3	1.66	0.03	10.17	1.00	0.81	46.11	F1NE63, E1BZC1, F1NNP2
GO:0043277~apoptotic cell clearance	3	1.66	0.03	10.17	1.00	0.81	46.11	F1NER9, F1NLR2, P26008
GO:0022603~regulation of anatomical structure morphogenesis	15	8.29	0.03	1.82	1.00	0.81	46.91	F1NE63, R4GJL4, Q5ZHM8, E1BYW1, F1NNP2, Q9PU45, F1NX90, E1BRS7, E1C7A6, F1NFN4, F1NER9, E1BQZ3, F1N871, F1P3I1, E1C8I6
GO:0006468~protein phosphorylation	22	12.15	0.03	1.58	1.00	0.81	47.10	F1NE63, E1C7H7, A3FMM9, Q5F420, E1C5S5, Q643S1, E1C066, Q5ZHM8, F1NLR2, P26008, E1C063, F1NNP2, F1N989, E1BS61, Q9DG07, F1NER9, O42391, F1NNJ1, E1C0E9, F1N9K6, F1N871, F1NKW3
GO:0032412~regulation of ion transmembrane transporter activity	5	2.76	0.04	4.01	1.00	0.81	47.21	F1NE63, F1P3S9, R4GIQ1, F1NGM0, E1BYZ2
GO:0032970~regulation of actin filament-based process	8	4.42	0.04	2.56	1.00	0.81	48.36	E1C066, E1C5S5, E1C6G9, E1C2V3, Q9PU45, F1NNP2, F1P3I1, F1NRM5
GO:0002040~sprouting angiogenesis	4	2.21	0.04	5.42	1.00	0.81	48.55	Q643S1, F1P5V9, F1N871, F1NX90
GO:0070371~ERK1 and ERK2 cascade	6	3.31	0.04	3.21	1.00	0.82	50.15	E1BS61, Q643S1, F1NER9, P26008, F1N871, F1N989

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0048015~phosphatidylinositol-mediated signaling	5	2.76	0.04	3.86	1.00	0.82	51.46	F1NE63, O42391, F1NNP2, E1C1G0, F1NSE0
GO:0002252~immune effector process	10	5.52	0.04	2.16	1.00	0.83	52.30	F1P0I1, E1C1A7, E1C066, F1P2D7, E1C5S5, F1NFN4, F1NER9, E1BR42, E1C063, F1NNP2
GO:0022898~regulation of transmembrane transporter activity	5	2.76	0.04	3.81	1.00	0.83	52.86	F1NE63, F1P3S9, R4GIQ1, F1NGM0, E1BYZ2
GO:0070997~neuron death	6	3.31	0.04	3.13	1.00	0.83	53.53	E1C135, O42391, F1NLR2, F1NNP2, R4GGA5, P19019
GO:0048017~inositol lipid-mediated signaling	5	2.76	0.04	3.77	1.00	0.83	54.26	F1NE63, O42391, F1NNP2, E1C1G0, F1NSE0
GO:0006006~glucose metabolic process	5	2.76	0.04	3.77	1.00	0.83	54.26	F1NA05, O42391, F1NIJ6, F1N9K6, E1C7A6
GO:0034764~positive regulation of transmembrane transport	4	2.21	0.04	5.08	1.00	0.83	54.38	F1NE63, E1BXI3, F1NGM0, Q6DMS2
GO:0042327~positive regulation of phosphorylation	14	7.73	0.04	1.81	1.00	0.82	54.46	F1NE63, A3FMM9, Q5F420, Q643S1, E1C5S5, Q5ZHM8, E1C063, F1NNP2, F1N989, Q9DG07, F1NER9, O42391, F1NKW3, F1N871
GO:0007423~sensory organ development	11	6.08	0.04	2.03	1.00	0.82	54.88	F1NIE7, F1NMD6, A3FMM9, Q5EES3, E1BYI1, Q8AV58, Q643S1, E1BYW1, Q3L254, F1NNP2, P19019
GO:0007215~glutamate receptor signaling pathway	3	1.66	0.05	8.72	1.00	0.83	56.26	F1NE63, R4GIQ1, E1BYZ2
GO:1901215~negative regulation of neuron death	5	2.76	0.05	3.68	1.00	0.83	57.03	E1C135, O42391, F1NLR2, R4GGA5, P19019
GO:0051129~negative regulation of cellular component organization	11	6.08	0.05	2.00	1.00	0.83	57.38	Q5ZIZ6, E1C6V5, Q90828, E1BZC1, E1C5S5, Q5ZHM8, Q5F363, Q9PU45, F1NNP2, Q5ZLJ8, E1C7A6

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0048699~generation of neurons	19	10.50	0.05	1.60	1.00	0.83	57.43	F1NE63, F1NMD6, E1BZC1, F1NHU1, F1NNP2, R4GGA5, E1C6D1, F1NIE7, E1BS61, Q5EES3, F1NBS7, F1NFN4, E1BQZ3, O42391, F1NYY0, Q3L254, F1NCB2, F1P3I1, P19019
GO:0048646~anatomical structure formation involved in morphogenesis	18	9.94	0.05	1.63	1.00	0.83	57.70	F1NE63, E1BYI1, E1BZC1, Q643S1, E1C066, F1NIJ6, E1BYW1, P26008, F1NNP2, R4GGA5, F1NX90, E1BRS7, F1NRM5, Q8AV58, F1NER9, F1NGM0, F1P5V9, F1N871
GO:0022008~neurogenesis	20	11.05	0.05	1.57	1.00	0.83	58.62	F1NE63, F1NMD6, E1BZC1, F1NHU1, F1NNP2, R4GGA5, E1C6D1, Q8QG58, F1NIE7, E1BS61, Q5EES3, F1NBS7, F1NFN4, E1BQZ3, O42391, F1NYY0, Q3L254, F1NCB2, F1P3I1, P19019
GO:0071695~anatomical structure maturation	3	1.66	0.05	8.32	1.00	0.83	59.42	F1NIE7, F1NNP2, E1BR21
GO:0022604~regulation of cell morphogenesis	10	5.52	0.05	2.08	1.00	0.84	60.40	F1NE63, R4GJL4, F1NFN4, Q5ZHM8, E1BQZ3, E1BYW1, Q9PU45, F1NNP2, F1P3I1, E1C8I6
GO:0010469~regulation of receptor activity	4	2.21	0.05	4.69	1.00	0.84	61.80	F1NE63, F1P3S9, R4GIQ1, E1BYZ2
GO:0051276~chromosome organization	15	8.29	0.05	1.71	1.00	0.84	62.12	Q5ZIZ6, Q90828, E1C4A8, F1ND07, E1C5S5, F1NV49, Q5F363, Q3YK19, F1NS98, E1C063, Q5ZJL7, R4GIZ7, E1C2H5, F1P2D7, F1NB03
GO:0016358~dendrite development	5	2.76	0.06	3.43	1.00	0.86	64.96	F1NE63, E1BQZ3, F1NHU1, F1NCB2, E1C6D1
GO:0045912~negative regulation of carbohydrate metabolic process	3	1.66	0.06	7.63	1.00	0.86	65.35	F1NA05, F1N9K6, Q5ZLJ8
GO:0010718~positive regulation of epithelial to mesenchymal transition	3	1.66	0.06	7.63	1.00	0.86	65.35	Q5ZHM8, E1BYW1, F1NNP2

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0000904~cell morphogenesis involved in differentiation	13	7.18	0.06	1.79	1.00	0.86	65.55	F1NE63, A3FMM9, Q5ZHM8, E1BQZ3, F1NYY0, E1BYW1, F1NLR2, P26008, F1NCB2, F1NNP2, F1P5V9, F1P3I1, E1C6D1
GO:0001816~cytokine production	9	4.97	0.06	2.13	1.00	0.87	66.65	E1C1A7, Q9DG07, E1C5S5, F1NER9, E1BRJ4, E1C063, F1NNP2, F1N871, E1BRS7
GO:0010256~endomembrane system organization	10	5.52	0.06	2.01	1.00	0.86	66.86	Q90965, E1C4Y9, E1C5S5, E1C2V3, F1NRD3, Q9PU45, F1NNP2, F1NGM0, Q5ZLJ8, F1NVE6
GO:0031532~actin cytoskeleton reorganization	4	2.21	0.06	4.44	1.00	0.86	66.97	F1NWB1, E1BQZ3, O42391, F1P5V9
GO:0051261~protein depolymerization	4	2.21	0.06	4.44	1.00	0.86	66.97	F1NMI2, E1BZC1, F1NB03, Q9PU45
GO:0034765~regulation of ion transmembrane transport	6	3.31	0.06	2.82	1.00	0.86	67.44	F1NE63, F1P3S9, R4GIQ1, F1NGM0, Q6DMS2, E1BYZ2
GO:0044723~single-organism carbohydrate metabolic process	10	5.52	0.06	1.99	1.00	0.86	68.11	F1N8Y0, F1NA05, O42391, F1NIJ6, E1BQH9, E1BZW3, F1N9K6, Q5ZLJ8, F1P5J6, E1C7A6
GO:0032956~regulation of actin cytoskeleton organization	7	3.87	0.06	2.47	1.00	0.87	68.81	E1C066, E1C5S5, E1C6G9, Q9PU45, F1NNP2, F1P3I1, F1NRM5
GO:0071447~cellular response to hydroperoxide	2	1.10	0.06	30.51	1.00	0.87	69.12	E1C5S5, F1NER9
GO:0030100~regulation of endocytosis	5	2.76	0.06	3.28	1.00	0.87	69.87	F1NMI2, Q5ZHM8, F1NER9, E1BR42, P26008
GO:0051130~positive regulation of cellular component organization	16	8.84	0.07	1.62	1.00	0.87	70.26	F1NE63, Q5ZIZ6, E1C066, E1C5S5, Q5ZHM8, E1BYW1, Q5F363, E1BR42, F1NNP2, F1NX90, F1NRM5, E1BS61, E1C6G9, F1NFN4, F1NER9, E1BXI3
GO:0007585~respiratory gaseous exchange	3	1.66	0.07	7.04	1.00	0.87	70.71	F1NMD6, F1P3S9, F1N871
GO:0019318~hexose metabolic process	5	2.76	0.07	3.21	1.00	0.88	72.18	F1NA05, O42391, F1NIJ6, F1N9K6, E1C7A6

