GREATER SAGE-GROUSE IN THE BI-STATE DISTINCT POPULATION SEGMENT: AN EVALUATUATION OF GENETIC STRUCTURE, CONNECTIVITY, AND VITAL RATES IN MONO COUNTY, CALIFORNIA

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AUTHORIZATION TO SUBMIT THESIS

This thesis of Joel M. Tebbenkamp, submitted for the degree of Master of Science with a Major in Natural Resources and titled "Greater Sage-Grouse in the Bi-State Distinct Population Segment: An Evaluation of Genetic Structure, Connectivity, and Vital Rates in Mono County, California," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit the final copies to the College of Graduate Studies for approval.

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ABSTRACT

The Bi-State Distinct Population segment (DPS) of greater sage-grouse (*Centrocercus urophasianus*) is genetically and geographically isolated from populations in other portions of the species range. In 2013, the Bi-State DPS was proposed to receive threatened status under the Endangered Species Act. To aid in conservation of this DPS we evaluated population genetic substructure, dispersal, and vital rates, including female survival, nest success, and brood survival. From 2007-2012, we radio-marked and monitored 112 greater sage-grouse and collected genetic data at 17 microsatellite loci for 334 individuals. We found evidence for 5 genetic populations. With telemetry data we did not document movements between populations but found genetic evidence that 10 individuals were likely recent dispersers. Female seasonal survival was highest during the winter and lowest during the breeding season, ranging from 0.68-0.97. Daily survival rate of nests decreased over the nesting season, ranging from 0.986-0.918. Apparent brood survival ranged from 30-100%.

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DEDICATION

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CHAPTER 1

INTRODUCTION

The greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse), while historically abundant and wide-ranging throughout western North America, has experienced marked population declines and range contractions since European settlement (Schroeder et al. 1999, Connelly et al. 2004, Schroeder et al. 2004). Across the species range annual rates of decline have been estimated to be from 2-10% (Garton et al. 2011) and their distribution has decreased by nearly 44% (Schroeder et al. 2004). During the early portion of the 1900s population declines can be largely attributed to over-harvest, however, during the latter part of the century declines have been more heavily influenced by habitat loss and degradation (Connelly & Braun 1997).

As a sagebrush (*Artemisia* spp.) obligate, requiring sagebrush throughout its seasonal cycle (Connelly et al. 2000), a variety of landscape-level changes in sagebrush habitats have negatively affected the species (Schroeder et al. 1999, Leonard et al. 2000, Connelly et al. 2004). These changes include, but are not limited to, land conversion for development or agriculture (Connelly et al. 2004), oil and mineral exploration (Doherty et al. 2011, Naugle et al. 2011), overgrazing (Beck & Mitchell 2000), invasive species (Miller et al. 2011) and piñon-juniper (*Pinus* spp. - *Juniperus* spp.) encroachment (Miller et al. 2005). Additionally, habitat alterations have the potential to directly or indirectly affect vital rates, as is the case with the erection of fences or other elevated structures which may directly contribute to mortalities through inadvertent collisions (Stevens et al. 2012*a*, *b*) or indirectly by providing perches for hunting raptors (Knight & Kawashima 1993, Freilich et al. 2003).

In addition to the loss of available habitat and changes that negatively affect vital rates, habitat fragmentation associated with habitat loss has indirect consequences that are a cause for concern (Knick & Hanser 2011). For grouse, the loss of connectivity has implications ranging from the loss of gene flow and genetic diversity (Johnson et al. 2004, Oyler-McCance et al. 2005) to challenges with repopulation of locally extirpated populations (Segelbacher et al. 2003). With the decrease in the species distribution, populations along the periphery of the species range are becoming increasingly isolated (Schroeder et al. 2004, Knick & Hanser 2011).

In 2010 the United States Fish and Wildlife Service (USFWS) ruled that range-wide sage-grouse were warranted for protection under the Endangered Species Act (ESA), however, they were precluded from protection by the need to invest limited resources on other species (United States Department of Interior 2010). The 2010 ruling also identified the sage-grouse populations occupying portions of Carson City, Lyon, Mineral, Esmeralda, and Douglas counties in Nevada, and of Alpine, Inyo, and Mono counties in California as a Distinct Population Segment (United States Department of Interior 2010; hereafter Bi-State DPS).

The justifications for elevating sage-grouse in the Bi-State area to DPS status was primarily based on genetic evidence (United States Department of Interior 2010). When comparing mitochondrial DNA (mtDNA) between the Bi-State DPS and populations found in northern California, Nevada, Oregon, and Washington, Benedict et al. (2003) found 87% of the haplotypes observed in the Bi-State DPS were unique to that region. Using mtDNA and nuclear DNA microsatellite loci, Oyler-McCance et al. (2005) conducted a range-wide study adding further evidence that the Bi-State DPS was genetically unique. Based on the degree of

genetic differentiation between the Bi-State DPS and other sage-grouse throughout the rest of their range, it is likely the Bi-State DPS has been isolated for thousands to tens of thousands of years (Benedict et al. 2003, Oyler-McCance et al. 2005). In 2013, due to isolation and other impending threats, the USFWS proposed listing the Bi-State DPS as threatened under the Endangered Species Act (United States Department of Interior 2013)

The area occupied by the Bi-State DPS is not a homogenous landscape with continuous suitable habitat, but rather a matrix of sagebrush-steppe with intervening forests, salt flats, bodies of water, and development. Consistent with the distribution of suitable and unsuitable habitats, the telemetry data of Kolada et al. (2009a, b) suggest the Bi-State DPS is subdivided into localized populations. These localized populations have different population sizes and population trends (Bi-State Local Planning Group 2004; hereafter BSPG 2004, Bi-State Technical Advisory Committee 2012; hereafter BSTAC 2012) as well as differences in vital rates such as nest success (Kolada et al. 2009b).

While it is important to identify and understand the site characteristics that are influencing population trends and vital rates within each localized population, it is also important to investigate the potential for movements and genetic exchange between localized populations. Telemetry-based studies have had, and will continue to have, an important role in monitoring individuals and documenting general movement patterns, however, they may fail to document rare but important movements due to the limited number of radio transmitters that can be deployed and effectively monitored (Fedy et al. 2008). While genetic-based methods do not allow one to directly monitor vital rates or movements, per se, they have proven to be useful in documenting functional connectivity, as inferred by gene flow

(Balkenhol et al. 2009), and therefore provide insight beyond what may be gleaned from telemetry data alone.

To address important questions about connectivity and vital rates for sage-grouse in the Bi-State DPS we combined traditional telemetry-based monitoring methods with molecular-based approaches. From 2007 to 2011 we captured, radio-marked, and monitored sage-grouse to assess movements and estimate vital rates including nest success, brood success, and adult survival. We obtained genetic samples from the birds that we captured and also collected noninvasive genetic samples (NGS) during the 2010 and 2011 field seasons. Using these data we: 1) identify the patterns of genetic structure and diversity, 2) evaluate dispersal between localized populations using molecular and telemetry-based methods, and 3) provide estimates of nest success, brood survival, and hen survival. This work will facilitate a greater understanding of the dynamics within the Bi-State DPS and provide information that can help guide management decisions.

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CHAPTER 2

A MULTI-METHOD EVALUATION OF CONNECTIVITY IN A THREATENED DISTINCT POPULATION SEGMENT OF GREATER SAGE-GROUSE

Abstract

Because isolation may imperil populations, maintaining demographic and genetic connectivity is a high priority for conservation and management. One population of conservation concern due to its high degree of isolation is the Bi-State Distinct Population Segment (DPS) of greater sage-grouse (*Centrocercus urophasianus*). Located on the periphery of their range, along the California-Nevada border, the Bi-State DPS is genetically isolated from other populations. Further, telemetry data suggest there is additional subdivision within the Bi-State DPS. Here, we combine telemetry and genetic data to investigate both demographic and genetic structuring within the Mono County, California portion of the Bi-State DPS. From 2007-2012, we radio-marked and monitored 122 greater sage-grouse and collected genetic data at 17 microsatellite loci for 334 individuals. Pairwise F_{ST} estimates (mean = 0.146, range = 0.090-0.205) along with 2 Bayesian clustering methods provided evidence for 5 genetic populations. We did not document any dispersal events between populations using radio-telemetry, however, using 4 genetic assignment methods found 10 individuals were likely recent dispersers. Combined, these data show that there is both demographic and genetic subdivision within the Bi-State DPS, and while demographic support between populations is unlikely due to the low number of dispersers, these infrequent dispersal events are capable of preventing genetic isolation. Thus, effective conservation of the Bi-State DPS will require maintaining genetic connectivity while also attending to demographic processes of each population.

Introduction

Maintenance of connectivity among natural populations is well recognized as an important conservation and management goal (Crooks & Sanjayan 2006). From a demographic perspective, connectivity between populations can promote stability for localized populations through source-sink interactions (Pulliam 1988) as well as at the metapopulation level through recolonization of locally extirpated populations (Hanski 1998). Genetic connectivity minimizes the risk of inbreeding and accumulation of genetic load (Keller & Waller 2002) and facilitates the spread of advantageous alleles (Mace & Purvis 2008), thus having important fitness and evolutionary implications.

Demographic and genetic connectivity, however, are not mutually inclusive (Palsbøll et al. 2007, Lowe & Allendorf 2010). While genetic subdivision may be observed as soon as populations deviate from panmixia, the benefits of genetic connectivity can be realized with as few as 1 effective migrant per generation (Mills & Allendorf 1996). Demographic connectivity in contrast is influenced by the number of dispersing individuals and their effects on a population's vital rates (Lowe & Allendorf 2010). Therefore, maintaining demographic connectivity generally requires a greater number of dispersers than is needed to maintain genetic connectivity. Given these differences, studies that consider both forms of connectivity can provide a more comprehensive understanding of the ecological and genetic processes that influence populations, and can be used to help delimit Population Management Units (Moritz 1994, Waples & Gaggiotti 2006), identify populations of conservation concern (Haig et al. 2006), and determine the best management practices (Hedrick 1995, Vierling 2000).

For greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse), a candidate for listing under the Endangered Species Act (United States Department of Interior

2010), connectivity has received increased attention. While habitat loss and degradation have directly contributed to the species decline and range contraction (Connelly et al. 2004, Schroeder et al. 2004), the associated increase in fragmentation resulting in decreased demographic and genetic connectivity also threatens their persistence (Knick & Hanser 2011, Oyler-McCance & Quinn 2011). Individual leks (strutting grounds) separated by as little as 13-18 km experience a decreased probability of persistence (Knick & Hanser 2011) and several isolated populations have been shown to exhibit depressed levels of genetic diversity (Oyler-McCance et al. 2005a).

The Bi-State population of sage-grouse, located at the edge of the species range, along the southern Nevada-central California border, is a conservation priority due to its high degree of geographic and genetic isolation. In 2010, the US Fish and Wildlife Service (USFWS) identified the Bi-State population as a Distinct Population Segment (DPS; United States Department of interior 2010) largely due to the genetic uniqueness suggesting long-term isolation (Benedict et al. 2003, Oyler-McCance et al. 2005a). In 2013, due to isolation and other impending threats, the USFWS proposed listing the Bi-State DPS as threatened under the Endangered Species Act (United States Department of Interior 2013).

Within the Bi-State DPS, telemetry data suggest that areas of unsuitable habitat are likely creating further subdivision (Koloda et al. 2009, Wiechman 2013). However, there is limited information on genetic connectivity among these apparently subdivided populations. To better understand the dynamics in Mono County, California, the core portion of the Bi-State DPS, we combined telemetry-based and genetic-based methods to investigate genetic and demographic connectivity. Specifically, we evaluated the (1) population genetic substructure, (2) level of genetic diversity within each genetic population, (3) relative

importance of barriers and distance in structuring populations, and (4) degree of contemporary connectivity using both molecular and telemetry-based methods.

Materials and Methods

Study Area

Our study area, located in Mono County, California, is bordered to the west by the eastern slope of the Sierra Nevada and to the east by the California-Nevada border (Fig. 2.1). Topographically variable, the study area contains a series of valleys and mountain ranges with elevations ranging from 1,660 m to 3,770 m. Temperature, precipitation, and vegetative communities generally follow an elevational gradient, and the most common cover types are sagebrush (*Artemisia* spp.)-steppe communities, coniferous forest, natural and artificially flooded meadows, and open water (Bi-State Local Planning Group 2004; hereafter BSPG 2004, Bi-State Technical Advisory Committee 2012; hereafter BSTAC 2012).

The study area encompasses 4,803 km^2, however, only 1,678 km^2 are considered to be suitable sage-grouse habitat (BSPG 2004). Non-habitat, which is mostly coniferous forests, frequently bisects the sagebrush-steppe/meadow habitats creating 6 spatially disjunct populations (hereafter subareas), each of which is thought to represent an independent lek complex (BSPG 2004, Kolada et al. 2009). From north to south the subareas are Jackass, Wheeler-Burcham, Bodie Hills, Granite Mountain, Parker, and Long Valley (Fig. 2.1). These 6 subareas vary greatly in their geographic extent, number of active leks, number of strutting males, and overall population trends (Table 2.1; BSTAC 2012).

Sampling

From 2007-2012, we collected genetic samples through capture and noninvasive genetic sampling (NGS). We captured adult sage-grouse using spotlighting techniques

(Wakkinen et al. 1992) and genetic samples were obtained by plucking feathers and by over-clipping the hallux nail to collect blood. We radio-marked the majority of captured females and a small number of males with ≤ 20 g ATS necklace -style radio transmitters (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA). The NGS samples included shed feathers and fecal pellets. When possible, samples were assigned to a lek of origin based on when (e.g. breeding season) and where (e.g. on or around a lek) they were collected.

Genetic Analysis

We extracted DNA from blood, feathers, and fecal pellets using Qiagen DNeasy blood and tissue kits (Qiagen, Inc., Valencia, California) following the protocols of Bush et al. (2005), Gebhardt et al. (2009), and Baumgart et al. (2013), respectively. A low-quantity DNA room was used when extracting DNA from fecal pellets and feathers, and extraction negative control samples were processed with all sets of extractions.

We amplified 19 polymorphic microsatellite loci and 1 avian sex identification locus (Appendix A; Table S2.1) using Qiagen multiplex kits (Qiagen, Inc., Valencia, California). For details on primers, reaction conditions, and genotyping see Appendix A. After finalizing consensus genotypes, we calculated false allele (FA) and allelic dropout (ADO) rates for NGS samples by comparing 3 replicate runs to the consensus genotype. For blood samples, we randomly selected 18 (12.2%) to rePCR and check for errors.

Using the lek as the unit of analysis, we tested for Hardy-Weinberg equilibrium (HWE) for each locus and linkage disequilibrium (LD) for each locus pair with GENEPOP (Raymond & Rousset 1995, Rousset 2008) using the default settings under the G-test and exact test options, respectively. Significance levels were adjusted to account for multiple comparisons using a sequential-Bonferroni correction (Holm 1979, Rice 1989), however, we

also noted any trends of disequilibria that were significant at unadjusted significance levels ($p < 0.05$ or $p < 0.01$).

Genetic Structure and Diversity

We estimated pairwise F_{ST} (Weir & Cockerham 1984) using MICROSATELLITE ANALYZER (Dieringer & Schlötterer 2003) between leks and subareas with ≥ 7 individuals sampled. Significant deviations from panmixia were assessed using 10,000 randomizations and significance levels were adjusted for multiple comparisons using the modified False Discovery Rate procedure (Benjamini & Yekutieli 2001, Narum 2006). We ran partial Mantel tests (Mantel 1967, Smouse et al. 1986) consisting of 10,000 randomizations using the Isolation By Distance Web Service (Jensen et al. 2005) to evaluate the relative importance of barriers and geographic distance on genetic structuring (Appendix A).