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0030182~neuron differentiation	17	9.39	0.07	1.57	1.00	0.88	72.30	F1NE63, F1NMD6, F1NHU1, F1NNP2, E1C6D1, F1NIE7, Q5EES3, E1BS61, F1NBS7, F1NFN4, E1BQZ3, O42391, F1NYY0, Q3L254, F1NCB2, F1P3I1, P19019
GO:0001654~eye development	8	4.42	0.07	2.20	1.00	0.88	72.84	F1NIE7, A3FMM9, Q5EES3, E1BYI1, Q8AV58, E1BYW1, Q3L254, F1NNP2
GO:1901615~organic hydroxy compound metabolic process	7	3.87	0.07	2.40	1.00	0.87	72.87	F1N8Y0, F1NIE7, F1NRD3, F1NNP2, Q6DMS2, F1NBD0, F1P5J6
GO:0043933~macromolecular complex subunit organization	26	14.36	0.07	1.40	1.00	0.87	72.91	Q5ZIZ6, E1BV28, E1C5S5, Q5F363, Q5ZJL7, R4GGA5, R4GIZ7, E1C2H5, F1NRM5, F1NMI2, F1P2D7, F1NER9, F1P1T5, F1NB03, F1NGM0, A3FMM9, E1C4A8, E1BZC1, F1ND07, E1C063, Q9PU45, F1NNP2, F1P140, E1C6G9, E1BWC6, F1NX76
GO:0042325~regulation of phosphorylation	18	9.94	0.07	1.54	1.00	0.87	73.60	F1NE63, A3FMM9, Q5F420, E1C5S5, F1NA05, Q643S1, E1C066, Q5ZHM8, E1C063, F1NNP2, F1NX90, F1N989, E1BS61, Q9DG07, F1NER9, O42391, F1NKW3, F1N871
GO:0007167~enzyme linked receptor protein signaling pathway	13	7.18	0.07	1.72	1.00	0.87	73.92	Q643S1, E1C066, E1C5S5, Q5ZHM8, E1BYW1, F1NNP2, E1BS61, Q9DG07, F1NFN4, E1BQZ3, E1C0E9, F1NCB2, F1N871
GO:0001568~blood vessel development	10	5.52	0.07	1.93	1.00	0.87	74.02	F1NIE7, E1BS61, E1BYI1, Q643S1, P26008, F1NNP2, F1P5V9, F1N871, F1NX90, E1BRS7
GO:0006897~endocytosis	8	4.42	0.07	2.18	1.00	0.87	74.21	F1NMI2, Q5ZHM8, F1NS31, F1NER9, E1BR42, F1NLR2, P26008, E1C1G0
GO:0030031~cell projection assembly	8	4.42	0.07	2.17	1.00	0.87	74.88	E1C5S5, E1C6G9, O42391, F1NYY0, Q9PU45, F1NGM0, F1P3I1, F1NRM5
GO:0051270~regulation of cellular component movement	12	6.63	0.08	1.76	1.00	0.88	75.43	F1NE63, E1BZC1, Q643S1, E1C2V3, Q5ZHM8, F1NYY0, P26008, Q9PU45, F1NNP2, F1N871, F1NX90, E1BRS7

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0071822~protein complex subunit organization	18	9.94	0.08	1.53	1.00	0.87	75.43	A3FMM9, E1BV28, E1BZC1, F1ND07, E1C5S5, F1NNP2, Q9PU45, R4GIZ7, F1P140, F1NRM5, F1NMI2, F1P2D7, E1C6G9, F1NER9, E1BWC6, F1NB03, F1NX76, F1NGM0
GO:0005996~monosaccharide metabolic process	5	2.76	0.08	3.11	1.00	0.87	75.45	F1NA05, O42391, F1NIJ6, F1N9K6, E1C7A6
GO:0006801~superoxide metabolic process	3	1.66	0.08	6.54	1.00	0.87	75.48	Q5ZM68, E1C5S5, F1NER9
GO:0008610~lipid biosynthetic process	9	4.97	0.08	2.02	1.00	0.87	75.65	F1N8Y0, F1NIE7, Q5F420, E1C5S5, Q5ZLL8, F1NRX7, Q5ZM65, F1NBD0, F1N989
GO:0048666~neuron development	14	7.73	0.08	1.66	1.00	0.87	75.75	F1NE63, F1NHU1, F1NNP2, E1C6D1, Q5EES3, E1BS61, F1NBS7, F1NFN4, E1BQZ3, O42391, F1NYY0, F1NCB2, F1P3I1, P19019
GO:0090150~establishment of protein localization to membrane	6	3.31	0.08	2.63	1.00	0.86	75.81	E1C2V3, E1BXI3, Q9PU45, F1NGM0, Q5ZLJ8, E1C8I6
GO:0030334~regulation of cell migration	11	6.08	0.08	1.82	1.00	0.87	76.75	F1NE63, E1BZC1, Q643S1, Q5ZHM8, F1NYY0, P26008, Q9PU45, F1NNP2, F1N871, F1NX90, E1BRS7
GO:0072383~plus-end-directed vesicle transport along microtubule	2	1.10	0.08	24.41	1.00	0.87	76.98	O42391, F1P140
GO:0072386~plus-end-directed organelle transport along microtubule	2	1.10	0.08	24.41	1.00	0.87	76.98	O42391, F1P140
GO:0044539~long-chain fatty acid import	2	1.10	0.08	24.41	1.00	0.87	76.98	Q5F420, F1NER9
GO:0035556~intracellular signal transduction	29	16.02	0.08	1.34	1.00	0.87	77.61	Q90965, F1NE63, F1P3S9, E1C5S5, Q5ZHM8, R4GL74, E1BR42, P26008, E1C900, E1C1A7, O42391, E1BQZ3, F1NER9, F1N871, E1C066, Q643S1, R4GJL4, F1NLR2, F1NX14, E1C063,

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
								Q5ZLL8, F1NNP2, E1C1G0, F1NSE0, F1N989, E1BS61, Q9DG07, E1C6G9, F1NKW3
GO:0070527~platelet aggregation	3	1.66	0.08	6.31	1.00	0.87	77.64	E1C5S5, F1NYY0, F1NLR2
GO:0023051~regulation of signaling	32	17.68	0.08	1.31	1.00	0.87	78.21	F1NE63, F1NMD6, F1P3S9, E1C5S5, Q5ZHM8, R4GL74, P26008, E1C900, R4GIQ1, E1C1A7, E1BSZ8, E1BQZ3, F1NER9, E1BXI3, F1NGM0, F1N871, F1NLF6, E1C066, Q643S1, E1BYW1, F1NLR2, E1C063, Q5ZLL8, F1NNP2, F1N989, E1BS61, F1NFN4, F1NX76, F1NCB2, F1N9K6, F1NKW3, E1BYZ2
GO:0042592~homeostatic process	20	11.05	0.08	1.46	1.00	0.87	78.74	E1C8S8, E1BYI1, Q5ZM68, F1P3S9, F1NA05, F1NIJ6, E1C085, F1NLR2, Q90743, F1NNP2, Q5F429, Q6DMS2, F1N989, E1C7A6, F1N8Y0, F1NER9, O42391, E1BWC6, F1NCB2, F1N9K6
GO:0043623~cellular protein complex assembly	9	4.97	0.08	1.97	1.00	0.88	79.61	A3FMM9, E1C5S5, E1C6G9, F1NER9, F1NX76, Q9PU45, R4GIZ7, F1P140, F1NRM5
GO:0002718~regulation of cytokine production involved in immune response	3	1.66	0.09	6.10	1.00	0.88	79.66	F1NER9, E1C063, F1NNP2
GO:0050764~regulation of phagocytosis	3	1.66	0.09	6.10	1.00	0.88	79.66	F1NER9, E1BR42, P26008
GO:0008654~phospholipid biosynthetic process	4	2.21	0.09	3.81	1.00	0.88	79.98	Q5ZLL8, F1NRX7, Q5ZM65, F1N989
GO:0006909~phagocytosis	4	2.21	0.09	3.81	1.00	0.88	79.98	F1NER9, E1BR42, F1NLR2, P26008
GO:0043624~cellular protein complex disassembly	4	2.21	0.09	3.81	1.00	0.88	79.98	F1NMI2, E1BZC1, F1NB03, Q9PU45