We performed Bayesian clustering analyses with the aspatial method in STRUCTURE 2.3.4 (Pritchard et al. 2000) and the spatial model in GENELAND (Guillot et al. 2005), using all samples that could be attributed to a single lek. With STRUCTURE, we performed 10 iterations of K = 1-10. Each iteration consisted of a 500,000 step Markov chain Monte Carlo (MCMC), a 100,000-step burn-in, and used the admixture model with correlated allele frequencies (F-model; Falush et al. 2003). We assessed the most likely number of genetic clusters (K) by identifying the K-value corresponding to the highest log likelihood of K (Pritchard et al. 2000) as well as by identifying where there was the greatest change in the log likelihood of K (ΔK; Evanno et al. 2005; hereafter Evanno method; Appendix A).

With GENELAND we identified the optimal number of genetic clusters by conducting 10 independent runs and choosing the K-value identified by the run with the highest posterior probability. Run parameters included 1,000,000 MCMC steps, a thinning parameter of 100,

burn-in of 1,000, a location uncertainty parameter of 2,000 m, and the uncorrelated allele frequencies model since the F-model failed to converge.

Because we used multiple methods for identifying genetic structure, we developed 2 criteria to define what we would consider a genetic population. First, a subarea or lek was required to have pairwise F_{ST} values that were significantly > 0 in pairwise comparisons with all other leks or subareas, respectively. Secondly, an area must have been identified as a unique genetic cluster with at least one of the Bayesian clustering methods.

Genetic diversity and inbreeding metrics were calculated for each genetic population using only samples from known leks of origin. Observed heterozygosity (H_O) and unbiased expected heterozygosity (H_E; Nei 1978) were calculated using GenAlEx 6.52 (Peakall & Smouse 2012). Allelic richness (AR) and the inbreeding coefficient (F_{IS}) were calculated using FSTAT (Goudet 1995). With H_E and AR we tested for equal population means using a 2-factor ANOVA or Kruskal-Wallis test, contingent on data meeting normality assumptions. Significant differences were further evaluated using Tukey's HSD. For F_{IS}, significant deviations from zero were evaluated using global tests of heterozygote deficiency or excess in GENEPOP (Raymond & Rousset 1995, Rousset 2008).

Contemporary Connectivity

Our molecular-based evaluation of contemporary connectivity between genetic populations included samples from all unique individuals and consisted of applying 4 different tests: (1) BAYESASS3 (Wilson & Rannala 2003), (2) STRUCTURE 2.3.4 (Pritchard et al. 2000) using the POPINFO option, (3) GENECLASS2 (Piry et al. 2004) using the L_home/L_max likelihood computation, and (4) GENECLASS2 using the exclusion-based L_home likelihood computation. Run parameters for each method are described in

Appendix A. For BAYESASS3 and STRUCTURE we flagged individuals as potential dispersers if the posterior probability of assignment to the population in which they were sampled was < 0.5 and they had a posterior probability of assignment of > 0.5 to one of the other sampled populations. With GENECLASS2 we flagged individuals as dispersers if the P-value was < 0.01. Taking a conservative approach, we only report individuals as likely dispersers if they were flagged as a disperser in a minimum of 2 of the first 3 tests or as a disperser with the exclusion-based L_home probability computation.

We monitored radio-marked sage-grouse in the Wheeler-Burcham, Bodie Hills, Parker, and Long Valley subareas to determine if these individuals emigrated from their subarea of capture. Monitoring consisted of locating individuals 1-3 times per week from the ground using a hand-held Yagi antenna and receiver from March through October, and periodically throughout the year via aerial telemetry from a fixed-winged aircraft when birds were missing or conditions did not permit ground tracking.

Results

Sample Collection and Genetic Analysis

Throughout the 6 subareas, we collected and analyzed 644 samples, including 168 from captured individuals, 347 from NGS feathers, and 129 from NGS fecal pellets. We successfully obtained consensus genotypes with at least 8 complete loci for 100% (168/168) of the samples from captured birds, 72% (249 /347) of the NGS feathers, and 33% (43/129) of the NGS fecal pellets. These 460 samples represented 334 unique individuals (Table 2.1), of which 265 were assigned to an individual lek (Table 2.2).

The TUD3 locus showed significant heterozygote deficiencies in 9/16 and 3/16 tests at $p < 0.01$ and after sequential Bonferroni correction, respectively, and therefore was removed

from further analysis. Only the SGCA5 and BG16 locus combination showed evidence of LD, with 3/15 and 1/15 tests crossing the significance threshold at $p < 0.05$ and after sequential Bonferroni correction, respectively. Therefore, we removed SGCA5 which was less polymorphic than BG16. For the 17 loci that were retained, consensus genotypes were on average 95.3% complete. Blood samples had a genotyping error rate of 2.0%. For feather samples ADO and FA was 5.5% and 0.6%, respectively. For fecal samples ADO and FA was 16.1% and 0.4%, respectively.

Genetic Structure and Diversity

Pairwise F_{ST} ranged from 0.000-0.235 for the 16 leks where we had ≥ 7 samples (Appendix A; Table S2.2). Pairwise F_{ST} estimates between leks located in different subareas generally rejected panmixia, whereas comparisons between leks within the same subarea did not. With the subarea as the unit of analysis, all pairwise F_{ST} estimates rejected panmixia (range = 0.064-0.232; Table 2.3). With the partial Mantel tests, the significance level and partial correlation coefficient was greater between genetic distance and the barrier matrix ($p = 0.0005$, $r = 0.4051$) than it was for genetic distance and geographic distance ($p = 0.0131$, $r = 0.2435$).

The peak log likelihood value using program STRUCTURE occurred at $K = 7$ (Appendix A; Fig. S2.1). However, for K-values above 4, the q-plots indicated over-splitting. Our iterative use of the Evanno method resulted in 3 hierarchically structured bifurcations, ultimately identifying $K = 4$ as the most likely number of genetic clusters (Appendix A; Fig. S2.1-S2.9). Most birds assigned strongly to 1 of the 4 clusters identified, which from north to south were comprised of individuals mainly from (1) Jackass/Wheeler-Bircham, (2) Bodie Hills, (3) Parker, and (4) Granite Mountain/Long Valley (Fig. 2.2a-d). With GENELAND, all

10 independent runs identified K = 5 to be the most likely number of genetic clusters, further delineating Granite Mountain and Long Valley as unique genetic clusters (Appendix A; Fig. S2.10).

Because all pairwise F_{ST} estimates between the 6 subareas were significantly > 0, all subareas met our first criteria for being identified as a genetic population. However, neither Bayesian clustering program separated the Jackass and Wheeler-Burcham subareas, therefore, based on our second criterion, they were considered one genetic population (hereafter the Fales genetic population). From north to south, the genetically-defined populations were Fales, Bodie Hills, Granite Mountain, Parker, and Long Valley (Fig. 2.1).

Between the 5 genetic populations, H_O, H_E, and AR ranged from 0.559-0.656, 0.578-0.604, and 3.359-4.224, respectively (Table 2.2). We found no significant differences in H_E between populations (Kruskal-Wallis, $p = 0.9807$), but we did detect significant differences between populations for AR (2-factor ANOVA, $p = 0.0026$). A post-hoc multiple comparison of means found that the only population pair in which AR differed significantly was Granite Mountain and Bodie Hills ($p = 0.0013$). F_{IS} ranged from -0.093-0.051, with only Parker (F_{IS} = -0.093, $p = 0.0248$) and Bodie Hills ($F_{IS} = 0.051$, $p = 0.0046$) showing significant deviations from zero (Table 2.2).

Contemporary Connectivity

Based on our combination of assignment tests we found evidence that 10 of the 334 sampled individuals were first or second generation (i.e. offspring of dispersers) dispersers, including 7 females, 2 males, and 1 individual of an undetermined sex (Table 2.4). However, because the different assignment methods were inconsistent in their evaluation of generations since dispersal, we labeled individuals as recent dispersers (e.g. first or second generation)

rather than attempting to infer the number of generations since dispersal. At least 1 recent disperser was found within each of the genetic populations and the identified source populations included Bodie Hills, Long Valley, and Parker. For individual Z215 the assigned source population differed between assignment tests, but 2 of the 3 tests strongly assigned this individual to Long Valley, and with the third test Granite Mountain had only slightly more support. Additionally, 4 individuals were identified as migrants only when using the exclusion-based L_home likelihood computation in GENECLASS2, suggesting that they likely came from unsampled populations.

We monitored 122 radio-marked individuals (Table 2.1). On average, individuals were monitored for 10.5 months (range = 1-36) and during that time were located a mean of 67 times (range = 2-201). However, even with more than 8,000 individual locations, no individuals were detected outside of the subarea in which they were captured.

Discussion

Population Structure

The 5 genetic populations we identified in the Mono County, California portion of the Bi-State DPS were generally consistent with the previously defined subareas and aligned closely with expectations based on previously collected telemetry data (Kolada et al. 2009, Wiechman 2013) and the spatial arrangement of habitat types thought to act as barriers. All pairwise F_{ST} comparisons between subareas were significant, suggesting that inter-subarea subdivision was strong enough to cause deviations from panmixia. Most subareas exhibited sufficient genetic differentiation to be identified as a unique genetic cluster with at least one of the Bayesian clustering methods, thereby meeting our criteria to be considered a genetic population. Only the Jackass and Wheeler-Burcham subarea distinction was inconsistent with

our genetically-defined populations. The Jackass and Wheeler-Burcham subareas are 19.2 km apart, potentially limiting movements due to distance alone (Knick & Hanser 2011). However, the lack of inhospitable habitat across the 19.2 km distance may have permitted occasional exchange between areas thereby explaining the deviation from panmixia but lack of sufficient genetic differentiation to be identified as unique genetic clusters with the Bayesian clustering programs. It is also possible that the Bayesian clustering programs were unable to differentiate between the Jackass and Wheeler-Burcham subareas due to the small sample size from Jackass (n = 7).

The 5 genetic populations identified represent higher levels of genetic structuring than previously documented for the species; the population units were smaller in geographic extent and the magnitude of genetic difference between the areas (e.g. pairwise F_{ST}) were greater. Leks separated by as little as 40 km typically had larger pairwise F_{ST} estimates then leks separated by up to 400 km in northern Alberta/southern Montana (Bush et al. 2011), an area the authors described as highly fragmented. We also found a greater number of genetic clusters relative to the size of our study area compared to previously published literature (e.g. Oyler-McCance et al. 2005a, Bush et al. 2011, Oyler-McCance & Casazza 2011). However, direct comparison of the Bayesian clustering analyses may be hampered since we used a larger number of loci, thereby providing us with greater power to detect genetic structure (Palsbøll et al. 2007, Ryman et al. 2006). For example, Oyler-McCance & Casazza (2011) genotyped 78 individuals at 7 loci and did not find convincing evidence for $K > 1$ (using program STRUCTURE) within the Mono County portion of the Bi-State area, whereas we genotyped 334 individuals at 17 loci and found $K = 4$.

Genetic processes are also undoubtedly influencing the high degree of genetic structure we detected. In northwestern Colorado and Lassen County, California genetic investigations have used the same (n = 17; Thompson 2012) or greater (n = 18; Davis 2012) number of loci, respectively, and found less genetic structure with both pairwise F_{ST} estimates and Bayesian clustering methods. Visual inspection of maps from these study areas reveals that the distribution of suitable habitat within Mono County is more patchy. In Mono County, forested areas, which are avoided by sage-grouse (Doherty et al. 2008), frequently bisect the study area. Other grouse species with patchy patterns of occupancy, such as the Gunnison sage-grouse (*Centrocercus minimus*; Oyler-McCance et al. 2005b), rock ptarmigan (*Lagopus muta pyrenaica*) in the sky islands of the French Pyrenees (Bech et al. 2009), and capercaillie (*Tetrao urogallus*) in fragmented forest patches in Western Europe (Segelbacher et al. 2003), have also shown high levels of genetic structuring indicating that landscape structure resulting in a patchy population distribution is likely to coincide with genetic structuring. The partial Mantel tests support this idea in that they indicate areas of non-habitat located between many of the subareas are acting as barriers and have a greater influence on genetic structure than distance alone.

Genetic Diversity

Regardless of population size, each of the genetic populations had similar levels of expected heterozygosity. Allelic richness tended to decrease with population size, however, the only statistically significant difference was between Bodie Hills and Granite Mountain which are the largest and smallest populations, respectively. The lack of major differentiation in diversity metrics between the genetic populations, despite differing population sizes and trends, provides evidence for genetic exchange between localized populations. However, the

Bi-State DPS is completely isolated from the remainder of the species range (Oyler-McCance et al. 2005a).

When comparing genetic diversity in the Bi-State area to other populations throughout the species range, the Bi-State DPS had some of the lowest levels of heterozygosity. Using the four common loci between our study and the range-wide analysis of Oyler-McCance et al. (2005a; ADL230, LLSD8, SGCA5, SGCA9), we found that even when all our Mono County samples were pooled, our study population had the fourth lowest level of heterozygosity out of the 44 populations sampled (Table S2.3). Only the 2 populations in Washington State and the Blue Mountain, Utah population had lower levels of heterozygosity. Consistent with the central-margin hypothesis (Eckert et al. 2008, Kark et al. 2008), each of these populations is located along the periphery of the species range. There are exceptions to this trend (e.g. Garner et al. 2004, Zigouris et al. 2012), and several peripheral populations of sage-grouse such as those in Alberta/northern Montana (Bush et al. 2011), northwestern Colorado (Thompson 2012), and Lassen County, California (Davis 2012), have average to high levels of heterozygosity. While peripheral location may have some influence on the level of genetic diversity in the Bi-State DPS, the long-term genetic isolation likely has a stronger influence on its comparatively low levels of heterozygosity.

Low levels of heterozygosity may incur negative fitness effects (Reed & Frankham 2003) and have been associated with low reproductive success due to hatching failures in the closely related greater prairie-chicken (*Tympanuchus cupido*; Bouzat et al. 1998, Westminster et al. 1998). Interestingly, only the Parker population experienced frequent hatching failures (9/13 monitored nests) due to nonviable eggs (Wiechman 2013), yet this population had one of the highest levels of heterozygosity and was outbred based on F_{IS} estimates (Table 2.3).

Paradoxically, small populations such as Parker may exhibit negative F_{IS} values even if inbreeding is occurring (Allendorf & Luikart 2007). Allelic richness estimates suggest the Parker population has suffered from a slight loss of genetic diversity, but the difference was not statistically significant. The Parker population, however, has shown low mitochondrial DNA gene diversity (Oyler-McCance & Casazza 2011) which has been directly linked to reproductive failures in other organisms (Gemmell et al. 2004). Although we did not find any indication of inbreeding or low genetic diversity with neutral microsatellite markers, genetic causes of these hatching failures should not be discounted.

Contemporary Connectivity

Consistent with previous reports (e.g. BSPG 2004, BSTAC 2012), our telemetry data indicated a lack of movement between subareas. However, our genetic data indicate that inter-subarea movements were occurring. Compared to our telemetry data, which found 0 of the 122 radio-marked individuals moving from the subarea in which they were marked, 10 of the 334 (2.99%) individuals that we sampled genetically appeared to be first or second generation dispersers (Table 2.4).

The greater number of recent dispersers identified using molecular methods is partially due to our ability to identify second-generation dispersers (ie. offspring of dispersers), but this is unlikely the sole reason for the differences. For white-tailed ptarmigan (*Lagopus leucura*), similar discrepancies have been seen between direct estimates of dispersal using genetic data and telemetry-based estimates (Fedy et al. 2008). Studies have also observed a lack of genetic structure despite telemetry data suggesting that populations were structured (Finnigan et al. 2012). Such differences are likely due to methodological limitations associated with documenting dispersal with telemetry-based monitoring (Koenig et al. 1996). With telemetry,

dispersing individuals may fail to be identified if they are captured after dispersal has already occurred, immigrate from outside the study area, or disperse long distances making it logistically difficult to document dispersal events (Koenig et al. 1996).

Inferring dispersal using molecular-based methods, however, is not without limitations as these methods may either fail to identify or incorrectly identify dispersing individuals (Manel et al. 2005). Despite potential concerns, many of the molecular-based methods of evaluating dispersal are well vetted and are considered reliable for use in forensic applications (Manel et al. 2002, DeYoung & Honeycut 2005). When model assumptions are met and F_{ST} is ≥ 0.05, both program STRUCTURE and BAYESASS3 are highly effective at identifying the source population of sampled individuals (Latch et al. 2006, Faubet et al. 2007), strengthening confidence in our assignments since all pairwise comparisons between populations had F_{ST} values > 0.05. To provide extra assurance that individuals were not erroneously identified as dispersers, we used 3 different assignment tests, requiring congruent results from at least 2 before reporting an individual as a disperser. Thus, if errors were made it was most likely in failing to identify an individual that had dispersed. However, we did violate the assumption embedded in each of the assignment tests that all potential source populations were sampled, and thus as recommended by Manel et al. (2002), included an exclusion-based test which does not assume all populations are sampled.

Four of the 10 birds that we identified as recent dispersers, were only identified as dispersers with the exclusion-based test. Although we cannot assign these individuals to a population of origin, it is highly likely that they came from one of the unsampled Population Management Units in the Bi-State area (Fig. 2.1). Along with our results that demonstrate inter-subarea dispersal does occur, independently collected genetic data (Oyler-McCance &

Casazza 2011) and satellite telemetry data (P. Coates, personal communication) have found evidence for birds immigrating into the study area from the White Mountain Population Management Unit (PMU) to the south and Pine Nut PMU to the north of our study area, respectively.

Four of the 6 birds whose population of origin (or parent's population of origin) was identified with the assignment tests, appeared to have moved between neighboring populations as is thought to be the general trend for sage-grouse when dispersal does occur (Dunn & Braun 1985, Oyler-McCance et al. 2005a). The other 2 individuals moved further and dispersed between non-neighboring populations, which although less common, is within the movement capability of the species given that direct observations of natal dispersal and seasonal movements have been shown to span distances up to 48 km (Thompson 2012) and 240 km (Smith 2013), respectively. Perhaps, more surprising, is that in most cases the dispersing birds would have been required to either pass through (or over) unsuitable habitat such as forested areas or large expanses of water, or would have needed to travel great distances to select a route consisting primarily of sagebrush steppe.

Dispersal events, although rare, appear sufficient to maintain genetic connectivity as only one effective migrant (e.g. a disperser that successfully produces offspring) per generation is needed for the genetic and evolutionary benefits of connectivity to be realized (Mills & Allendorf 1996). While not all dispersing individuals will successfully reproduce, there is evidence that at least some have. Program STRUCTURE found several individuals had nearly a 50-50 split in their population ancestry (Fig. 2.2a-d), suggesting they are offspring of parents from different populations. Also, despite experiencing demographic bottlenecks, the Parker, Granite Mountain, and Fales populations had similar levels of

heterozygosity and only slightly lower allelic richness compared to the larger populations at Bodie Hills and Long Valley. These comparable levels of genetic diversity are consistent with theoretical (Mills & Allendorf 1996) and empirical (Keller et al. 2001) results showing that low levels of dispersal are capable of maintaining or restoring genetic diversity after demographic bottlenecks. Although the level of dispersal appears sufficient for populations to incur the benefits of genetic connectivity, it is too infrequent for populations to be considered demographically connected. Simulations suggest when the proportion of individuals exchanging between populations is less than 10%, they have limited influence on each other's demographics (Hastings 1993). Even if all 10 individuals identified as dispersers are assumed first-generation dispersers, this would only represent 2.99% exchange.

Conservation Implications

Our results revealed that with the exception of the Jackass and Wheeler-Burcham subareas, each of the subareas fit the genetic criterion of Moritz (1994) as well as the demographic criterion of Palsbøll et al. (2007) for classification as separate management units, illustrating the importance of continued monitoring, conservation, and management efforts at the subarea-scale. Because it seems unlikely for populations to receive demographic support from their neighbors, it will be important to control or mitigate factors such as fire (Blomberg et al. 2012), disease (Christiansen & Tate 2011), and an increasing human footprint (Leu & Hanser 2011) which may weaken a population's resilience and cause population declines. The smaller populations, especially Parker and Granite Mountain, each of which only have one lek, are inherently at a greater risk of extirpation and therefore will require careful monitoring. Within Bodie Hills and Long Valley, the large core populations which have multiple well-connected leks, management decisions that maintain inter-lek

connectivity and healthy populations will be paramount to the persistence of the Bi-State DPS, especially if birds are needed for translocation efforts.

Conservation and management efforts focused solely at the subarea-scale, however, will fail to conserve the Bi-State DPS as a whole. Grouse species have a tendency to become subdivided, or even isolated, by natural and/or anthropogenic factors, and as a result have been shown to experience negative fitness effects (Westminster et al. 1998, Stiver et al. 2008). Although populations within much of the Bi-State area are clearly subdivided, under current conditions there is sufficient gene flow to maintain genetic diversity and avoid inbreeding. To ensure continued gene flow it will be important to consider how landscape-level changes such as piñon-juniper (*Pinus* spp.-*Juniperus* spp.) encroachment or removal and urban development may influence genetic connectivity. Maintaining as many populations as possible, even the smaller populations, will also be important since each population can act as an important linkage in facilitating gene flow. Ultimately, conservation efforts in the Bi-State area must consider population-level processes and connectivity between populations, and will require developing, carefully evaluating, and implementing management plans that attend to both.

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Figure Captions

Fig. 2.1 Mono County, California study area and the location of areas occupied by greater sage-grouse (modified from Schroeder et al. (2004)) and the sampled subareas which include Jackass (JA), Wheeler-Burcham (WB), Bodie Hills (BH), Granite Mountain (GM), Parker (PA), and Long Valley (LV). Jackass and Wheeler-Burcham constitute one genetic population (Fales) while the other subareas each represent unique genetic populations

Fig. 2.2 STRUCTURE plots displaying K = 4 for greater sage-grouse sampled in the a) Jackass (first 7 individuals) and Wheeler-Burcham, b) Parker, c) Bodie Hills, and d) Granite Mountain (first 13 individuals) and Long Valley subareas of Mono County, California between 2007–2012. Each bar represents a unique individual and different shades indicate the proportion of an individual's ancestry belonging to each of the 4 clusters

Figures

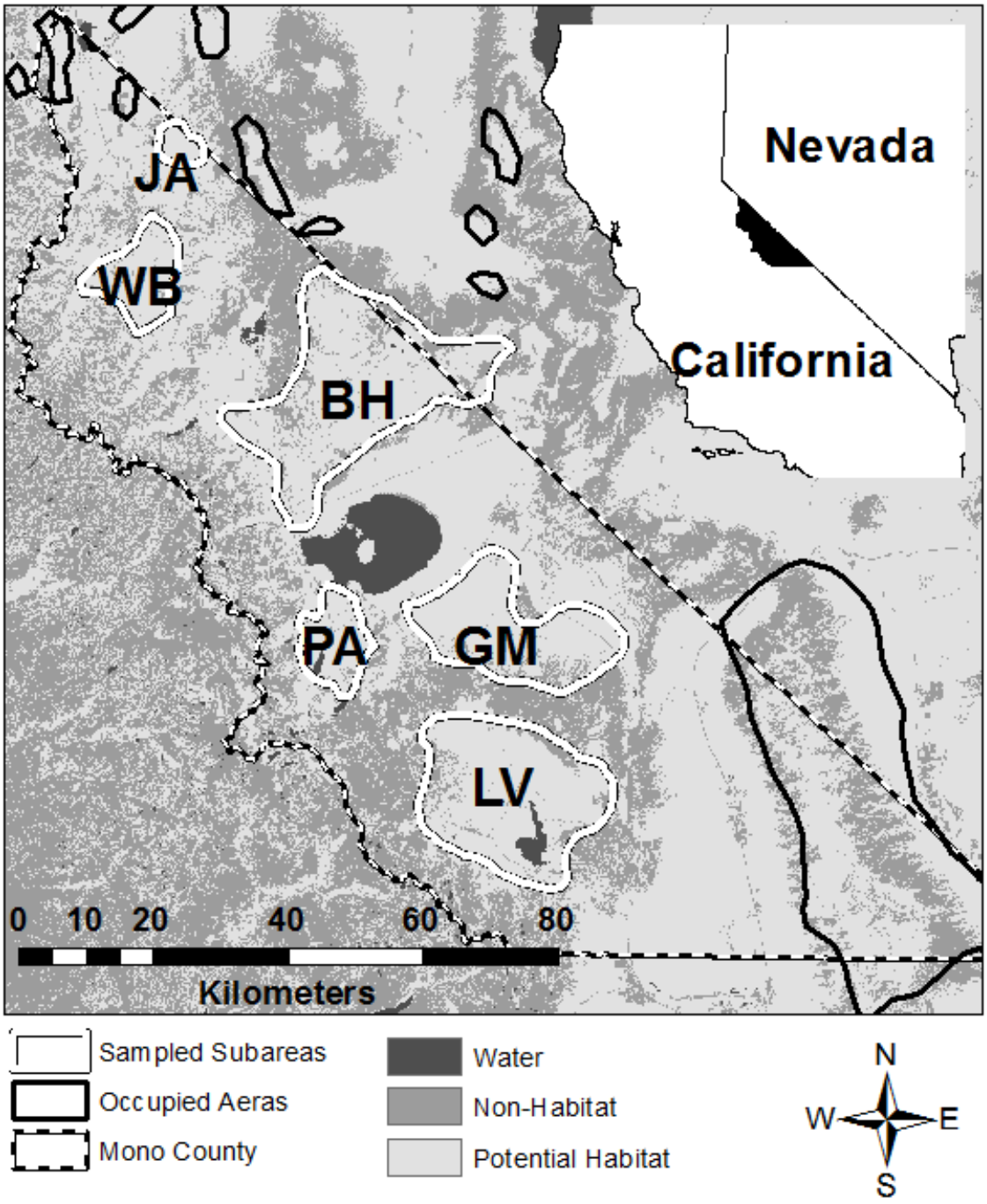

Fig. 2.1

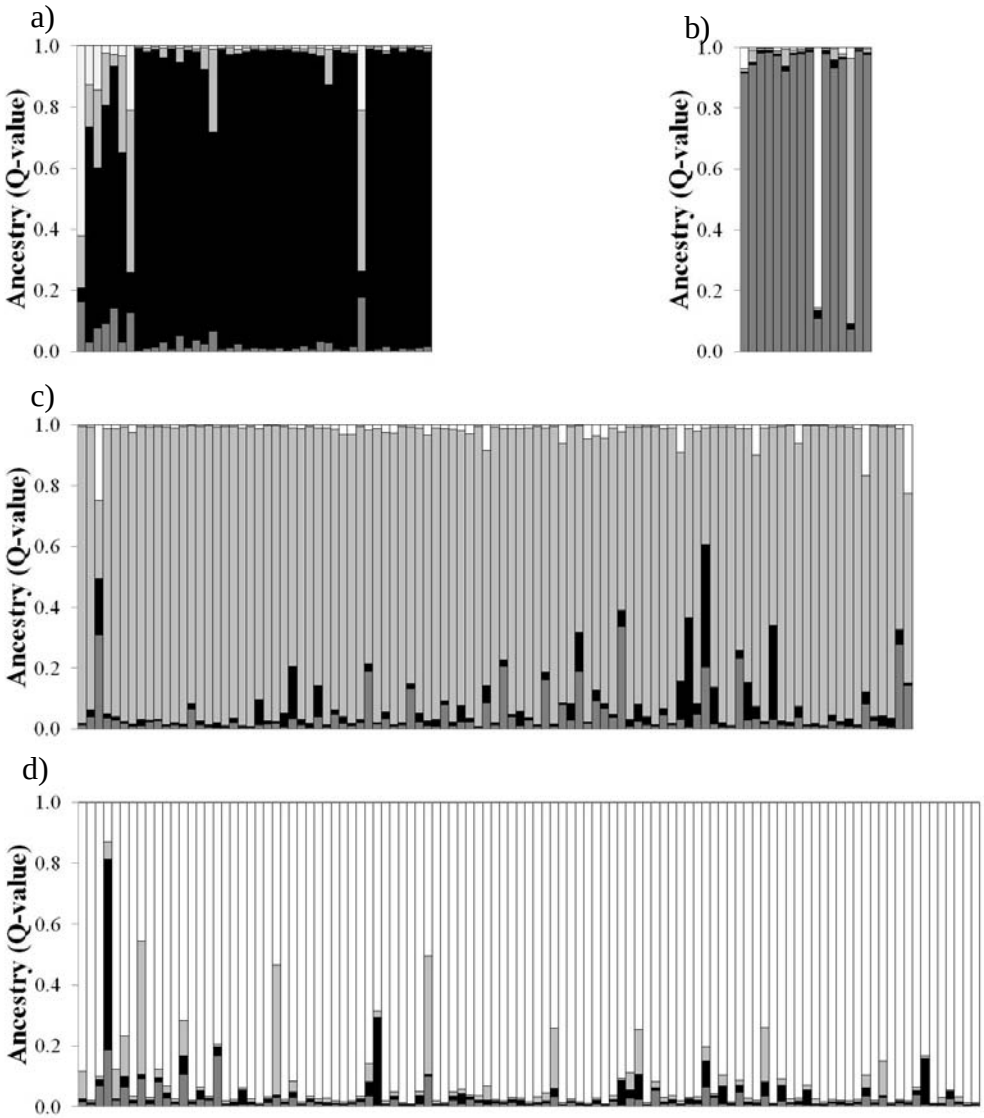

Fig. 2.2

Tables

Table 2.1 Number of unique individuals genetically sampled, radio-marked greater sage-grouse, and subarea-level information for each of the sampled subareas in the Mono County, California portion of the Bi-State Distinct Population Segment.

Subarea	Unique Individuals	Radio-Marked (M/F)	Leks	Peak Male Count[a]	Area (km^2)	Population Trend[b]
Jackass	7	0	1	18	34	Unknown[c]
Wheeler-Burcham	40	4 (3/1)	2	36	145	Stable, below long-term average
Bodie Hills	136	54 (1/53)	12	432	489	Stable, above long-term average
Granite Mt.	13	0	1	4	365	Declining, below long-term average
Parker	16	9 (2/7)	1	7	121	Declining, below long-term average[d]
Long Valley	122	55 (3/52)	10	386	524	Stable, above long-term average

[a] Lek count data from 2011 for Wheeler-Burcham, Bodie Hills, Long Valley, and Parker, from 2012 for Jackass, and from 2013 for Granite Mt.

[b]Data from Bi-State Technical Advisory Committee (2012)

[c]Trend data is lacking due to infrequent counts because of limited access

[d]Population declines in Parker are largely attributed to hatching failures caused by nonviable eggs

Table 2.2 Summary statistics for sample size (N), observed heterozygosity (H_O), expected heterozygosity (H_E), allelic richness (AR), and inbreeding coefficient (F_{IS}) from each of the genetic populations of greater sage-grouse identified in Mono County, California.