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0031399~regulation of protein modification process	20	11.05	0.09	1.45	1.00	0.88	80.28	F1NE63, Q5ZIZ6, A3FMM9, Q5F420, E1C5S5, Q643S1, E1C066, Q5ZHM8, Q5F363, E1C063, F1NNP2, Q5ZLJ8, F1N989, E1BS61, Q9DG07, F1NFN4, F1NER9, O42391, F1N871, F1NKW3
GO:0010562~positive regulation of phosphorus metabolic process	14	7.73	0.09	1.62	1.00	0.88	80.55	F1NE63, A3FMM9, Q5F420, Q643S1, E1C5S5, Q5ZHM8, E1C063, F1NNP2, F1N989, Q9DG07, F1NER9, O42391, F1NKW3, F1N871
GO:0045937~positive regulation of phosphate metabolic process	14	7.73	0.09	1.62	1.00	0.88	80.55	F1NE63, A3FMM9, Q5F420, Q643S1, E1C5S5, Q5ZHM8, E1C063, F1NNP2, F1N989, Q9DG07, F1NER9, O42391, F1NKW3, F1N871
GO:0009966~regulation of signal transduction	29	16.02	0.09	1.33	1.00	0.88	80.61	F1NE63, F1NMD6, F1P3S9, E1C5S5, Q5ZHM8, R4GL74, P26008, E1C900, R4GIQ1, E1C1A7, E1BSZ8, E1BQZ3, F1NER9, E1BXI3, F1N871, F1NLF6, E1C066, Q643S1, E1BYW1, F1NLR2, E1C063, Q5ZLL8, F1NNP2, F1N989, E1BS61, F1NFN4, F1NCB2, F1NKW3, E1BYZ2
GO:0031175~neuron projection development	12	6.63	0.09	1.71	1.00	0.88	80.79	F1NE63, Q5EES3, E1BS61, F1NFN4, E1BQZ3, O42391, F1NYY0, F1NHU1, F1NNP2, F1NCB2, F1P3I1, E1C6D1
GO:0072359~circulatory system development	14	7.73	0.09	1.62	1.00	0.87	80.92	F1NIE7, E1BS61, E1BQN0, E1BYI1, E1C066, Q643S1, E1C2V3, E1BYW1, P26008, F1NNP2, F1P5V9, F1N871, F1NX90, E1BRS7
GO:0072358~cardiovascular system development	14	7.73	0.09	1.62	1.00	0.87	80.92	F1NIE7, E1BS61, E1BQN0, E1BYI1, E1C066, Q643S1, E1C2V3, E1BYW1, P26008, F1NNP2, F1P5V9, F1N871, F1NX90, E1BRS7
GO:0008064~regulation of actin polymerization or depolymerization	5	2.76	0.09	2.93	1.00	0.87	81.27	E1C5S5, E1C6G9, Q9PU45, F1P3I1, F1NRM5
GO:0030832~regulation of actin filament length	5	2.76	0.09	2.93	1.00	0.87	81.27	E1C5S5, E1C6G9, Q9PU45, F1P3I1, F1NRM5
GO:0071495~cellular response to endogenous stimulus	14	7.73	0.09	1.61	1.00	0.87	81.29	F1P3S9, Q643S1, E1C5S5, E1C066, Q5F420, Q5ZHM8, E1BYW1, Q9PU45, F1NNP2, E1BS61,

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
								F1NFN4, F1NER9, E1BXI3, P19019
GO:2000311~regulation of alpha-amino-3-hydroxy-5-methyl-4-isoxazole propionate selective glutamate receptor activity	2	1.10	0.09	20.34	1.00	0.88	82.85	F1NE63, R4GIQ1
GO:0045792~negative regulation of cell size	2	1.10	0.09	20.34	1.00	0.88	82.85	E1C066, Q9PU45
GO:0051493~regulation of cytoskeleton organization	8	4.42	0.09	2.04	1.00	0.89	83.24	E1BZC1, E1C066, E1C5S5, E1C6G9, Q9PU45, F1NNP2, F1P3I1, F1NRM5
GO:0032411~positive regulation of transporter activity	3	1.66	0.10	5.72	1.00	0.88	83.28	F1NE63, E1C5S5, F1NGM0
GO:2000145~regulation of cell motility	11	6.08	0.10	1.75	1.00	0.88	83.49	F1NE63, E1BZC1, Q643S1, Q5ZHM8, F1NYY0, P26008, Q9PU45, F1NNP2, F1N871, F1NX90, E1BRS7
GO:0001944~vasculature development	10	5.52	0.10	1.82	1.00	0.88	83.52	F1NIE7, E1BS61, E1BYI1, Q643S1, P26008, F1NNP2, F1P5V9, F1N871, F1NX90, E1BRS7
GO:0051235~maintenance of location	6	3.31	0.10	2.44	1.00	0.89	84.14	F1P3S9, F1NER9, P26008, Q6DMS2, F1N989, E1C8I6
Cellular Component (GOTERM_CC_FAT)								
GO:0030027~lamellipodium	6	3.31	0.02	4.09	1.00	1.00	18.87	E1C066, O42391, P26008, F1NX14, Q9PU45, F1P5V9
GO:0030054~cell junction	18	9.94	0.02	1.85	1.00	0.94	19.35	E1C5S5, E1C2V3, F1NWB1, P26008, F1NS97, Q9PU45, Q6ITC7, Q5ZJL7, E1C890, F1NRM5, E1C4Y9, Q9DG07, Q8AV58, E1C6G9, F1NYY0, F1NGM0, F1P5V9, P19019
GO:0031984~organelle subcompartment	7	3.87	0.03	2.93	1.00	0.98	35.46	E1C4Y9, F1NLF6, F1NAK6, F1NRD3, F1NTJ5, E1BZW3, Q5ZLJ8

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0005942~phosphatidylinositol 3-kinase complex	3	1.66	0.03	10.34	1.00	0.95	36.80	O42391, E1C1G0, F1NSE0
GO:0030175~filopodium	4	2.21	0.04	5.45	1.00	0.93	39.49	E1C7H7, F1NTJ5, P26008, Q9PU45
GO:0043235~receptor complex	8	4.42	0.04	2.44	1.00	0.94	46.34	R4GIQ1, Q5ZHM8, F1NS31, P26008, F1N871, E1C890, Q6DMS2, P19019
GO:0098857~membrane microdomain	6	3.31	0.05	3.06	1.00	0.91	47.16	Q9DG07, Q5ZHM8, F1NS31, F1NER9, F1NHU1, F1NBD0
GO:0045121~membrane raft	6	3.31	0.05	3.06	1.00	0.91	47.16	Q9DG07, Q5ZHM8, F1NS31, F1NER9, F1NHU1, F1NBD0
GO:0005768~endosome	12	6.63	0.05	1.91	1.00	0.89	48.61	F1P4R5, E1C4Y9, E1BS61, F1NLF6, F1NHW2, F1NHU1, F1NTJ5, F1NNP2, F1NGM0, F1NCB2, F1P140, Q5ZLJ8
GO:0005875~microtubule associated complex	5	2.76	0.05	3.57	1.00	0.88	50.64	Q90828, F1NA05, F1NB03, F1P140, E1C6D1
GO:0098791~Golgi subcompartment	6	3.31	0.07	2.66	1.00	0.94	64.80	E1C4Y9, F1NLF6, F1NAK6, F1NTJ5, E1BZW3, Q5ZLJ8
GO:0015629~actin cytoskeleton	9	4.97	0.08	1.99	1.00	0.94	68.42	E1C7H7, E1C066, F1P0K3, F1NYY0, F1NTJ5, E1BXA7, Q9PU45, E1BR21, F1NRM5
GO:0030864~cortical actin cytoskeleton	3	1.66	0.09	6.06	1.00	0.93	70.96	F1NYY0, Q9PU45, F1NRM5
GO:0045202~synapse	10	5.52	0.09	1.86	1.00	0.92	71.04	F1NMI2, Q8AV58, F1NWB1, F1NYY0, F1NX76, F1NCB2, F1NS97, E1C890, E1BYZ2, P19019
GO:0098589~membrane region	6	3.31	0.09	2.51	1.00	0.91	72.18	Q9DG07, Q5ZHM8, F1NS31, F1NER9, F1NHU1, F1NBD0
GO:0061695~transferase complex, transferring phosphorus-containing groups	6	3.31	0.10	2.44	1.00	0.92	75.53	O42391, E1BRJ4, E1C063, E1C1G0, F1NSE0, E1C1Z0
Molecular Function (GOTERM_MF_FAT)								