Population	N	H_O	H_E	AR	F_{IS}
Fales	43	0.569	0.578	3.882	0.017
Bodie Hills	99	0.559	0.588	4.224	0.051*
Granite Mt.	13	0.624	0.591	3.359	-0.059
Parker	16	0.656	0.602	3.645	-0.093*
Long Valley	94	0.605	0.604	3.914	-0.003

*Significantly different from zero

Table 2.3 Pairwise F_{ST} (lower diagonal) and distance (km; upper diagonal) between subareas for greater sage-grouse in Mono County, California. All pairwise F_{ST} comparisons were significant after the B-Y FDR[a] correction ($p < 0.015$).

Subarea	1	2	3	4	5	6
1. Jackass	--	19.2	35.5	84.4	75.8	100.3
2. Wheeler-Burcham	0.090	--	29.9	69.8	56.1	83.4
3. Bodie Hills	0.064	0.108	--	35.5	28.2	50.8
4. Granite Mt.	0.157	0.232	0.176	--	23.2	17.6
5. Parker	0.120	0.149	0.122	0.205	--	29.3
6. Long Valley	0.121	0.202	0.156	0.100	0.183	--

[a]Benjamini-Yekutieli False Discovery Rate significance correction for multiple comparisons (Benjamini & Yekutieli 2001)

Table 2.4 Population sampled, probability of residency in the sampled population, and most likely population of origin for sage-grouse that met our criteria for dispersers based on the one exclusion-based test (L_Home; in GENECLASS2) and three assignment tests (L_Home/LHomeMax; in GENECLASS2, BAYESASS3, and STRUCTURE).

			L_Home	L_Home/L_HomeMax		BAYESASS3		STRUCTURE	
ID	Sex[a]	Sampled Population	P-value	P-value	Assigned Population	PP of Residency[c]	Assigned Population	PP of Residency[c]	Assigned Population
Z006	F	Long Valley	0.010	0.504	NA[b]	0.895	NA[b]	0.858	NA[b]
Z051	M	Long Valley	0.001	0.504	NA[b]	0.982	NA[b]	0.982	NA[b]
Z108	M	Fales	0.000	0.022	NA[b]	0.032	Bodie Hills	0.022	Bodie Hills
Z118	F	Long Valley	0.006	0.505	NA[b]	1.000	NA[b]	0.998	NA[b]
Z144	F	Long Valley	0.140	0.011	NA[b]	0.355	Bodie Hills	0.238	Bodie Hills
Z204	F	Bodie Hills	0.008	0.513	NA[b]	0.974	NA[b]	0.987	NA[b]
Z215	F	Parker	0.001	0.000	Long Valley	0.000	Long Valley	0.000	Granite Mt.
Z265	Unk	Parker	0.014	0.013	NA[b]	0.065	Bodie Hills	0.234	Bodie Hills
Z306	F	Fales	0.073	0.002	Long Valley	0.174	Long Valley	0.515	NA[b]
Z312	F	Granite Mt.	0.002	0.020	NA[b]	0.000	Parker	0.067	Parker

[a]F = female, M = male, Unk = unknown

[b]NA = not identified as a migrant and not assigned to a population of origin based on the method used

[c]Bayesian posterior probability (PP) of residency in sampled population

CHAPTER 3

VITAL RATES OF GREATER SAGE-GROUSE IN THE BI-STATE DISTINCT POPULATION SEGMENT

Abstract

The Bi-State Distinct Population segment (DPS) of greater sage-grouse (*Centrocercus urophasianus*), located along the border of central California and eastern Nevada, is genetically and geographically isolated from populations in other portions of the species range. In 2013, the Bi-State DPS was proposed to receive threatened status under the Endangered Species Act. To assess vital rates, we radio-marked and monitored 112 female greater sage-grouse in 3 of the localized populations within the Mono County, California portion of the Bi-State DPS from 2007 to 2011. From 2009 to 2011 we also monitored 41 broods. We used program MARK to model monthly survival for females and daily survival of nests, and estimated apparent brood survival until 60 days post-hatch. Female survival was best explained by a model with a season and year effect, with season receiving overwhelming support throughout the candidate set of models (cumulative AIC_c weight = 0.950). Monthly survival was highest during the winter (0.980-0.994) and the lowest during the breeding season (0.924-0.998). Daily nest survival was best explained by a decreasing linear time trend over the nesting season (AIC_c weight = 0.507), and ranged from 0.986 to 0.918. The Parker subarea had a 0% apparent nest success largely due to nonviable eggs. For years in which we had an adequate sample size of broods, apparent brood success ranged from 30% to 100%. These results provide key baseline information as well as insight into the factors driving population performance.

Introduction

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) have experienced range-wide population declines over the last 50 years (Schroder et al. 1999, Connelly et al. 2004). Habitat loss and degradation are leading causes of population reductions (Holloran et al. 2005, Leu & Hanser 2011), as altered landscapes may fail to meet the birds' life requisites, thus affecting population vital rates and trajectory (Blomberg et al. 2012). Predator subsidies have increased the concentration of predators in some areas exacerbating the risk of depredation (Coates & Delehanty 2010, Hagen 2011), and the placement of infrastructure, especially fences, presents birds with the risk of structure collisions, potentially leading to injury or death (Wolfe et al. 2007, Stevens et al. 2012a, b).

Different threats, whether natural or anthropogenic, are likely to influence vital rates such as nest success, brood survival, and adult survival differently. A resulting change in any one vital rate will impact a populations' trajectory differently depending on the species' life history (Wisdom et al. 2000). While many galliform species tend to rely on high reproductive effort to maintain population levels (Taylor et al. 2012), sage-grouse have comparatively low reproductive effort and high adult survival (Schroder et al. 1999, Connelly et al. 2000), making adult survival especially influential on population trends (Johnson & Braun 1999, Sæther & Bakke 2000). Indeed, Taylor et al. (2012) reported that population growth was most sensitive to differences in adult female survival. Consistent with the important vital rates for many galliform species, reduced nest (Schroder 1997) and chick survival (Aldridge & Brigham 2001) have also been identified as likely causes for population declines in sage-grouse.

Along with declining populations, the distribution of sage-grouse has been reduced nearly 44% (Schroeder et al. 2004). This range contraction has reduced connectivity among

populations, especially those along the periphery of the species range, resulting in an increased risk of local extirpation (Knick & Hanser 2011). The Bi-State population, a peripheral population located along the border of central California and southern Nevada, has been isolated from the remainder of the species range predating European settlement (Oyler-McCance et al. 2005). This population has been identified as a Distinct Population Segment (DPS) by the United States Fish and Wildlife Service (USFWS) largely due to its genetic isolation and uniqueness (Benedict et al. 2003, Oyler McCance et al. 2005, United States Department of Interior 2010). In 2013, the USFWS proposed listing the Bi-State DPS as threatened under the Endangered Species Act (United States Department of Interior 2013).

As a population of conservation concern, it is important to have up-to-date vital rate data for the Bi-State DPS, as these types of data can act as important baseline information and provide insight about a population's trajectory (Taylor & Gerrodette 1993). Here, we use program Mark (White & Burnham 1999) to estimate female and nest survival rates, and investigate influential factors using an information theoretic approach (Burnham and Anderson 2002) for 3 of the localized populations within the Mono County, California portion of the Bi-State DPS between 2007 and 2011. Because the Bi-State population is geographically and genetically isolated, and thus susceptible to genetic impoverishment which may have a deleterious effect on fitness (Reed & Frankham 2003, Gemmell et al. 2004), we assess the influence of individual-level genetic diversity on survival and nest success. We also report apparent brood success for 2 of the localized populations between 2009 and 2011.

Study Area

Our study area in Mono County, California is bordered to the west by the eastern slope of the Sierra Nevada and to the east by the California-Nevada state line (Fig. 3.1).

Topographically variable, the study area contains a series of valleys and mountain ranges with elevations from 1,660 m to 3,770 m. Temperature, precipitation, and vegetative communities generally follow an elevational gradient, and the most common cover types are sagebrush (*Artemisia* spp.)-steppe communities, coniferous forest, natural and artificially flooded meadows, and open water (Bi-State Local Planning Group 2004; hereafter BSPG 2004, Kolada et al. 2009b). Non-habitat, which is mostly coniferous forests, frequently bisects the sagebrush-steppe/meadow habitats creating 6 spatially disjunct populations (hereafter subareas), each of which is thought to represent an independent lek complex (BSPG 2004, Kolada et al. 2009a,b). From north to south the subareas are Jackass, Wheeler-Burcham, Bodie Hills, Granite Mountain, Parker, and Long Valley.

All subareas, except Parker, are used for seasonal grazing by sheep or cattle (BSPG 2004). Recreational activities such as hiking, fishing, and use of off-road vehicles are common in the Long Valley and Parker subareas (Bi-State Technical Advisory Committee 2012; hereafter BSTAC 2012). Human impacts also include a series of roadways ranging from 2-tracks to a 4-lane highway, infrastructure such as power lines and fences, as well as an airport and landfill in the Long Valley subarea (BSTAC 2012). Predators include California gulls (*Larus californicus*), common ravens (*Corvus corax*), raptors, coyotes (*Canis latrans*), and American badgers (*Taxidea taxus*).

Methods

Field Methods

From 2007 through 2011 we captured female sage-grouse using spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992). Most hens were captured on and around leks during the breeding season, but we also opportunistically captured individuals

during the late summer and fall. Upon capture, each individual was banded with a uniquely-numbered California Department of Fish and Wildlife aluminum leg band and fitted with a ≤ 20 g ATS necklace-style radio transmitter equipped with an 8-hour activity sensor (Advanced Telemetry Systems, Inc., Isanti, MN, USA). We classified each individual as a yearling (< 1 yr old, first breeding season) or adult (≥ 2 yr old, second or later breeding season) based on the feather wear of the outer primaries (Eng 1955), and checked for the presence of a brood patch to determine if the hen had nested prior to capture. We obtained genetic samples from each bird by collecting 2-3 breast feathers and by over-clipping the hallux nail to collect 3-4 drops of blood in a microfuge tube. After collecting blood, we stopped bleeding using a cotton swab and styptic powder. Until DNA was extracted, we preserved the genetic samples by desiccating the feathers with indicator silica and freezing the blood.

We located radio-marked individuals 1-3 times per week from the ground using a hand-held 3-pronged Yagi antenna and receiver from March through October, and periodically throughout the year via aerial telemetry from a fixed-winged aircraft when birds were missing or conditions did not permit ground tracking. When we detected a mortality signal, indicating 8 hours of inactivity, we attempted to locate the radio-transmitter and any signs of the carcass as soon as logistically feasible to confirm the individual's fate. We did not assign a specific cause of mortality because the apparent cause of death may be misleading (Bumann & Stauffer 2002, Hennefer 2007).

From April to July we took note of localized movements as this is often indicative of nest initiation (Webb et al. 2012). Once localized movements were observed, we attempted to visually locate the radio-marked bird without causing it to flush. After the discovery of an apparent nest, we returned within 1-4 days to visually confirm the nesting status. If a hen was

flushed upon discovery of a nest, and had abandoned by the time we returned to confirm the nest, we censored the nest from our analysis. After we confirmed a female was on a nest, we monitored the nest 2-3 times per week from a designated listening point, at a distance of approximately 100 m, assuming the female was on her nest if the signal remained in the same direction. When the direction or magnitude of the signal changed we investigated the fate of the nest. When monitoring nests of unmarked females that had been incidentally discovered, we visually assessed the status of the nest 2 - 3 times per week from a distance of 10 - 20 m. We considered a nest to be successful if at least 1 egg membrane was detached from the shell, indicating the egg had hatched (Wallestad & Pyrah 1974). If we determined the nest failed, we continued monitoring the nest hen for any re-nesting attempts.

Genetic Analysis

Blood and feather samples were extracted and genotyped at 17 microsatellite loci following the methods described in Chapter 2. To provide a comparative measure of genetic diversity we the homozygosity by loci metric (HL; Aparicio et al. 2006) because it has greater statistical power with moderate sample sizes compared to the other individual heterozygosity metrics. We calculated HL for each individual using the Rhh package (Alho et al. 2010) in R (R Development Core Team 2011).

Data Analysis

Hen Survival

Using the RMark package (Laake & Rexstad 2007) in program R (R Development Core Team 2011), we used the nest survival model (Dinsmore et al. 2002) of program MARK (White & Burnham 1999) to estimate hen survival rates and to test competing hypotheses about factors influencing survival using an information theoretic approach (Burnham &

Anderson 2002). Because the sample size and temporal scale of monitoring would not permit estimating daily survival rates we used months as the temporal unit of analysis. We converted telemetry records into a format compatible with the nest survival model with the first possible occasion starting on 1 April and the last possible occasion ending on 31 March of the following year. We considered 1 month to equal 30 days, therefore, when processing the data with RMark we used the intervals argument to assign a length of 1 time unit to months with 30 days and to adjust the units of time allotted to shorter and longer months accordingly. For a capture history to be usable an individual must be observed over at least one interval (e.g. between months). Because April, the first month of the breeding season, was defined as the first occasion and March was defined as a last occasion each of these months only had the capability of allowing a bird to be observed over an interval in one direction; from April to May and from February to March. Thus, if a bird was found dead in April the data would not be usable because it was not observed over an interval. Similarly, data from any individual captured in March, regardless of the fate, would be unusable because it could not be observed over an interval. Therefore, to increase the amount of usable data we divided both April and March into 4 equal-length occasions and adjusted the units of time each of these occasions represented accordingly using the intervals argument under the process.data command.

Using Akaike's Information Criterion adjusted for small sample size (AIC_c),we took a 2-stage modeling approach (Coates & Delehanty 2010) because we were unable to obtain genetic data from all individuals, and were therefore unable to test the possible influence of genetic diversity on survival when using the full data set. All variables used in the first stage were factor variables and were considered group covariates. These variables were: year (2007-2011), season (breeding = 1 April-30 June, summer/fall = 1 July-31 October, winter =

1 November-31 March), subarea (Bodie Hills, Parker, Long Valley), age class (yearling or adult), and a variable indicating if a hen was successful or unsuccessful in hatching a nest during the year for which survival was being modeled. If either age class or nest fate was unknown, as was typical of birds captured during late summer and fall, we excluded the individual from survival analysis for the year with the missing data. We built and compared models comprised of biologically relevant combinations of these variables but ultimately included only additive models during model selection since preliminary data analysis indicated insufficient data for modeling interactions.

The second step was to determine if adding a term for genetic diversity improved model fit. During stage 2 we used a reduced data set that included only birds from which we were successfully able to obtain a genetic sample. We evaluated the support received by the top model identified in step 1 in comparison to an equivalent model, but with the addition of a individual covariate corresponding to the level of genetic diversity for each bird (HL).

During each stage of model selection, we calculated c-hat by dividing the deviance by the deviance degrees of freedom. Although this method of calculating c-hat may produce positively biased estimates (Moynahan et al. 2007), it is the only method of calculating c-hat for the nest survival model. If the estimate of c-hat was ≤ 1 we did not apply an adjustment to the AIC_c values, but if c-hat was > 1 we adjusted the AIC_c values to produce $QAIC_c$ values (Burnham & Anderson 2002). After identifying the most parsimonious model we calculated seasonal survival rates by raising the estimate of monthly survival by the number of months contained within the season and calculated the confidence intervals with the delta method using the msm package (Jackson 2011) in program R (R Development Core Team 2011).

Nest Survival

Using the RMark package (Laake & Rexstad 2007) in program R (R Development Core Team 2011), we used the nest survival model (Dinsmore et al. 2002) of program MARK (White & Burnham 1999) to estimate daily survival rates (DSR) and evaluate factors affecting nest survival. Based on the date of the earliest discovered nest and the latest documented hatch or failure during any year of the study, we defined the nesting season as a 101-day period starting on 12 April and ending on 21 July. We included a linear time trend of the day of nesting season (Time) as a variable in our models to assess potential changes in DSR over the nesting season. Since we were unable to accurately determine the date of initiation or first day of incubation, the "Time" variable may also help account for some of the possible variability associated with initiation date and nest age (Moynahan et al. 2007). Additional variables included year (2007-2011), study area (Bodie Hills, Parker, and Long Valley), nest attempt (attempt; initial or renest), and age class (yearling or adult) of the nesting hen. Using combinations of these variables we developed a set of biologically plausible a priori models representing hypotheses about the relationship between daily survival rate and the variables of interest (Burnham & Anderson 2002). Since the nest attempt and Time variable were confounded, we did not build any models that contained both variables. Additionally, we restricted our models to additive models since models with interactions did not converge.

Using Akaike's Information Criterion adjusted for small sample size (AIC_c), we took a 2-stage modeling approach (Coates & Delehanty 2010) since we were unable to obtain genetic data from all nesting hens, and were therefore unable to test the possible influence of genetic diversity when using the full data set. During stage 1 we used the full data set to evaluate our a priori models that did not include the genetic diversity variable for individual

heterozygosity. The second stage was to determine if adding a term for genetic diversity improved model fit. During stage 2 we used a reduced data set that included only nests from hens that we were able to genetically sample. With the reduced data set, we evaluated the support received by the top model identified in step one in comparison to an equivalent model, but with the addition of an individual covariate corresponding to the level of genetic diversity of the hen for each nest.

During each stage of model selection, we calculated c-hat by dividing the deviance by the deviance degrees of freedom. Although this method of calculating c-hat may produce positively biased estimates (Monahan et al. 2007), it is the only method of calculating c-hat for the nest survival model. If the estimate of c-hat was ≤ 1 we did not apply an adjustment to the AIC_c values, but if c-hat was > 1 we adjusted the AIC_c values to produce $QAIC_c$ values (Burnham & Anderson 2002). When appropriate we used the model.average function in RMark to produce model averaged DSR estimates and 95% confidence intervals. To calculate nest success we assumed laying occurred over 10 days and that the incubation period was 28 days (Schroeder et al. 1999), resulting in a 38 day exposure period. We calculated nest survival and the associated confidence intervals with the delta method using the msm package (Jackson 2011) in program R (R Development Core Team 2011).

Brood Survival

During 2009 through 2011 we monitored brood survival of the radio-marked hens that successfully nested. At 30 and 50-60 days (± 5 days) post-hatch we determined if hens were still brooded and counted chicks by either flushing the hen at first light or locating the hen at night using a spotlight. If no chicks were observed during the first brood count, we assumed

the brood had failed and did not conduct a second brood count. We considered a brood to be successful if there was ≥ 1 chick observed during the second brood count.

Results

Hen Survival

From 1 April 2007 through 31 October 2011, we captured and radio-marked 112 hens within the Bodie Hills, Parker, and Long Valley subareas (Table 3.1) and obtained genetic samples from 89. After excluding the capture histories that were missing data on age class or nest success status, we had a total of 184 year-long capture histories (Table 3.2). Forty-eight individuals were monitored for 1 year, 45 individuals were monitored for 2 years, 14 individuals were monitored for 3 years, and 1 hen was monitored for 4 years.

During the first stage of model selection for monthly survival rates of females, the best model included a season and year effect (Table 3.3). In the second round of model selection adding the individual covariate representing heterozygosity did not improve model fit. The model that included HL was 1.472 ΔAIC_c from the previously identified top model, and the Akaike weights indicated the model that did not include HL was 2.09 times more likely to be the best approximating model (Table 3.4). The beta estimate for HL was 1.055, suggesting a positive relationship between heterozygosity and survival, however, the 95% confidence interval showed substantial overlap of zero (LCL = -1.759, UCL = 3.861) making it difficult to determine if HL truly had an effect on survival, and if so, the directionality of the effect. Thus, because the model without HL provided a better fit and because the effect of HL proved ambiguous, we excluded the genetic diversity metric and report results based on the full data set.

With the full data set, 3 models had $\Delta AIC_c < 2$ (Table 3.3). The top model only included season and year effects. For this model the 95% confidence intervals for beta estimates that modify the effect of year all overlap zero, whereas the 95% confidence intervals on the beta estimates that modify the effect of season do not (Table 3.5). The other 2 models within 2 ΔAIC_c of the top model, and therefore worthy of consideration (Burnham & Anderson 2002), also included a season and year effect, once again with the beta estimates that modified year and season overlapping and not overlapping 0, respectively (Table 3.5). The second best model also included a term indicating whether or not a hen had successfully hatched a nest, and the other model containing the effect of subarea (Table 3.3). In both cases, however, the 95% confidence intervals on the beta estimates for the additional terms overlapped zero (Table 3.5).

The top model that contained only season and year effects had an Akaike weight of 0.230 and the sum of the Akaike weights for all models containing both a season and year effect was 0.675. More notably, the sum of the Akaike weights for models that contained a seasonal effect was 0.950, with all models that contained season outperforming any model that did not (Table 3.3), providing strong support for a seasonal effect. For each year the monthly survival rate during the breeding season was the lowest and the monthly survival rate during the winter was the highest (Fig. 3.2a-j). Despite the fact that the breeding, summer/fall, and winter seasons had different lengths of 3, 4, and 5 months, respectively, the monthly survival rates differed such that estimates for seasonal survival were still the lowest during the breeding season and greatest during the winter (Fig. 3.2f-j).

Nest Survival

Of 112 female sage-grouse that were radio marked, mortality or radio failure prevented us from monitoring 13 of these individuals during any portion of the breeding

season, leaving 99 birds for which we could possibly discover a nest. These hens were monitored over 1-3 breeding seasons resulting in a sample size of between 18-40 birds for each breeding season (Table 3.6). Across subareas, nest initiation rate ranged from 22.7% for yearlings in 2007 to 100% for both yearlings and adults in 2010 and 2011 (Table 3.7). For each year that the total nest initiation rate was under 100%, the initiation rate for adults exceeded that of yearlings (Table 3.7). Based on the number of potential re-nesting opportunities (e.g. a nest failed and the hen was not killed), the re-nesting rate for years and age classes combined was 33%. As with initial nesting attempts, the rate of re-nesting for adults (39%) was greater than that of yearlings (13%) (Table 3.8).

With the exclusion of 9 nests from radio-marked hens censored due to researcher-induced abandonment, we found and monitored a total of 142 nests (Table 3.9). One hundred forty of these nests belonged to radio-marked birds, and 2 were from unmarked birds incidentally discovered during 2011. Across years the apparent nest success in the Bodie Hills, Parker, and Long Valley was 44.62%, 0%, and 52.31%, respectively (Table 3.10). The 0% nest success in the Parker subarea was a result of many of the nests containing nonviable eggs. Nine of 12 Parker nests failed to hatch even after the standard 28-day incubation period.

During the first stage of model selection for daily nest survival, the top model was a linear time trend over the course of the nesting season (Table 3.11). In the second round of model selection adding the individual covariate representing heterozygosity did not improve model fit. The model that included HL was 1.538 AIC_c units from the previously identified top model, and the Akaike model weights indicated the model that did not include HL was 2.16 times more likely to be the best approximating model (Table 3.12). The beta estimate for HL was 0.727, suggesting a positive relationship between heterozygosity and survival,

however, the 95% confidence interval showed substantial overlap of zero (LCL = -1.363, UCL = 2.818) making it difficult to determine if HL truly had an effect on survival, and if so, the directionality of the effect. Thus, because the model without HL provided a better fit and because the effect of HL proved ambiguous, we excluded the genetic diversity metric and report results based on the full data set.

With the full data set, 2 models had $\Delta AIC_c < 2$ (Table 3.11). The top model received an AIC weight of 0.507 and described daily nest survival as a linear function of day of nesting season. The second best approximating model, which was 1.959 ΔAIC_c from the top model and had an AIC weight of 0.191, contained a linear time trend over the nesting season as well as an age class effect. For both models beta estimate of the time trend had 95% confidence intervals that did not overlap zero, and indicated a decrease in DSR over the nesting season (Table 3.13). For the second best model the beta estimate for the age class variable suggested yearlings had a higher DSR then adults, however, the 95% confidence intervals for this beta estimate overlapped zero (LCL = -0.519, UCL = 0.645; Table 3.13). The model averaged survival estimates for the top 2 models contain point estimates of DSR that are similar between both age classes and confidence intervals between age classes always overlap. Therefore, we graphically display only DSR estimates as a function of date of nesting season for adults, which while similar between age classes, provides a slightly more conservative estimate of DSR (Figure 3.3).

Brood Survival

From 2009 through 2011, 41 radio-marked hens nested successfully; 20 from Bodie Hills and 21 from Long Valley. Across years, the percentage of broods that survived to 30 days post-hatch in Bodie Hills and Long Valley was 85% and 76%, respectively (Table 3.14).

In 2010, 100% of the broods in both areas reached 30 days of age. In the Bodie Hills apparent brood survival (e.g. brood observed at 60 day brood check) ranged from 0% in 2011 to 82% in 2009. In Long Valley apparent brood survival ranged from 30% in 2009 to 66% in 2011. Across years the percentage of broods surviving until 60 days post-hatch in the Bodie Hills and Long Valley was 60% and 47%, respectively (Table 3.14).

Discussion

Hen Survival

Based on our model selection results we found season to be the most supported main effect. For all years, seasonal survival was highest during the winter, followed by the summer-fall, and lowest for the breeding season. Ranging from 80.9-91.6%, our winter seasonal survival estimates (Fig. 3.2) were slightly lower than most reviewed by Connelly et al. (2011) and those observed in Utah by Baxter et al. (2013) and in eastern Nevada by Blomberg et al. (2013). In Montana, Moynahan et al. (2006) documented seasonal winter survival of 93% during a mild winter but only 58% during a severe winter. Despite the above average snow fall (3.5 m) during the 2010-2011 winter (NCDC Station Historical Listing for NWS Cooperative Network, Lee Vining, CA), we did not see a decrease in survival as was observed by Moynahan et al. (2006).

Contrary to the observations in Eastern Nevada (Blomberg et al. 2013), Montana (Moynahan et al. 2006), and throughout Nevada, including the Bi-State area (Sedinger et al. 2011), we did not observe any decrease in survival during the late summer and fall. Our Summer-fall and winter seasonal survival estimates never differed by more than 1% within a year, suggesting that in the Bi-State DPS the bulk of the predation risk, which is a major source of mortality for sage-grouse (Schroeder et al. 1999, BSTAC 2012), is associated with

nesting and brood-rearing activities (Hagen 2011). Unlike Eastern Nevada, which is located along the major raptor migration route (Goodrich & Smith 2008), the Bi-State area does not experience a major influx of raptors during the late summer and fall, likely explaining why survival did not decrease as was seen by Blomberg et al. (2013). The low survival during the late summer in Montana observed by Moynahan et al. (2006) was attributed to West Nile virus, which has not been documented in the Bi-State DPS. In Nevada, specifically during October, Sedinger et al. (2011) found a decrease in survival that was correlated with increased hunting pressure. In the Mono County, California portion of the Bi-State DPS hunting is restricted under limited quota permit system, and less than 3% of the fall population is harvested annually (BSTAC 2012). Interestingly, Sedinger et al. (2011) documented low monthly survival during November and December (0.71) as well as annual survival (0.16) in the Bi-State DPS, however, as they acknowledge, these may be spurious results due to a low sample size (n = 6).

A year effect was also included in our top model, suggesting there was some variability between years. The beta estimates for the year parameter, however, always had 95% confidence intervals that overlapped 0 (Table 3.5). Similarly, annual variation in survival was not well supported for either juveniles in Table Butte, ID (Beck et al. 2006) or yearling and adult females in eastern Nevada (Blomberg et al. 2013). An effect of year was well supported by Moynahan et al. (2006) and Baxter et al. (2013) when modeling survival using a season-year interaction. Since it appears there are differences in seasonal estimates between years (Fig. 3.2), our beta parameters may have been significant if our data set was large enough to allow us to model a season-year interaction.

Nest Survival

Over the duration of our 5-year study nest initiation rates were highly variable. Pooling age classes, there was only 34% nest initiation in 2007 whereas in 2010 and 2011 it was 100% (Table 3.7). Nest initiation rates have previously been documented as low as 63% (Bunnell 2000), but our 2007 estimates were lower than this and well below the approximately 80% average documented for the species (Connelly et al. 2011). During the 2006-2007 winter only 89 cm of snow fell, less than one half of the 20 year average (NCDC Station Historical Listing for NWS Cooperative Network, Lee Vining, CA), likely leading to sub-optimal dietary conditions due to the lack of forbs (Pyle & Crawford 1996, Guttery et al. 2013) and lower reproductive effort (Blomberg about 2013). Also, the majority of the birds radio-marked were yearlings, which frequently have lower nest initiation rates than adults (Baxter et al. 2009, Connelly et al. 2011). However, our 2007 estimate of nest initiation is likely an underestimate since 7 of the birds were radio-marked in late April presenting a situation in which we may have missed their first and only nesting attempt.

During 2010 and 2011 both nesting and re-nesting rates were high for what is commonly observed for the species (Connelly et al. 2011). While many studies likely underestimate nest initiation due to missing nests that are deprecated early (Schroeder et al. 1999), evidence of a breeding attempt, based on follicle scars, were not present in all hens examined by Dalke et al. (1963). The only other study populations that have been observed to have a 100% nest initiation rate are those in Washington State (Schroeder 1997) and Alberta, Canada (Aldridge & Brigham 2001), both of which are also peripheral populations.

The high nest initiation rate, and subsequently the high re-nesting rate, in 2010 and 2011 was likely because of favorable conditions due to above average winter snowfall,

leading to greater plant productivity (Bates et al. 2006). Mechanistically, this can promote reproductive effort because with increased food resources a hen may invest more energy in reproduction (Barnett & Crawford 1994). From a life history perspective, it is advantageous for a hen to forgo nesting during poor conditions, when a brood is less likely to survive, since an increase in reproductive effort decreases survival in sage-grouse (Blomberg et al. 2013). Conversely, when conditions are favorable for reproduction, as was the case in 2010 and 2011, it is advantageous for an individual to increase its reproductive effort (Hirshfield & Tinkel 1975).

While there were large differences in nest initiation rates for each year, a year effect on nest success was not apparent. During model selection, the top model that contained year was less supported than the null, intercept only, model (Table 3.11). The most influential variable, and the best supported model, was a linear effect of time, with DSR decreasing over the duration of the 101 day nesting season. Based on the product of the model averaged DSR for adults, a nest found on day 1 of the nesting season had a 46.7% chance of surviving the 38-day exposure period, whereas a nest discovered on day 68, the last day we discovered a nest, only had a 11.8% chance of surviving the exposure period. This decreasing chance of nest success over the season is contrary to the trend seen in Montana, where Moynahan et al. (2007) found that nests during the last 28 days of the nesting season had a higher chance of survival than those during the first 28 days. The decreasing trend of DSR is, however, is similar to that observed in Strawberry Valley, UT (Baxter et al. 2008) and within the Bi-State population (Kolada et al. 2009a). Although Kolada et al. (2009a) based their trend on nest age, the date of nesting season and nest age are interrelated (Moynahan et al. 2007). Since nest attendance may decrease as the nesting season progresses (Coates & Delehanty 2008),

the risk of nest depredation, especially by visual predators, such as ravens and gulls, which are especially common in the Long Valley subarea due to a landfill, may increase. Similarly, predators, both visual and olfactory, may develop a search image (Cornell 1976, Ishii & Shimada 2010), keying in on this seasonally abundant resource as the season progresses.