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0098772~molecular function regulator	22	12.15	0.00	2.09	0.54	0.54	2.20	F1NLF6, E1C2K7, E1C5S5, F1NWB1, E1C066, F1ND07, R4GL74, E1BYW1, E1BR42, E1BTF2, F1NI67, E1BRS7, E1C0R6, E1BS61, R4GIQ1, F1NAK6, O42391, E1BQZ3, F1NN85, F1NEW8, E1BXI3, E1C3U0
GO:0030234~enzyme regulator activity	18	9.94	0.00	2.30	0.60	0.37	2.60	F1NLF6, E1C2K7, E1C5S5, F1NWB1, E1C066, F1ND07, E1BYW1, E1BR42, E1BTF2, E1BRS7, F1NI67, E1C0R6, E1BQZ3, F1NN85, O42391, F1NEW8, E1BXI3, E1C3U0
GO:0016773~phosphotransferase activity, alcohol group as acceptor	18	9.94	0.00	2.16	0.83	0.44	4.99	F1NE63, E1C7H7, E1C5S5, F1NLR2, F1NX14, E1C063, F1NNP2, E1C1G0, F1NSE0, E1C1A7, F1NHW2, O42391, F1NNJ1, E1C0E9, F1N9K6, F1NKW3, F1N871, E1C116
GO:0061134~peptidase regulator activity	7	3.87	0.01	4.27	0.94	0.50	7.83	F1NLF6, F1ND07, F1NN85, F1NEW8, E1BYW1, E1BTF2, E1BRS7
GO:0035005~1-phosphatidylinositol-4-phosphate 3-kinase activity	3	1.66	0.01	25.12	0.94	0.43	7.84	O42391, E1C1G0, F1NSE0
GO:0005524~ATP binding	27	14.92	0.01	1.69	0.97	0.45	9.90	E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0035091~phosphatidylinositol binding	8	4.42	0.01	3.50	0.98	0.42	10.39	R4GL74, F1NQ91, F1NTJ5, F1N9K6, E1C1G0, E1BTV4, F1NSE0, E1C116
GO:0032559~adenyl ribonucleotide binding	27	14.92	0.01	1.66	0.99	0.43	12.28	E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0036094~small molecule binding	40	22.10	0.01	1.46	0.99	0.40	12.32	Q90965, E1C7H7, Q5ZIZ6, E1BV28, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, Q6DMS2, E1C1A7, F1NB03, Q5ZJC9, F1P374, F1NGM0, F1N871, F1NBD0, E1C735, F1P0I1, F1NLY0, A0A547, Q5ZLC4, Q5ZM68, F1NHR6, F1NV49, F1NLR2, Q3YK19, E1C063, F1NX14, Q5ZMC5, F1NHN3, F1P140, F1NNJ1, E1BRJ4, E1C0E9, E1BXA7, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0030554~adenyl nucleotide binding	27	14.92	0.01	1.66	0.99	0.37	12.59	E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0016301~kinase activity	18	9.94	0.01	1.94	0.99	0.37	13.60	F1NE63, E1C7H7, E1C5S5, F1NLR2, F1NX14, E1C063, F1NNP2, E1C1G0, F1NSE0, E1C1A7, F1NHW2, O42391, F1NNJ1, E1C0E9, F1N9K6, F1NKW3, F1N871, E1C116
GO:0004866~endopeptidase inhibitor activity	6	3.31	0.01	4.45	1.00	0.36	14.40	F1NLF6, F1NN85, F1NEW8, E1BYW1, E1BTF2, E1BRS7
GO:0004672~protein kinase activity	15	8.29	0.01	2.11	1.00	0.34	14.61	F1NE63, E1C7H7, E1C5S5, F1NLR2, E1C063, F1NNP2, E1C1A7, F1NHW2, O42391, F1NNJ1, E1C0E9, F1N9K6, F1NKW3, F1N871, E1C116
GO:0016303~1-phosphatidylinositol-3-kinase activity	3	1.66	0.01	17.58	1.00	0.34	15.61	O42391, E1C1G0, F1NSE0
GO:0030414~peptidase inhibitor activity	6	3.31	0.01	4.34	1.00	0.33	15.82	F1NLF6, F1NN85, F1NEW8, E1BYW1, E1BTF2, E1BRS7
GO:0003774~motor activity	6	3.31	0.01	4.34	1.00	0.33	15.82	E1C7H7, Q90828, F1NB03, F1NTJ5, E1BXA7, F1P140
GO:0008047~enzyme activator activity	10	5.52	0.01	2.68	1.00	0.31	15.90	E1C0R6, E1C2K7, F1ND07, E1C5S5, E1BQZ3, O42391, E1BR42, E1BXI3, E1C3U0, F1NI67

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0061135~endopeptidase regulator activity	6	3.31	0.01	4.24	1.00	0.32	17.31	F1NLF6, F1NN85, F1NEW8, E1BYW1, E1BTF2, E1BRS7
GO:0035004~phosphatidylinositol 3-kinase activity	3	1.66	0.01	15.99	1.00	0.32	18.57	O42391, E1C1G0, F1NSE0
GO:0046906~tetrapyrrole binding	6	3.31	0.01	4.14	1.00	0.32	18.88	F1NLY0, F1NNN4, Q5ZM68, F1P4G4, P20678, F1NB14
GO:0016307~phosphatidylinositol phosphate kinase activity	3	1.66	0.02	14.65	1.00	0.34	21.66	O42391, E1C1G0, F1NSE0
GO:0097367~carbohydrate derivative binding	34	18.78	0.02	1.47	1.00	0.34	22.08	Q90965, E1C7H7, Q90828, E1C5S5, F1NTJ5, F1NS97, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1NYY0, F1P374, E1BXI3, F1NGM0, F1N871, E1C9I1, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BRJ4, E1C0E9, E1BXA7, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0052742~phosphatidylinositol kinase activity	3	1.66	0.02	13.53	1.00	0.36	24.85	O42391, E1C1G0, F1NSE0
GO:0032549~ribonucleoside binding	30	16.57	0.02	1.51	1.00	0.36	25.56	Q90965, E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1NGM0, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BRJ4, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0008289~lipid binding	12	6.63	0.02	2.18	1.00	0.35	26.34	Q5ZLC4, F1NER9, R4GL74, F1NQ91, F1NTJ5, F1N9K6, E1C1G0, E1BTV4, F1NSE0, F1NBD0, F1NHY3, E1C116
GO:0001882~nucleoside binding	30	16.57	0.02	1.50	1.00	0.35	26.52	Q90965, E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1NGM0, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BRJ4, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0003779~actin binding	6	3.31	0.03	3.55	1.00	0.40	31.68	F1NWB1, F1NYY0, Q9PU45, F1NS97, F1P3I1, F1NRM5
GO:0035639~purine ribonucleoside triphosphate binding	29	16.02	0.03	1.46	1.00	0.45	37.13	Q90965, E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1NGM0, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0032550~purine ribonucleoside binding	29	16.02	0.03	1.46	1.00	0.45	38.31	Q90965, E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1NGM0, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0001883~purine nucleoside binding	29	16.02	0.03	1.46	1.00	0.44	38.60	Q90965, E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1NGM0, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0005262~calcium channel activity	5	2.76	0.03	4.01	1.00	0.44	40.06	R4GIQ1, F1NAK6, P26008, F1NAX8, Q6DMS2
GO:0030695~GTPase regulator activity	7	3.87	0.04	2.81	1.00	0.46	42.24	E1C0R6, E1C2K7, E1C066, E1BQZ3, E1BR42, E1C3U0, F1NI67
GO:0032555~purine ribonucleotide binding	29	16.02	0.04	1.44	1.00	0.46	43.76	Q90965, E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1NGM0, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0000166~nucleotide binding	35	19.34	0.04	1.37	1.00	0.46	44.64	Q90965, E1C7H7, Q5ZIZ6, E1BV28, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, Q5ZJC9, F1P374, F1NGM0, F1N871, E1C735, F1P0I1, A0A547, Q5ZM68, F1NHR6, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1NHN3, F1P140, F1NNJ1, E1C0E9, E1BXA7, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:1901265~nucleoside phosphate binding	35	19.34	0.04	1.37	1.00	0.46	44.64	Q90965, E1C7H7, Q5ZIZ6, E1BV28, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, Q5ZJC9, F1P374, F1NGM0, F1N871, E1C735, F1P0I1, A0A547, Q5ZM68, F1NHR6, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1NHN3, F1P140, F1NNJ1, E1C0E9, E1BXA7, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0017076~purine nucleotide binding	29	16.02	0.04	1.43	1.00	0.45	44.69	Q90965, E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1NGM0, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0032553~ribonucleotide binding	29	16.02	0.04	1.42	1.00	0.47	47.19	Q90965, E1C7H7, Q90828, E1C5S5, F1NTJ5, R4GGA5, F1NRM5, E1C1A7, F1NB03, F1P374, F1NGM0, F1N871, E1C735, F1P0I1, A0A547, F1NV49, F1NLR2, Q3YK19, F1NX14, E1C063, Q5ZMC5, F1P140, F1NNJ1, E1BXA7, E1C0E9, F1N9K6, E1BZT9, F1NKW3, E1C116
GO:0020037~heme binding	5	2.76	0.05	3.57	1.00	0.51	52.25	F1NNN4, Q5ZM68, F1P4G4, P20678, F1NB14
GO:0060589~nucleoside-triphosphatase regulator activity	7	3.87	0.05	2.61	1.00	0.50	52.39	E1C0R6, E1C2K7, E1C066, E1BQZ3, E1BR42, E1C3U0, F1NI67
GO:0005543~phospholipid binding	8	4.42	0.05	2.34	1.00	0.51	54.45	R4GL74, F1NQ91, F1NTJ5, F1N9K6, E1C1G0, E1BTV4, F1NSE0, E1C116