Unlike the previous work in the Bi-State area (Kolada et al. 2009a) the effect of subarea was not well supported by our models. Across subareas and years the mean date of nest discovery was 5 May, the 24th day of the nesting season. Assuming a 38-day exposure period, with nest initiation starting 10 days prior to the date of discovery (7 eggs laid at a rate of 1.5 eggs per day; Schroeder et al. 1999) the expected nest success rate would be 37.3%, slightly lower than our estimated apparent nest success rate of 44.4% (Table 3.10). While direct comparisons of nest success may be hindered due to the different methodologies that have been used to produce estimates, nest survival rates are highly variable. Telemetry studies have found rates as high as 70% in Montana (Wallestad & Pyrah 1974) and as low as 15% in Oregon (Gregg et al. 1994). Based on DSR, our estimate of nest survival is slightly lower than the previous estimate of 43% in the Bi-State area (Kolada et al. 1999a). Both these estimates are similar to the mean nest survival in altered habitats of 37% (Connelly et al. 2011). With extensive grazing, infrastructure, and recreational opportunities (BSTAC 2012) the Bi-State area has a large human footprint (Leu & Hanser 2011).

Our estimates of nest survival using DSR do not show the 0% nest survival in the Parker subarea (Table 3.10) which is a result of many of the clutches containing nonviable eggs. Although similar hatching failures have been observed in closely related species such as the greater prairie-chicken (*Tympanuchus cupido*; Bouzat et al. 1998, Westemeier et al. 1998) and the Gunnison sage-grouse (*Centrocercus minimus*; Stiver et al. 2008) with small

population sizes and low genetic diversity, the hatching failures in the Parker subarea could not definitively be linked to a genetic cause (Chapter 2). We, however, had a small sample size of both individual sage-grouse and nests. Thus, further research on the cause of the hatching failures is necessary.

Brood Survival

As a component of recruitment, low brood survival has been identified as a factor leading to poor population performance (Aldridge & Brigham 2001, Gregg & Crawford 2009). Because habitat at the edge of a species range is often marginal, recruitment in peripheral populations may be limited (Kawecki 2008). Sveum et al. (1998) found brood survival, in Washington State, as defined as the presence of the brood after 1 August, to be 10% and 50% during 2002 and 2003, respectively. In Alberta, Aldridge and Brigham (2001) found brood survival to be 43%, which they defined as ≥ 1 chick surviving until 50 days post-hatch. In South Dakota, brood survival until 3 weeks post-hatch was 52% and brood survival during 2006 and 2007 until 7 weeks post-hatch was 31% and 43%, respectively (Kaczor 2008).

Although brood survival in our study was highly variable between years and subareas, survival to 30 and 60 days post-hatch was generally greater than observed in other peripheral populations (e.g. Washington State, Alberta, and South Dakota). We also found brood survival to be comparable, if not above, that of other stable populations such as those in the northern Great Basin (Gregg & Crawford 2009) and western Wyoming (Bui et al. 2010). Thus, it seems brood survival is not a limiting factor. Survival from brood breakup until the following spring, however, can range from 6% (Kaczor 2008) to 86% (Beck et al. 2006).

Thus, despite high brood survival it is difficult to infer recruitment into the next year's population without further investigation of juvenile survival.

Conservation Implications

Based on lek count data (BSTAC 2012) and the assessment of Garton et al. (2011), both the Bodie Hills and Long Valley populations appear to be stable to increasing. These trends are detected despite high variability in vital rates between years. Thus, it appears the reduction in one vital rate may be compensated by an increase in another. This is likely especially true in the case of low nest success and brood survival which could lead to increased hen survival (Blomberg et al. 2013), which is a vital rate to which population trends are most sensitive (Johnson & Braun 1999, Taylor et al. 2012).

The Parker population , in contrast has been in decline (BSTAC 2012). This is likely due to high frequency of nest failing because they contain nonviable eggs. However, the small number of unique hens monitored in the Parker subarea (n = 7) makes it difficult to draw firm inferences. The prevalence of nests with nonviable eggs and brood production is difficult to judge based on lek count data. Because sage-grouse are long-lived (Schroeder et al. 1999) and exhibit high site fidelity (Dunn & Braun 1985), potentially resulting in a time lag after a perturbation (Walker et al. 2007). Determining the cause of the nonviable eggs should be of high priority since translocation efforts may help the population if hatching failures are due to genetic causes (Gemmell et al. 2004, Tallmon et al. 2004) or Allee effects (Courchamp et al. 1999), but might fail if they were a result of unknown site-specific factors.

Recently, Coates et al. (2013) developed utilization distributions from radio-marked sage-grouse in the Bi-State area to recommend the optimal size of surface use designations (e.g. restrictions on land usage) in relation to leks. In the surface use designations areas,

however, there are certain areas or habitat types that sage-grouse select and use to maximize their survival and reproductive success. Within the Bi-State DPS sage-grouse selected nest sites with greater shrub canopy cover then at randomly selected sites (Kolada et al. 2009b) and the percentage of non-sagebrush shrub had the greatest influence on nest survival (Kolada et al. 2009a). Casazza et al. (2011) found that brood survival was positively correlated with the percentage of perennial shrubs, species richness, and amount of meadow edge at a 7.9 ha scale. Information gained from these types of studies can help facilitate targeted management actions. Here, we described nest survival, brood survival, and hen survival but future work is still needed to evaluate juvenile survival as well as the factors that affect the survival of both juveniles and hens.

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Figure Captions

Fig. 3.1 Mono County, California study area and the location of areas occupied by greater sage-grouse (modified from Schroeder et al. (2004)), which from north to south are Jackass (JA), Wheeler-Burcham (WB), Bodie Hills (BH), Granite Mountain (GM), Parker (PA), and Long Valley (LV). Greater sage-grouse were monitored in the Bodie Hills, Parker, and Long Valley subareas

Fig. 3.2 Monthly survival rate (MSR; a-e) and seasonal survival rate (SSR; f-j) estimates based on the top model for female greater sage-grouse survival during the breeding (1 April-30 June), summer/fall (1 July-31 October), and winter (1 November-31 March) seasons from April 2007 through October 2011 in the Bodie Hills, Parker, and Long Valley portions of the Bi-State Distinct Population Segment in Mono County, California, USA

Fig. 3.3 Estimates of daily survival rate (DSR) as a trend over time for greater sage-grouse nests in the Mono County, California portion of the Bi-State Distinct Population Segment between 2007-2011 using the model averaged results from the 2 most parsimonious models of the set of candidate models

Figures

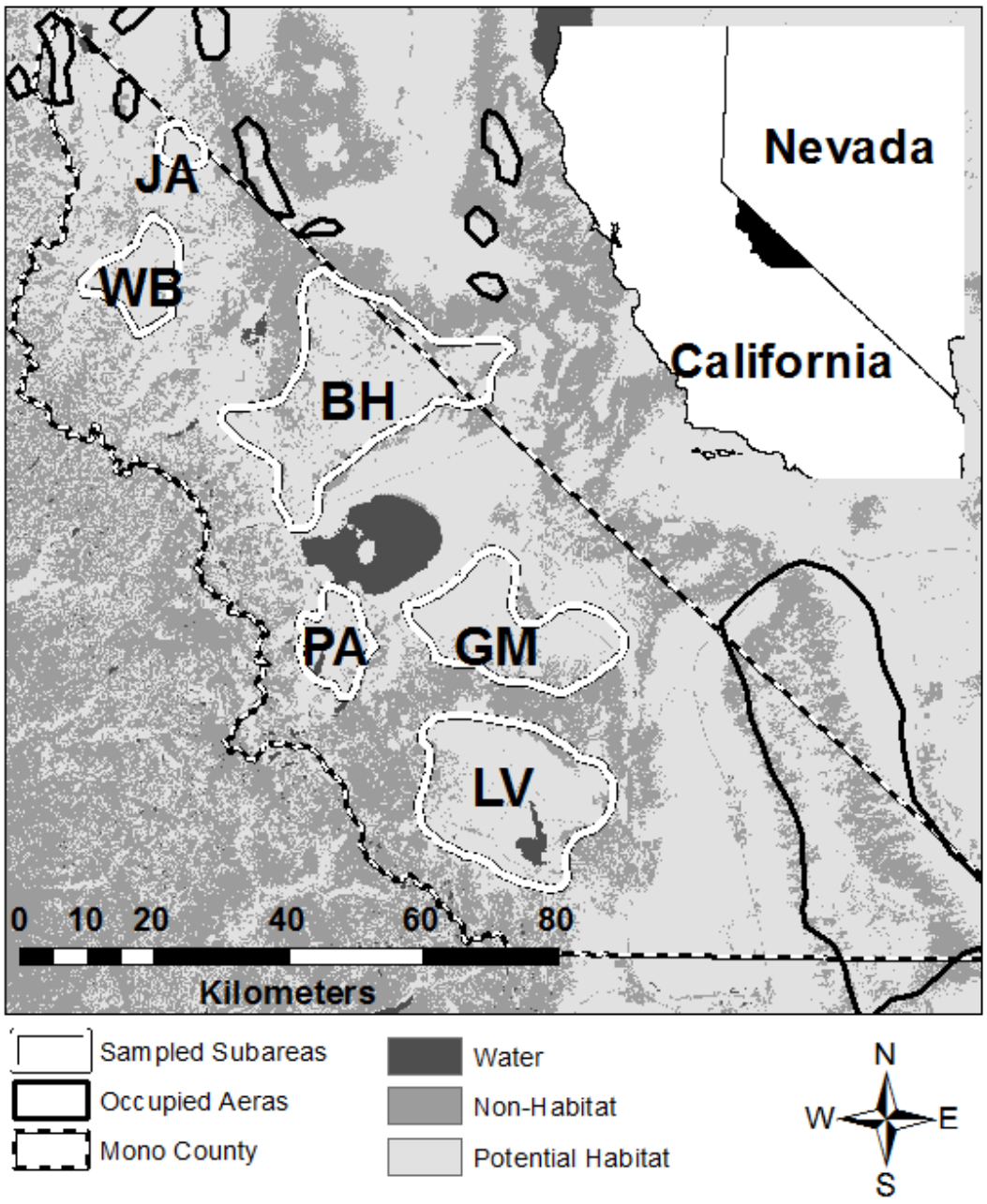

Fig. 3.1

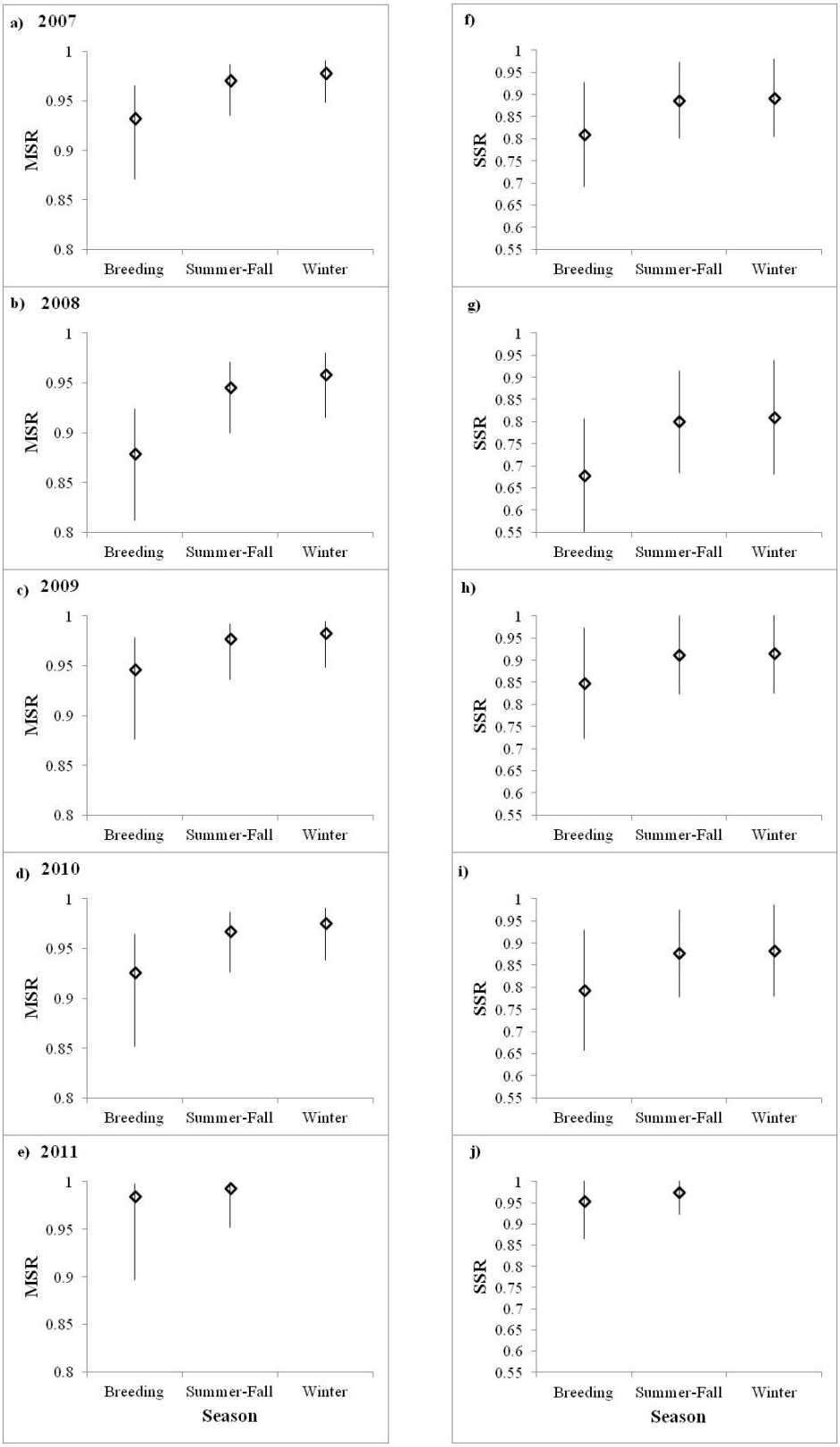
a) 2007
b) 2008
c) 2009
d) 2010
e) 2011
f)
g)
h)
i)
j)
MSR
SSR
Breeding
Summer-Fall
Winter
Season

Fig. 3.2

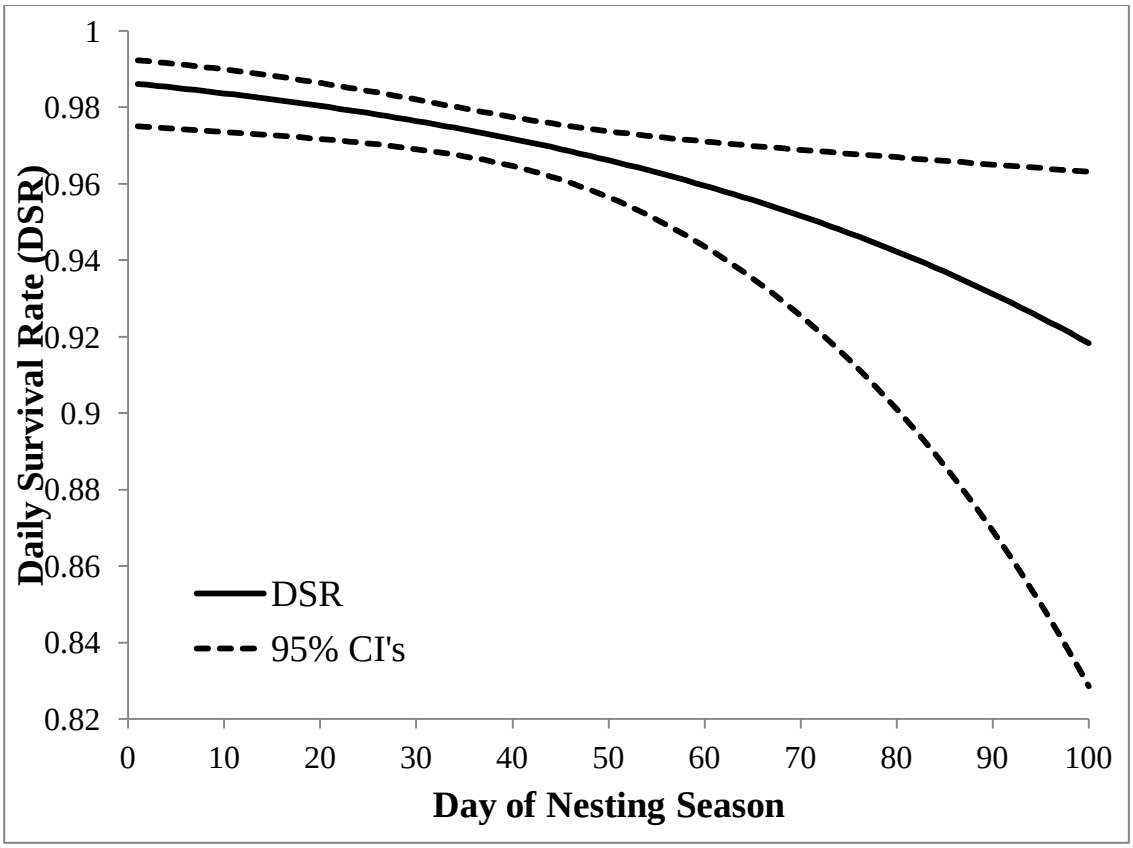
1
0.98
0.96
0.94
0.92
0.9
0.88
0.86
0.84
0.82
Daily Survival Rate (DSR)
DSR
95% CI's
0
10
20
30
40
50
60
70
80
90
100
Day of Nesting Season

Fig. 3.3

Tables

Table 3.1 Number of female greater sage-grouse radio-marked in the Bodie Hills (BH), Parker (PA), and Long Valley (LV) subareas of the Bi-State Distinct Population Segment in Mono County, California, USA from 2007-2011.