Category Term	Count	%	*P*-Value	Fold Enrichment	Bonferroni	Benjamini	*FDR*	Genes
GO:0015085~calcium ion transmembrane transporter activity	5	2.76	0.06	3.45	1.00	0.52	56.22	R4GIQ1, F1NAK6, P26008, F1NAX8, Q6DMS2
GO:0004857~enzyme inhibitor activity	7	3.87	0.07	2.43	1.00	0.58	63.16	F1NLF6, F1NWB1, F1NN85, F1NEW8, E1BYW1, E1BTF2, E1BRS7
GO:0017016~Ras GTPase binding	4	2.21	0.07	4.19	1.00	0.58	64.19	E1C2K7, F1NA05, E1C3U0, F1NI67
GO:0031267~small GTPase binding	4	2.21	0.07	4.11	1.00	0.58	65.79	E1C2K7, F1NA05, E1C3U0, F1NI67
GO:0051020~GTPase binding	4	2.21	0.08	3.97	1.00	0.61	68.88	E1C2K7, F1NA05, E1C3U0, F1NI67
GO:0005096~GTPase activator activity	6	3.31	0.08	2.61	1.00	0.60	69.34	E1C0R6, E1C2K7, E1BQZ3, E1BR42, E1C3U0, F1NI67
GO:0002162~dystroglycan binding	2	1.10	0.08	23.45	1.00	0.61	70.74	F1NYY0, F1NS97
GO:0005216~ion channel activity	9	4.97	0.09	1.93	1.00	0.65	75.03	R4GIQ1, F1NAK6, F1NHW2, P26008, F1NAX8, E1C890, Q6DMS2, F1NVE6, P19019
GO:0030228~lipoprotein particle receptor activity	2	1.10	0.10	19.54	1.00	0.66	77.11	F1NS31, F1NER9
Orthologous Groups (COG_ONTOLOGY)								
Secondary metabolites biosynthesis, transport, and catabolism	4	2.21	0.07	3.84	0.60	0.60	38.97	F1NNN4, F1P4G4, P20678, F1NB14
Proteins (GENE3D)								
1.10.630.10:Cytochrome p450	4	2.21	0.01	8.39	0.93	0.93	13.49	F1NNN4, F1P4G4, P20678, F1NB14
1.10.1070.11:Phosphatidylinositol 3-kinase Catalytic Subunit; Chain A, domain 5	3	1.66	0.02	12.20	1.00	0.94	26.71	O42391, E1C1G0, F1NSE0
2.60.40.150:C2- domain Calcium/lipid binding domain	5	2.76	0.07	3.22	1.00	1.00	58.94	E1C5S5, F1NFN4, O42391, E1C1G0, F1NSE0

APPENDIX XXI

Custom R Function for counting SNPs in a sliding window; used to produce figures

#Number of SNPs with *XtX*/*BF* > thresh along binned scaffolds

```
###
### Function
###
sw.count<-function(bin,overlap,input){
  size=unique(input[,2]) #column of scaffold sizes
  scaff=unique(input[,1]) #column of scaffold numbers
  out=list(NA)
  for(i in 1:length(size)){
    loc=input[input[,1]==scaff[i],3]
    tmp.scaff=rep(0,size[i])
    tmp.scaff[loc]=tmp.scaff[loc]+1
    new.scaff=NA
    if(size[i] < bin){
      n.bin=1
      }else{
      n.bin=ceiling(size[i]/overlap)}
    b=1
    for(n in 1:n.bin){
      if((b+bin) <= size[i]){
        new.scaff[n]=sum(tmp.scaff[c(b:(b+bin))])
        }else if(size[i] < bin){
        new.scaff=sum(tmp.scaff)
        }else{
          new.scaff[n]=sum(tmp.scaff[-c(1:(b+bin))])}
      b=b+overlap
    }
    out[[i]]=new.scaff
  }
  new.out=list(out,scaff)
}
###
### End Function
###
```

APPENDIX XXII

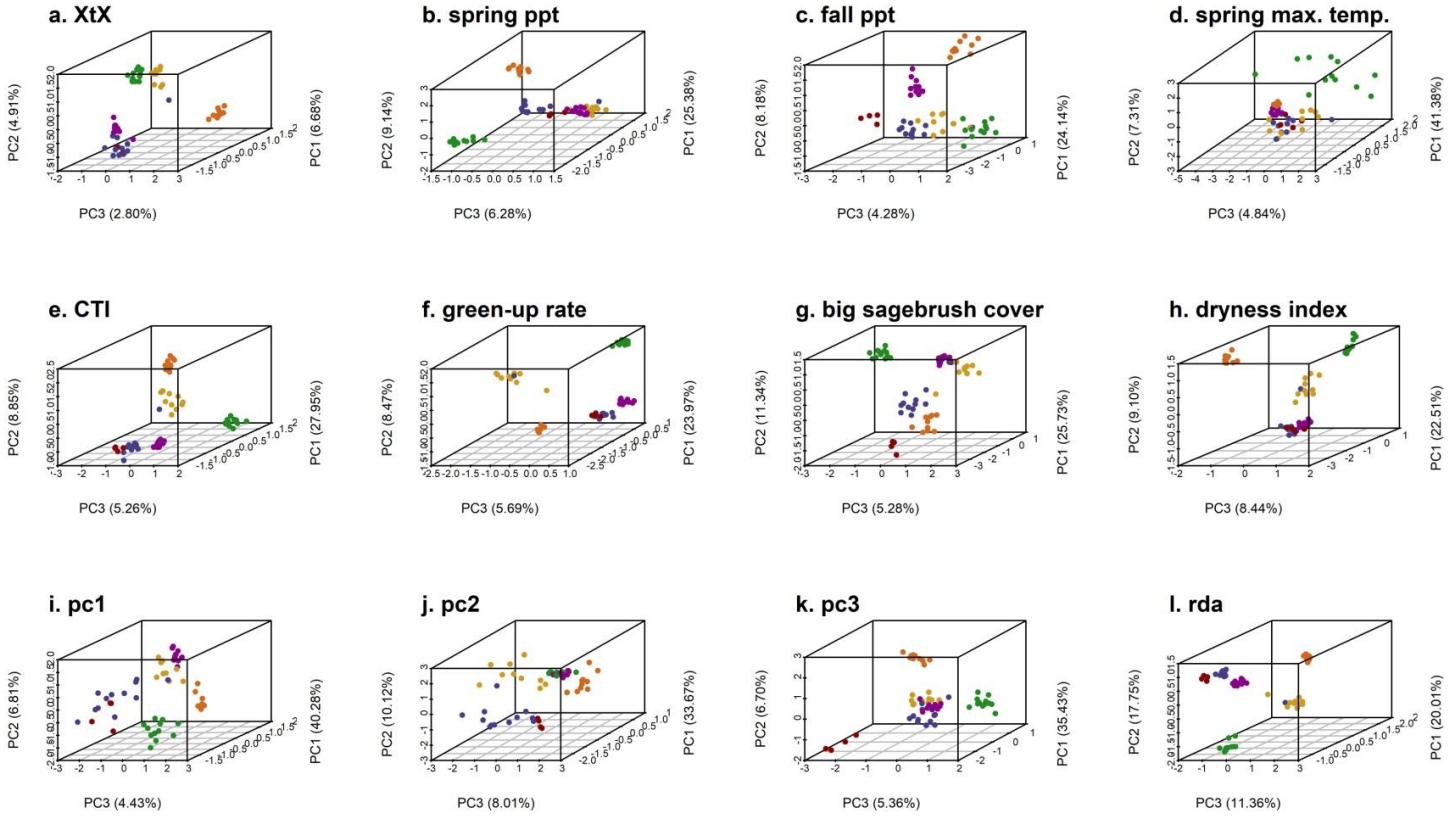

Figure S22.1. Three-dimensional plots of the first three principal components for each PCA analysis on SNPs under divergent selection from different methods. Each point represents an individual color coded by the population where the sample was collected: Red = Cimarron, Blue = Crawford, Green = Dove Creek, Purple = Gunnison Basin, Orange = Piñon Mesa, Yellow = San Miguel. Percentage of variation accounted for by each PC is labeled in parentheses on each axis.