Year	BH	PA	LV	Total
2007	30	0	14	44
2008	2	3	14	19
2009	15	3	10	28
2010	3	1	9	13
2011	3	0	5	8
Total	53	7	52	112

Table 3.2 Number of year-long capture histories from female greater sage-grouse used to model survival from 2007 through 2011 in the Bodie Hills (BH), Parker (PA), and Long Valley (LV) subareas of the Bi-State Distinct Population Segment in Mono County, California, USA.

Year	BH	PA	LV	Total
2007	20	0	14	34
2008	19	4	33	56
2009	22	6	16	44
2010	13	5	13	31
2011	8	3	8	19
Total	82	18	84	184

Table 3.3 Candidate models of monthly survival rates for female greater sage-grouse in the Bodie Hills, Parker, and Long Valley subareas (SA) in the Mono County, California, USA portion of the Bi-State Distinct Population Segment during 2007-2011. Models were evaluated using the nest survival model and are ranked in ascending order based on their AIC_c values.

Model[a]	K[b]	AIC_c	ΔAIC_c	Model weight	Deviance
season + Yr	7	377.896	0.000	0.230	363.818
season + Yr + nest	8	379.367	1.471	0.110	363.268
season + Yr + SA	9	379.379	1.484	0.110	361.255
season + Yr + age class	8	379.900	2.004	0.084	363.801
season + Yr + nest + SA	10	380.165	2.269	0.074	360.013
season	3	380.276	2.380	0.070	374.259
season + SA	5	380.404	2.508	0.066	370.362
season + Yr + SA + age class	10	381.400	3.504	0.040	361.248
season + nest + SA	6	381.733	3.837	0.034	369.675
season + nest	4	382.121	4.226	0.028	374.094
season + Yr + nest + SA + age class	11	382.179	4.283	0.027	359.996
season + SA + age class	6	382.239	4.343	0.026	370.181
season + age class	4	382.270	4.374	0.026	374.242
season + nest + SA + age class	7	383.317	5.421	0.015	369.240
season + nest + age class	5	384.089	6.193	0.010	374.047
Yr	5	384.895	6.999	0.007	374.854
SA	3	385.072	7.177	0.006	379.056
Yr + SA	7	385.334	7.438	0.006	371.257
Null	1	385.414	7.518	0.005	383.411
Yr + nest + SA)	8	386.142	8.246	0.004	370.042
SA + age class	4	386.401	8.505	0.003	378.373
Yr + nest	6	386.467	8.571	0.003	374.409
nest + SA	4	386.545	8.649	0.003	378.518
Yr + age class	6	386.873	8.977	0.003	374.815
age class	2	387.155	9.259	0.002	383.147
Yr + SA + age class	8	387.271	9.375	0.002	371.172
nest + SA + age class	5	387.413	9.518	0.002	377.372
Yr + nest + SA + age class	9	387.873	9.977	0.002	369.749
Yr + nest + age class	7	388.379	10.484	0.001	374.302
nest + age class	3	388.968	11.072	0.001	382.951

[a] season: breeding = 1 April-30 June, summer/fall = 1 July-31 October, winter = 1 November-31 March; nest: success or failure in hatching, SA: subarea (Bodie Hills, Parker, Long Valley), age class: yearling or adult

[b] K = number of parameters

Table 3.4 Comparison of the top model for female greater sage-grouse monthly survival identified in stage 1 of model selection with an equivalent model that includes a term representing genetic diversity for each individual using the reduced data set that contained only genetically sampled females from the Bi-State Distinct Population Segment in Mono County, California, USA from 2007-2011 to determine if genetic diversity influences survival.

Model[a]	K[b]	AIC_c	ΔAIC_c	Model weight	Deviance
season + Yr	7	377.896	0.000	0.676	363.818
season + Yr + HL	8	379.367	1.472	0.324	363.268

[a] season: breeding = 1 April-30 June, summer/fall = 1 July-31 October, winter = 1 November-31 March; HL: homozygosity by loci metric (Aparicio et al. 2006) measure of genetic diversity

[b] K = number of parameters

Table 3.5 Beta estimates, standard errors, and lower and upper 95% confidence intervals for the 3 models with an ΔAIC_c value < 2 from the set of candidate models explaining monthly survival rates for female greater sage-grouse in the Bodie Hills, Parker, and Long Valley subareas (SA) in the Mono County, California, USA portion of the Bi-State Distinct Population Segment during 2007-2011.

				95% CI	
Model[a]	**Parameter**[b]	**Estimate**	**SE**	**Lower**	**Upper**
season + Yr					
	$\beta_{Intercept}$	2.616	0.363	1.905	3.328
	β_{2008}	-0.633	0.391	-1.400	0.133
	β_{2009}	0.261	0.564	-0.844	1.365
	β_{2010}	-0.091	0.487	-1.046	0.864
	β_{2011}	1.529	1.063	-0.554	3.612
	$\beta_{Summer/Fall}$	0.874	0.370	0.150	1.599
	β_{Winter}	1.158	0.418	0.339	1.976
season + Yr + nest					
	$\beta_{Intercept}$	2.577	0.366	1.859	3.294
	β_{2008}	-0.696	0.400	-1.479	0.088
	β_{2009}	0.207	0.568	-0.905	1.319
	β_{2010}	-0.142	0.492	-1.105	0.822
	β_{2011}	1.496	1.064	-0.589	3.580
	$\beta_{Hatched\ nest}$	0.243	0.331	-0.406	0.892
	$\beta_{Summer/Fall}$	0.874	0.370	0.149	1.598
	β_{Winter}	1.167	0.418	0.348	1.986
season + Yr + SA					
	$\beta_{Intercept}$	2.770	0.406	1.974	3.567
	β_{2008}	-0.669	0.392	-1.437	0.099
	β_{2009}	0.012	0.582	-1.129	1.152
	β_{2010}	-0.203	0.492	-1.167	0.761
	β_{2011}	1.414	1.065	-0.674	3.501
	$\beta_{Long\ Valley}$	-0.243	0.314	-0.858	0.372
	β_{Parker}	0.811	0.773	-0.704	2.327
	$\beta_{Summer/Fall}$	0.862	0.371	0.135	1.589
	β_{Winter}	1.091	0.419	0.270	1.912

[a] season: breeding = 1 April-30 June, summer/fall = 1 July-31 October, winter = 1 November-31 March, nest: success or failure in hatching

[b] the estimate for the $\beta_{Intercept}$ parameter models the influence of the breeding season and the year 2007, and when applicable, a failed nest or the Bodie Hills sub area

Table 3.6 Number of female greater sage-grouse (yearling/adult) monitored during the 2007-2011 breeding seasons in the Bodie Hills, Parker, and Long Valley subareas in the Mono County, California portion of the Bi-State Distinct Population Segment.

Year	Bodie Hills	Parker	Long Valley	Total
2007	13 (12/1)	0 (0/0)	13 (10/3)	26 (22/4)
2008	18 (5/13)	1 (1/0)	21 (2/19)	40 (8/32)
2009	18 (9/9)	5 (1/4)	15 (7/8)	38 (17/21)
2010	12 (0/12)	3 (0/3)	13 (0/13)	28 (0/28)
2011	12 (0/8)	2 (0/2)	8 (2/6)	18 (2/16)
Total	69 (26/43)	11 (2/9)	70 (21/49)	150 (49/101)

Table 3.7 Nest initiation rate for yearling and adult greater sage-grouse in the Bodie Hills, Parker, and Long Valley subareas in the Mono County, California portion of the Bi-State Distinct Population Segment from 2007-2011.

	Yearling			Adult		
Year	Initiation Rate (%)	Initial Nests	Monitored	Initiation Rate (%)	Initial Nests	Monitored
2007	22.7	5	22	100.0	4	4
2008	75.0	6	8	90.6	29	32
2009	88.2	15	17	95.2	20	21
2010	100.0	3	3	100.0	25	25
2011	100.0	2	2	100.0	14	14
Total	59.6	31	52	95.8	92	96

Table 3.8 Re-nesting rate for yearling and adult greater sage-grouse in the Bodie Hills, Parker, and Long Valley subareas in the Mono County, California portion of the Bi-State Distinct Population Segment from 2007-2011.

	Yearling			Adult		
Year	Re-Nesting Rate (%)	Re-Nesting Attempts	Available to Renest	Re-Nesting Rate (%)	Re-Nesting Attempts	Available to Renest
2007	0.0	0	2	0.0	0	3
2008	33.3	1	3	29.4	5	17
2009	14.3	1	7	11.1	1	9
2010	0.0	0	2	64.3	9	14
2011	0.0	0	1	54.6	6	11
Total	13.3	2	15	39.0	21	54

Table 3.9 Number of greater sage-grouse nests from the Bodie Hills, Parker, and Long Valley subareas used to model nest success in the Mono County, California portion of the Bi-State Distinct Population Segment from 2007-2011.

Year	Bodie Hills	Parker	Long Valley	Total
2007	3	0	6	9
2008	20	1	18	39
2009	17	5	15	37
2010	15	3	15	33
2011	10	3	11[a]	24
Total	65	12	54	142

[a] Two nests were from unmarked birds

Table 3.10 Apparent nest success rate and sample size (successful nests/total nests) of greater sage-grouse in the Bodie Hills, Parker, and Long Valley subareas of the Mono County, California portion of the Bi-State Distinct Population Segment that were monitored between 2007-2011.

Year	Bodie Hills	Parker	Long Valley	Total
2007	33.3% (1/3)	NA	50.0% (3/6)	44.4% (4/9)
2008	40.0% (8/20)	0.0% (0/1)	44.4% (8/18)	41.0% (16/39)
2009	64.7% (11/17)	0.0% (0/5)	66.7% (10/15)	56.8% (21/37)
2010	53.3% (8/15)	0.0% (0/3)	40.0% (6/15)	42.4% (14/33)
2011	10.0% (1/10)	0.0% (0/3)	63.6% (7/11)	33.3% (8/24)
Total	44.6% (29/65)	0.0% (0/12)	52.3 (34/65)	44.4% (63/142)

Table 3.11 Candidate models of daily survival rates for greater sage-grouse nests in the Bodie Hills, Parker, and Long Valley subareas in the Mono County, California portion of the Bi-State Distinct Population Segment during 2007-2011. Models were evaluated using the nest survival model and are ranked in ascending order based on their AIC_c values.

Model[a]	K[b]	AIC_c	ΔAIC_c	Model weight	Deviance
Time	2	553.809	0.000	0.507	549.804
Time + age class	3	555.768	1.959	0.191	549.759
Time + SA	4	557.604	3.795	0.076	549.589
Null (intercept only)	1	558.476	4.668	0.049	556.475
Time + year	6	559.319	5.510	0.032	547.289
Time + age class + SA	5	559.545	5.736	0.029	549.523
attempt	2	559.727	5.919	0.026	555.723
age class	2	560.037	6.229	0.023	556.033
age class + attempt	3	560.997	7.189	0.014	554.989
Time + age class + year	7	561.277	7.469	0.012	547.237
SA	3	561.761	7.952	0.010	555.752
SA + attempt	4	563.013	9.204	0.005	554.999
year	5	563.053	9.244	0.005	553.031
Time + year + SA	8	563.262	9.454	0.004	547.211
year + attempt	6	563.286	9.477	0.004	551.256
age class + SA	4	563.314	9.505	0.004	555.300
age class + SA + attempt	5	564.280	10.471	0.003	554.258
age class + year + attempt	7	565.122	11.314	0.002	551.082
Time + age class + SA + year	9	565.206	11.397	0.002	547.141
SA + year + attempt	8	566.217	12.409	0.001	550.165
age class + SA + year	8	568.010	14.201	0.000	551.958
age class + SA + year + attempt	9	568.072	14.264	0.000	550.007

[a] Time = linear time trend over the nesting season, age class = yearling or adult, SA = subarea (Bodie Hills, Parker, Long Valley), year = 2007-2009, attempt = initial nest or re-nesting attempt

[b] K = number of parameters

Table 3.12 Comparison of the top model identified in stage 1 of model selection for daily nest survival with an equivalent model that includes a term representing genetic diversity of the nesting greater sage-grouse hen. Nest were monitored from 2007-2011 within the Mono County, California portion of the Bi-State Distinct Population Segment.

Model[a]	K[b]	AIC_c	ΔAIC_c	Model weight	Deviance
Time	2	473.771	0.000	0.683	469.766
Time + HL	3	475.310	1.538	0.317	469.299

[a] Time = linear time trend over the nesting season, ; HL: homozygosity by loci metric (Aparicio et al. 2006) measure of genetic diversity
[b] K = number of parameters

Table 3.13 Beta estimates, standard errors, and lower and upper 95% confidence intervals for the 2 models with a ΔAIC_c value < 2 from the set of candidate models explaining the daily survival rate for greater sage-grouse nests in the Bodie Hills, Parker, and Long Valley subareas (SA) in the Mono County, California, USA portion of the Bi-State Distinct Population Segment during 2007-2011.

				95% CI	
Model[a]	Parameter	Estimate	SE	Lower	Upper
Time	$\beta_{Intercept}$	4.271	0.300	3.683	4.860
	β_{Time}	-0.019	0.007	-0.032	-0.005
Time + age class					
	$\beta_{Intercept}$	4.246	0.321	3.617	4.875
	β_{Time}	-0.018	0.007	-0.032	-0.004
	$\beta_{age\ class}$	0.063	0.297	-0.519	0.645

[a] Time = linear trend of time over nesting season, age class = yearling or adult (Beta estimates are for the yearling age class)

Table 3.14 Number of broods and apparent brood survival to 30 and 60 days for greater sage-grouse broods in the Bodie Hills and Long Valley subareas within Mono County, California between 2009-2011.