APPENDIX XXIII

Table S23.1. West Nile virus detection in counties supporting Gunnison sage-grouse populations. Detections = total number of organisms (animals and mosquitos) detected with WNV from 2006-2017. Colorado data source: https://www.colorado.gov/pacific/cdphe/west-nile-virus-data; Utah data source: http://health.utah.gov/epi/diseases/WNV/surveillance.

County	Population	Detections
Montrose	Cimarron & Crawford	5
Delta	Crawford	27
Dolores	Dove Creek	0
San Juan (UT)	Dove Creek	0
Gunnison	Gunnison Basin	0
Saguache	Gunnison Basin	0
Mesa	Piñon Mesa	46
Grand (UT)	Piñon Mesa	93
San Miguel	San Miguel	0

APPENDIX XXIV

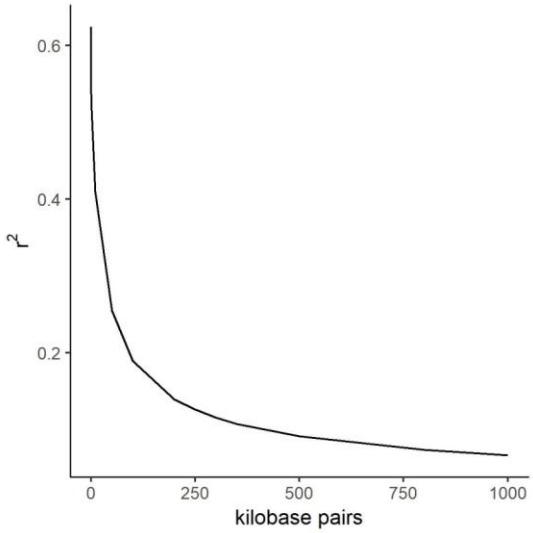

Figure S24.1. Linkage disequilibrium decay (in kbp) for Gunnison sage-grouse.

APPENDIX XXV

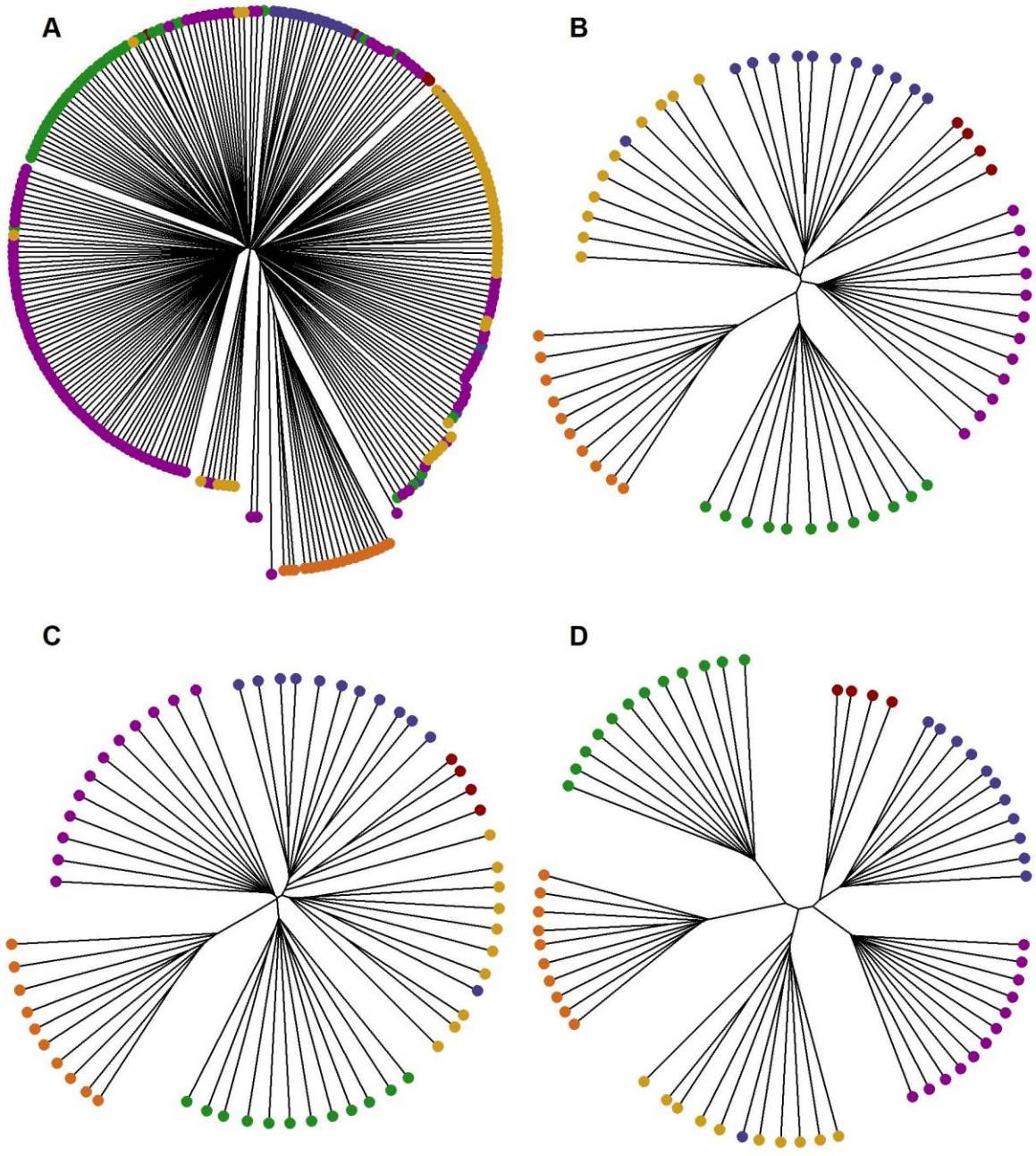

Figure S25.1. Dendrograms created using the single (based on closest pair) method for (A) microsatellites, (B) all SNPs, (C) putatively neutral SNPs, and (D) candidate adaptive loci. Colors indicate sampling origin: Cimarron = red, Crawford = blue, Dove Creek =green, Gunnison Basin = purple, Piñon Mesa = orange, San Miguel = yellow.

APPENDIX XXVI

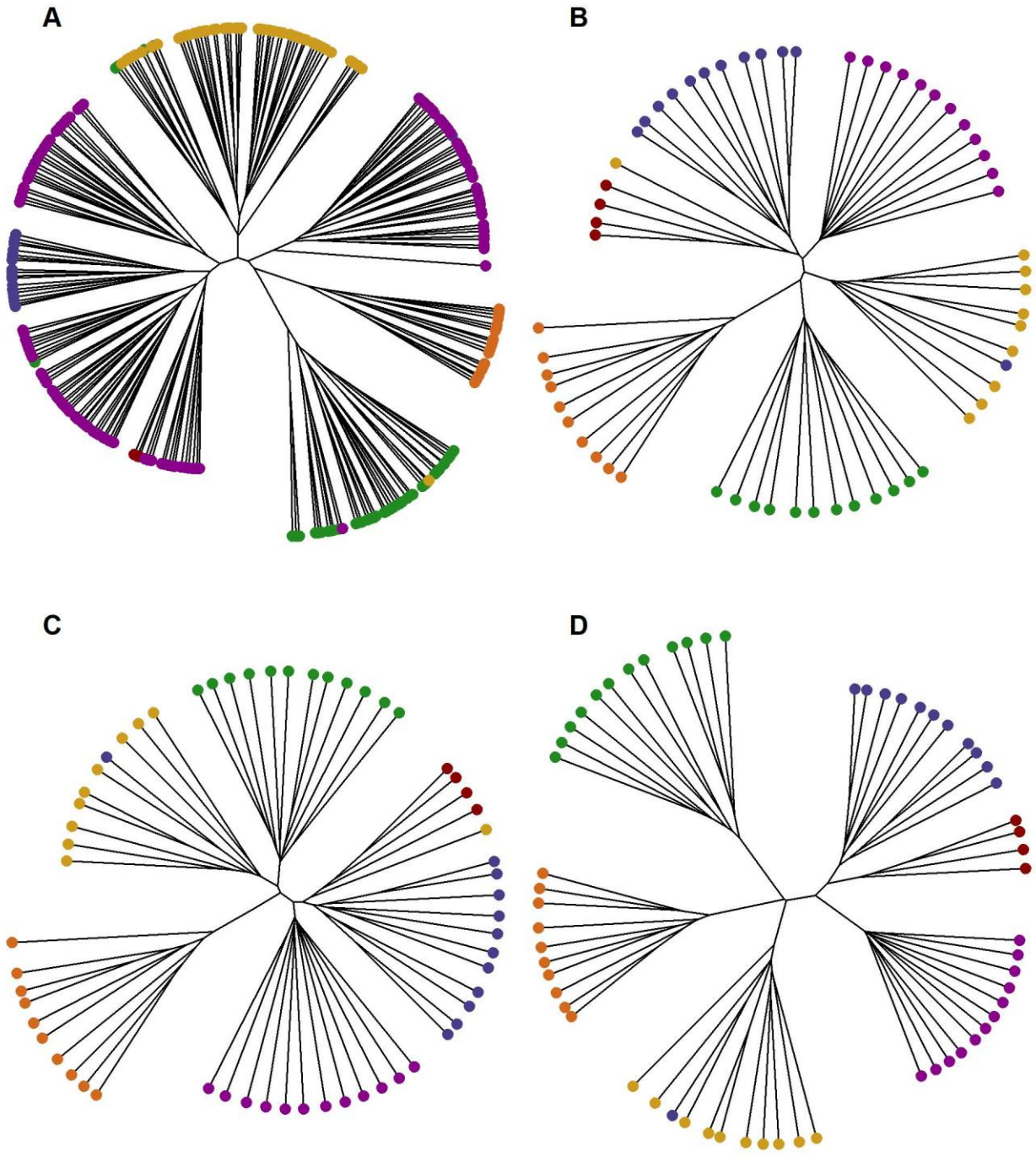

Figure S26.1. Dendrograms created using the complete (based on furthest pair) method for (A) microsatellites, (B) all SNPs, (C) putatively neutral SNPs, and (D) candidate adaptive loci. Colors indicate sampling origin: Cimarron = red, Crawford = blue, Dove Creek =green, Gunnison Basin = purple, Piñon Mesa = orange, San Miguel = yellow.

APPENDIX XXVII

Table S27.1. Means and *SE*s for all diversity metrics (H_O = observed heterozygosity, $\underline{H}_E$ = expected heterozygosity, F_{IS} = inbreeding coefficient, A_R = allelic richness) for each population and each data type (microsatellites or putatively neutral SNPs).

		H_O		H_E		F_{IS}		A_R	
Population	Data	Mean	*SE*	Mean	*SE*	Mean	*SE*	Mean	*SE*
Cimarron	microsatellite	0.534	0.067	0.413	0.046	-0.279	0.109	2.183	0.155
Crawford	microsatellite	0.517	0.047	0.51	0.042	-0.022	0.065	2.605	0.170
Dove Creek	microsatellite	0.464	0.036	0.514	0.043	0.071	0.049	2.602	0.165
Gunnison Basin	microsatellite	0.529	0.042	0.559	0.044	0.045	0.021	2.924	0.213
Pinon Mesa	microsatellite	0.498	0.041	0.505	0.036	0.007	0.047	2.428	0.128
San Miguel	microsatellite	0.548	0.034	0.578	0.037	0.038	0.022	2.853	0.171
Cimarron	SNP	0.227	0.004	0.183	0.003	-0.193	0.006	1.419	0.005
Crawford	SNP	0.23	0.003	0.226	0.003	-0.022	0.004	1.490	0.004
Dove Creek	SNP	0.227	0.003	0.225	0.003	-0.006	0.003	1.481	0.004
Gunnison Basin	SNP	0.226	0.003	0.222	0.003	-0.021	0.003	1.524	0.004
Pinon Mesa	SNP	0.207	0.003	0.198	0.003	-0.043	0.004	1.473	0.004
San Miguel	SNP	0.228	0.003	0.227	0.003	-0.024	0.004	1.501	0.004

APPENDIX XXVIII

Table S28.1. Means and 95% CIs for all differentiation metrics (G_{ST}, D_{Jost}, F_{ST}) for each population pair (Comparison) and each data type (microsatellites, putatively neutral SNPs, and all SNPs).

		G_{ST}		D_{Jost}		F_{ST}	
Comparison	Data	Mean	95% CI	Mean	95% CI	Mean	95% CI
Cimarron-Crawford	microsatellite	0.255	[0.176 - 0.374]	0.073	[0.034 - 0.131]	0.158	[0.103 - 0.240]
Cimarron-Dove Creek	microsatellite	0.366	[0.283 - 0.493]	0.153	[0.115 - 0.210]	0.211	[0.162 - 0.286]
Cimarron-Gunnison Basin	microsatellite	0.275	[0.193 - 0.413]	0.102	[0.061 - 0.172]	0.145	[0.100 - 0.223]
Cimarron-Pinon Mesa	microsatellite	0.562	[0.484 - 0.673]	0.284	[0.213 - 0.384]	0.326	[0.275 - 0.401]
Cimarron-San Miguel	microsatellite	0.345	[0.274 - 0.444]	0.110	[0.077 - 0.163]	0.177	[0.135 - 0.236]
Crawford-Dove Creek	microsatellite	0.333	[0.282 - 0.381]	0.175	[0.138 - 0.211]	0.194	[0.162 - 0.224]
Crawford-Gunnison Basin	microsatellite	0.179	[0.149 - 0.215]	0.086	[0.069 - 0.109]	0.100	[0.082 - 0.121]
Crawford-Pinon Mesa	microsatellite	0.563	[0.515 - 0.618]	0.339	[0.289 - 0.400]	0.310	[0.278 - 0.348]
Crawford-San Miguel	microsatellite	0.295	[0.237 - 0.348]	0.137	[0.098 - 0.177]	0.157	[0.124 - 0.188]
Dove Creek-Gunnison Basin	microsatellite	0.319	[0.286 - 0.353]	0.178	[0.155 - 0.202]	0.173	[0.155 - 0.192]
Dove Creek-Pinon Mesa	microsatellite	0.505	[0.468 - 0.547]	0.279	[0.243 - 0.319]	0.281	[0.259 - 0.306]
Dove Creek-San Miguel	microsatellite	0.288	[0.242 - 0.333]	0.151	[0.120 - 0.180]	0.155	[0.130 - 0.180]
Gunnison Basin-Pinon Mesa	microsatellite	0.493	[0.462 - 0.529]	0.272	[0.238 - 0.309]	0.254	[0.237 - 0.274]
Gunnison Basin-San Miguel	microsatellite	0.294	[0.263 - 0.325]	0.147	[0.124 - 0.170]	0.151	[0.134 - 0.168]
Pinon Mesa-San Miguel	microsatellite	0.477	[0.441 - 0.515]	0.250	[0.215 - 0.288]	0.242	[0.220 - 0.265]
Cimarron-Crawford	neutral SNPs	0.111	[0.075 - 0.168]	0.004	[0.002 - 0.008]	0.139	[0.093 - 0.209]
Cimarron-Dove Creek	neutral SNPs	0.215	[0.182 - 0.263]	0.014	[0.011 - 0.018]	0.253	[0.218 - 0.303]
Cimarron-Gunnison Basin	neutral SNPs	0.150	[0.116 - 0.203]	0.008	[0.005 - 0.013]	0.176	[0.138 - 0.235]
Cimarron-Pinon Mesa	neutral SNPs	0.304	[0.270 - 0.353]	0.027	[0.023 - 0.033]	0.348	[0.311 - 0.400]
Cimarron-San Miguel	neutral SNPs	0.165	[0.123 - 0.227]	0.009	[0.005 - 0.014]	0.199	[0.149 - 0.270]
Crawford-Dove Creek	neutral SNPs	0.162	[0.138 - 0.191]	0.013	[0.010 - 0.016]	0.197	[0.168 - 0.235]
Crawford-Gunnison Basin	neutral SNPs	0.093	[0.077 - 0.118]	0.005	[0.004 - 0.008]	0.117	[0.095 - 0.148]
Crawford-Pinon Mesa	neutral SNPs	0.265	[0.241 - 0.296]	0.028	[0.025 - 0.032]	0.305	[0.277 - 0.342]

		G_{ST}		D_{Jost}		F_{ST}	
Comparison	Data	Mean	95% CI	Mean	95% CI	Mean	95% CI
Crawford-San Miguel	neutral SNPs	0.111	[0.076 - 0.150]	0.007	[0.004 - 0.010]	0.139	[0.095 - 0.189]
Dove Creek-Gunnison Basin	neutral SNPs	0.166	[0.151 - 0.187]	0.014	[0.012 - 0.016]	0.199	[0.181 - 0.226]
Dove Creek-Pinon Mesa	neutral SNPs	0.264	[0.246 - 0.288]	0.027	[0.024 - 0.030]	0.305	[0.285 - 0.334]
Dove Creek-San Miguel	neutral SNPs	0.134	[0.115 - 0.159]	0.009	[0.008 - 0.012]	0.166	[0.142 - 0.198]
Gunnison Basin-Pinon Mesa	neutral SNPs	0.270	[0.254 - 0.294]	0.029	[0.027 - 0.033]	0.306	[0.287 - 0.334]
Gunnison Basin-San Miguel	neutral SNPs	0.129	[0.109 - 0.155]	0.009	[0.007 - 0.012]	0.157	[0.132 - 0.189]
Pinon Mesa-San Miguel	neutral SNPs	0.248	[0.228 - 0.278]	0.024	[0.022 - 0.028]	0.289	[0.264 - 0.323]
Cimarron-Crawford	all SNPs	0.125	[0.087 - 0.188]	0.005	[0.003 - 0.010]	0.157	[0.108 - 0.232]
Cimarron-Dove Creek	all SNPs	0.253	[0.220 - 0.305]	0.019	[0.016 - 0.025]	0.292	[0.256 - 0.346]
Cimarron-Gunnison Basin	all SNPs	0.180	[0.145 - 0.240]	0.010	[0.007 - 0.016]	0.217	[0.177 - 0.282]
Cimarron-Pinon Mesa	all SNPs	0.327	[0.294 - 0.384]	0.029	[0.025 - 0.036]	0.378	[0.341 - 0.438]
Cimarron-San Miguel	all SNPs	0.206	[0.162 - 0.271]	0.013	[0.009 - 0.019]	0.246	[0.196 - 0.318]
Crawford-Dove Creek	all SNPs	0.193	[0.166 - 0.221]	0.016	[0.013 - 0.019]	0.233	[0.199 - 0.267]
Crawford-Gunnison Basin	all SNPs	0.116	[0.099 - 0.139]	0.007	[0.006 - 0.009]	0.147	[0.124 - 0.178]
Crawford-Pinon Mesa	all SNPs	0.276	[0.251 - 0.306]	0.027	[0.024 - 0.031]	0.320	[0.290 - 0.357]
Crawford-San Miguel	all SNPs	0.143	[0.102 - 0.189]	0.010	[0.006 - 0.014]	0.177	[0.127 - 0.234]
Dove Creek-Gunnison Basin	all SNPs	0.195	[0.181 - 0.215]	0.016	[0.015 - 0.019]	0.234	[0.217 - 0.259]
Dove Creek-Pinon Mesa	all SNPs	0.292	[0.275 - 0.313]	0.030	[0.028 - 0.033]	0.335	[0.315 - 0.360]
Dove Creek-San Miguel	all SNPs	0.172	[0.152 - 0.200]	0.013	[0.011 - 0.017]	0.209	[0.184 - 0.245]
Gunnison Basin-Pinon Mesa	all SNPs	0.286	[0.269 - 0.309]	0.028	[0.026 - 0.031]	0.330	[0.311 - 0.357]
Gunnison Basin-San Miguel	all SNPs	0.164	[0.142 - 0.197]	0.012	[0.010 - 0.016]	0.201	[0.174 - 0.241]
Pinon Mesa-San Miguel	all SNPs	0.268	[0.246 - 0.297]	0.026	[0.023 - 0.029]	0.313	[0.288 - 0.348]

APPENDIX XXIX

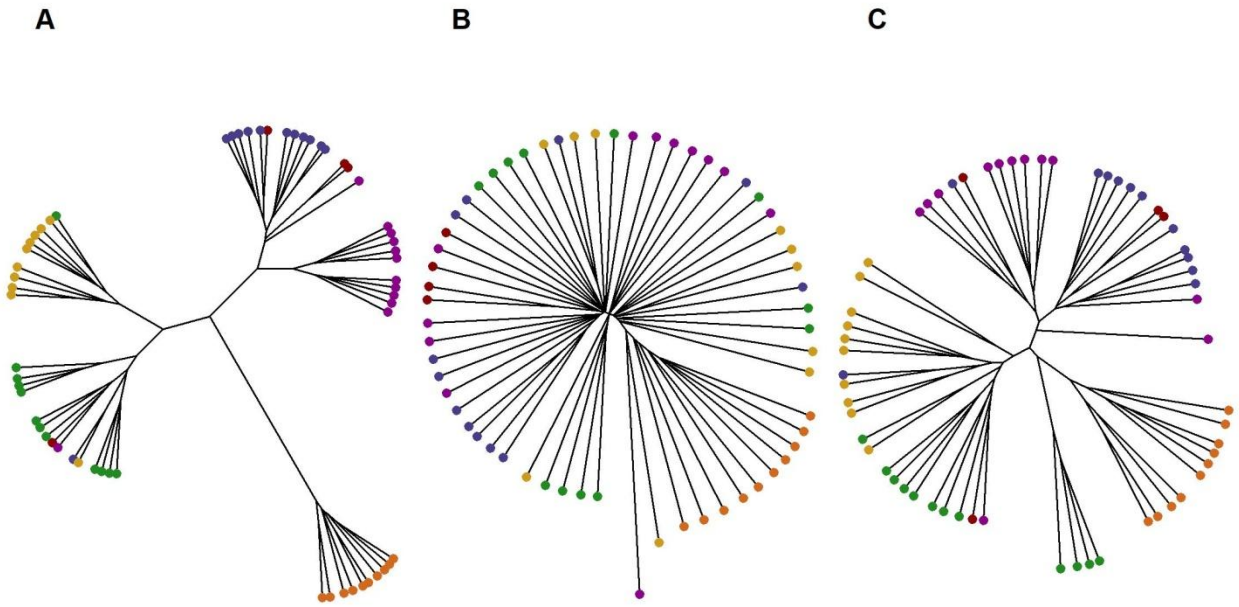

Figure S29.1. Dendrograms created using microsatellite loci from the 60 individuals included in the SNP data set using the (A) ward.D2 method, (B) single (based on closest pair), and (C) complete (based on furthest pair) method. Colors indicate sampling origin: Cimarron = red, Crawford = blue, Dove Creek =green, Gunnison Basin = purple, Piñon Mesa = orange, San Miguel = yellow.

APPENDIX XXX

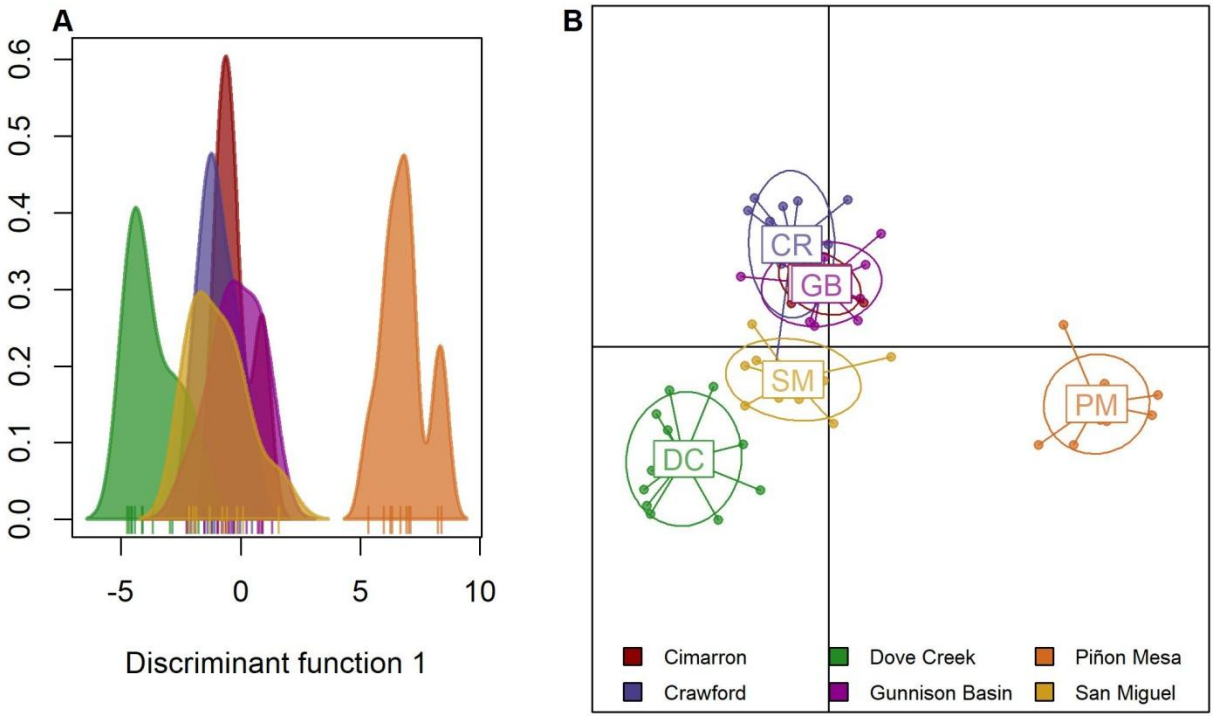

Figure S30.1. Separation of Gunnison sage-grouse populations (individual density) along discriminant function one (A) and star plots of the first two axes from discriminant analysis of principle components (DAPC) (B) for microsatellite from the 60 individuals included in the SNP data set. Colors indicate sampling origin: Cimarron = red, Crawford = blue, Dove Creek =green, Gunnison Basin = purple, Piñon Mesa = orange, San Miguel = yellow.