	Bodie Hills			Long Valley			Total		
Year	**Broods**	**30-d**	**60-d**	**Broods**	**30-d**	**60-d**	**Broods**	**30-d**	**60-d**
2009	11	82%	82%	10	70%	30%	21	76%	52%
2010	8	100%	38%	6	100%	66%	14	100%	50%
2011	1	0%	0%	5	60%	60%	6	50%	50%
Total	20	85%	60%	21	76%	47%	41	80%	51%

APPENDICES

Appendix A: Online Supplementary Material From "A Multi-method Evaluation of Connectivity in a Threatened Distinct Population Segment of Greater Sage-Grouse

PCR and Genotyping

The loci used were developed from sage-grouse (SGCA5, SGCA9; Taylor et al. 2003), capercaillie (*Tetrao urogallus*; TUD1, TUD3, TUD4, TUT3, TUT4; Segelbacher et al. 2000), black grouse (*Tetrao tetrix*; TTD1, TTD2, TTD6, TTT1; Caizergues et al. 2001, BG6, BG14, BG15, BG16; Piertney & Höglund 2001, TTT3; Caizergues et al. 2003), red grouse (*Lagopus lagopus*; LLSD8; Piertney & Dallas 1997), turkey (*Meleagris gallopavo*; RHT0094, Burt et al. 2003), and domestic chicken (*Gallus gallus*; ADL230; Cheng et al. 1995) (Table S2.1). When amplifying noninvasive genetic samples (NGS), which were the fecal and feather samples, we also included the avian sex identification locus developed by Kahn et al. (1998; hereafter Kahn) in the multiplex reactions (Table S2.1). For all PCR reactions we included positive and negative control samples to test for amplification and contamination, respectively.

All multiplex PCR reactions contained 3.50 µL of 1x Qiagen master mix, 0.70 µL 0.5x Q-solution, 1 µL DNA, dye-labeled primers (Table S2.1), and the necessary amount of molecular-grade water so that each well contained a total volume of 7.00 µL. The temperature cycles for all multiplexes started with an initial denaturing step of 95°C for 15 min and subsequent denaturing steps of 94°C for 30 s. All multiplex reactions also had elongation steps of 1 min where the temperature was held at 72°C and a final elongation step where the temperature was held at 60°C for 60 min.

For Multiplex 1 the annealing steps were 90 s. Starting at 56°C, we used 11 touchdown cycles with 1°C increments followed by an additional 31 and 37 cycles for blood and NGS, respectively, with an annealing temperature of 45°C. For Multiplex 2 annealing steps were 90 s. Starting at 60°C, we used 11 touchdown cycles with 0.3°C increments

followed by an additional 19 and 35 cycles for blood and NGS samples, respectively, with an annealing temperature of 57°C. For Multiplex 3 annealing steps were 90 s. Starting at 65°C, we used 11 touchdown cycles with 1°C increments followed by an additional 30 and 37 cycles for blood and NGS samples, respectively, with an annealing temperature of 55°C. For Multiplex 4, which was only used for NGS samples, the annealing steps were 90 s. Starting at 61°C, we used 11 touchdown cycles with 0.8°C increments followed by an additional 37 cycles with an annealing temperature of 53°C. For Multiplex 5, which was also only used for NGS samples, the annealing steps were 135 s. Starting at 61°C, we used 11 touchdown cycles with 1.0°C increments followed by an additional 40 cycles with an annealing temperature of 50°C.

We separated the PCR products by size using an Applied Biosystems 3130xl sequencer (Applied Biosystems, Foster City, California) and scored them using the associated GeneMapper 3.7 software. Because noninvasively collected samples have an increased potential for allelic dropout and false alleles (Taberlet et al. 1999, Waits & Paetkau 2005), we required an allele to be observed in 3 PCR replicates if it was homozygous or twice if it was heterozygous. We considered blood to produce high-quality DNA and therefore accepted the genotype after only 1 run. The probability of identity between siblings statistic ($P_{(ID)}$sibs; Waits et al. 2001), calculated using GenAlEx 6.41 (Peakall & Smouse 2006), indicated we needed a minimum of 8 loci to obtain a < 0.01 probability of siblings having identical genotypes. Therefore, we removed samples in which we could not obtain a consensus genotype for at least 8 loci. GenAlEx6.41 (Peakall & Smouse 2006) was used to compare and match genotypes from all samples that were retained.

Partial Mantel Tests

The straight-line distance between each pair of leks was measured using proximity tools in ArcGIS 10 (ESRI, Redlands, CA) and lek pairs were considered to be separated by a barrier if an unsuitable habitat (e.g. forested areas or large bodies of water) bisected the line along which distance was measured. The barrier matrix was populated with a binary variable to account for the presence or absence of putative barriers with the other two matrices containing the values for linearized pairwise F_{ST} and the logarithm of pairwise geographic distances (Rousset 1997).

Hierarchical Evanno Method

Since the Evanno method typically identifies the highest hierarchical level of genetic structure as the optimal K-value (Evanno et al. 2005), we identified further substructure by splitting the data into the number of clusters recommended, assigning individuals to each cluster based on their highest proportion of inferred ancestry (q-value), and then re-analyzing each cluster separately using the parameters previously described. We repeated this process until most individuals had a 50-50 split in ancestry when K = 2, indicating there was no further substructure (Pritchard et al. 2010), or until the maximum log likelihood occurred at K = 1.

Assignment Test Run Parameters

With BayesAss3, we used 10,000,000 MCMC iterations, sampling the chain every 100 steps after a 1,000,000 step burn-in. We set the mixing parameters for the migration rate (m), allele frequency (a), and inbreeding coefficient (f) to 0.12, 0.40, and 0.35, respectively, resulting in acceptance rates along the chain between 20% and 60%, thereby increasing the likelihood that the chains converged (Rannala 2007). To diagnose potential convergence

problems and to ensure the chains were not getting stuck at local optima, we conducted 5 independent runs and evaluated the consistency of the results. Under the POPINFO option in program STRUCTURE, we set GENSBACK = 1 and the MIGPRIOR = 0.05. Using these settings we conducted 5 independent runs consisting of 500,000 MCMC iterations and a 100,000 step burn-in with K = 5. With GENECLASS2 we used the frequency-based assignment method (Paetkau et al. 1995) with both the L_home/L_max and L_home likelihood computations. We used the default frequency of 0.01 for missing alleles and calculated P-values using the Monte Carlo resampling algorithm (Paetkau et al. 2004).

Results of Hierarchical Evanno Method

Level 1

Using the run parameters for program STRUCTURE described in the body of the paper we found $\Delta K = 2$ when all samples from a known lek of origin were included in the analysis (Fig. S2.1). This first split produced one group of birds whose origins were mainly from Jackass, Wheeler-Burcham, Bodie Hills, and Parker (Cluster 2.1) and another group with birds mainly from Granite Mountain and Long Valley (Cluster 2.2; Fig. S2.2).

Level 2

Running STRUCTURE with the birds that were placed in the Jackass, Wheeler-Burcham, Bodie Hills, and Parker group (Cluster 2.1) resulted in $\Delta K = 2$ (Fig. S2.3). This produced one group of birds whose origins were mainly from the Bodie Hills (Cluster 3.1) and a second group of birds whose origins mainly included Jackass, Wheeler-Burcham, and Parker (Cluster 3.2; Fig. S2.4). Running STRUCTURE with birds from the Granite Mountain and Long Valley (Cluster 2.2) resulted in $\Delta K = 3$ (Fig. S2.5). While the structure plot of K = 3 (Fig. S2.6) shows the birds from Granite Mountain constitute their own cluster, most birds

from Long Valley showed ancestry values that were split between the remaining two clusters in roughly equal proportions, suggesting the data were over-split. Structure plots showing K = 2 were also over-split (data not shown), and therefore, we determined Granite Mountain and Long Valley represented one cluster.

Level 3

Running STRUCTURE with the birds that were placed in the Bodie Hills cluster (Cluster 3.1) resulted in the maximum log likelihood occurring at K = 1 (Fig. S2.7), indicating there was no further structure. Therefore, we determined the Bodie Hills represented one cluster. Running STRUCTURE with the birds from Jackass, Wheeler-Burcham, and Parker that were placed into cluster 3.2 resulted in $\Delta K = 2$ (Fig. S2.8). One group consisted of birds primarily from Jackass and Wheeler-Burcham and the other group consisted of birds mainly from Parker (Fig. S2.9). When running STRUCTURE with each of these cluster separately, we found, despite each resulting in $\Delta K = 2$, that neither had any further subdivision based on the structure plots for K = 2 which showed most individuals were symmetrically assigned to each of the two possible clusters, indicating the data were over split (data not shown). Therefore, the final two clusters with our STRUCTURE analysis consisted of a group with birds mostly from the Jackass and Wheeler-Burcham subareas (the Fales genetic population) and a group with birds mostly from the Parker subarea.

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Supplementary Tables and Figures

Table S2.1 Locus name and primer concentration (µM; blood/NGS) for each multiplex used to amplify 19 microsatellite markers and 1 sex identification locus for greater sage-grouse samples collected in Mono County, California, 2007-2012.

Multiplex 1	Multiplex 2	Multiplex 3	Multiplex 4	Multiplex 5
ADL230 (0.071/0.100)	Kahn (NA/0.171)	BG6 (0.021/0.057)	BG16 (NA/0.038)	ADL230 (NA/0.077)
BG14 (0.129/0.129)	TUD1 (0.057/0.029)	RHT0094 (0.047/0.043)	Kahn (NA/0.069)	BG14 (NA/0.154)
BG15 (0.071/0.071)	TUD3 (0.086/0.029)	TTD1 (0.036/0.057)	TTD1 (NA/0.015)	BG15 (NA/0.069)
BG16 (0.143/0.143)	TUD4 (0.429/0.043)	TTD2 (0.041/0.071)	TUT3 (NA/0.010)	BG6 (NA/0.069)
LLSD8 (0.029/0.143)	TUT3 (0.029/0.021)	TTD6 (0.027/0.057)	TUT4 (NA/0.017)	LLSD8 (NA/0.023)
SGCA5 (0.086/0.129)	TUT4 (0.043/0.021)	TTT1 (0.043/0.071)		RHT0094 (NA/0.077)
SGCA9 (0.086/0.129)		TTT3 (0.071/0.086)		SGCA5 (NA/0.115)
				SGCA9 (NA/0.092)
				TTD2 (NA/0.115)
				TTD6 (NA/0.031)
				TTT1 (NA/0.069)
				TTT3 (NA/0.046)
				TUD1 (NA/0.023)
				TUD4 (NA/0.085)

Table S2.2 Pairwise F_{ST} (lower diagonal) and distance (km; upper diagonal) between greater sage-grouse leks in Mono County, California, 2007-2012. Bold numbers indicate significance after B-Y FDR[a] correction ($p < 0.0093$) and italicized numbers indicate significance at $p < 0.05$.

Subarea	Jackass	Wheeler-Burcham		Bodie Hills						Granite Mt.	Parker	Long Valley				
Lek	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. Jackass	--	19.2	24.8	35.5	43.8	48.4	48.5	46.1	49.5	84.4	75.8	100.3	106.7	110.5	112.9	114.1
2. Burcham	**0.067**	--	5.7	30.7	39.4	40.9	38.9	33.5	38.0	73.4	60.8	87.6	93.8	97.5	100.3	101.0
3. Wheeler	**0.099**	0.000	--	30.2	38.3	39.0	36.3	29.9	34.7	69.8	56.1	83.4	89.5	93.2	96.1	96.7
4. Big Flat	**0.026**	**0.088**	**0.105**	--	8.8	13.1	14.9	17.9	18.2	49.8	46.3	66.5	73.2	76.8	79.0	80.5
5. Dry Lakes	**0.015**	**0.108**	**0.118**	0.000	--	7.7	12.5	19.5	17.5	43.3	43.6	60.6	67.3	70.9	72.7	74.5
6. Racetrack	**0.050**	**0.100**	**0.109**	0.000	0.000	--	5.6	14.2	10.8	36.8	35.9	65.7	60.4	64.0	66.0	67.6
7. Beiderman	**0.081**	**0.128**	**0.134**	0.003	0.008	0.000	--	8.9	5.2	35.9	31.7	52.0	58.6	62.3	64.6	66.0
8. Highway	**0.074**	**0.084**	**0.087**	0.000	**0.033**	0.010	0.012	--	5.0	39.9	30.2	54.6	60.9	64.7	67.3	68.2
9. Bridgeport Canyon	**0.071**	**0.127**	**0.121**	0.009	0.010	0.010	0.008	0.004	--	35.5	28.2	50.8	57.2	60.9	63.4	64.5
10. Granite Mt.	**0.157**	**0.235**	**0.224**	**0.155**	**0.171**	**0.200**	**0.185**	**0.192**	**0.154**	--	23.2	17.6	24.2	27.7	29.4	31.3
11. Parker	**0.120**	**0.138**	**0.156**	**0.109**	**0.100**	**0.133**	**0.154**	**0.130**	**0.140**	**0.205**	--	23.2	34.5	38.1	41.3	41.4
12. LV9	**0.154**	**0.231**	**0.219**	**0.147**	**0.170**	**0.182**	**0.194**	**0.163**	**0.145**	**0.106**	**0.196**	--	6.7	10.3	12.7	13.9
13. LV8	**0.065**	**0.172**	**0.178**	**0.091**	**0.134**	**0.148**	**0.169**	**0.138**	**0.129**	**0.124**	**0.176**	*0.016*	--	3.7	6.8	7.3
14. LV1	**0.083**	**0.197**	**0.191**	**0.130**	**0.156**	**0.192**	**0.199**	**0.161**	**0.166**	**0.114**	**0.179**	0.012	0.000	--	3.6	3.6
15. LV4	**0.063**	**0.187**	**0.175**	**0.087**	**0.104**	**0.132**	**0.144**	**0.116**	**0.100**	**0.092**	**0.172**	0.000	0.000	0.000	--	3.3
16. LV2	**0.122**	**0.211**	**0.201**	**0.128**	**0.160**	**0.181**	**0.184**	**0.156**	**0.154**	**0.088**	**0.190**	0.005	*0.011*	0.000	0.002	--

[a]Benjamini-Yekutieli False Discovery Rate significance correction for multiple comparisons (Benjamini & Yekutieli 2001)

Table S2.3 Comparison of expected heterozygosity for greater sage-grouse between data collected in Mono County, California during 2007-2012 (in bold) and the 44 populations reported by Oyler-McCance et al. (2005). Data sorted in ascending order by mean expected heterozygosity.

			Expected Heterozygosity				
Population	State/Province	N	SGCA5	SGCA9	LLSD8	ADL0230	Mean
Douglas/Grant	WA	21	0.07	0.58	0.09	0.73	0.37
Yakima	WA	29	0.07	0.62	0.41	0.58	0.42
Blue Mountain	UT	18	0.55	0.72	0.57	0.62	0.62
Mono County	**CA**	**267**	**0.76**	**0.43**	**0.66**	**0.72**	**0.64**
Lyon/Mono[a b]	NV/CA	68	0.78	0.42	0.69	0.68	0.64
Wayne	UT	27	0.59	0.83	0.49	0.70	0.65
Strawberry Valley	UT	23	0.77	0.77	0.57	0.58	0.67
Warner	OR	22	0.83	0.28	0.77	0.83	0.68
Churchill	NV	19	0.79	0.63	0.65	0.69	0.69
North Park	CO	22	0.79	0.77	0.64	0.61	0.70
Wagontire	OR	22	0.85	0.49	0.76	0.78	0.72
Bighorn	WY	20	0.77	0.61	0.68	0.83	0.72
Harding	SD	26	0.54	0.88	0.78	0.69	0.72
Washoe	NV	22	0.81	0.64	0.75	0.70	0.73
Lasson	CA	55	0.74	0.64	0.79	0.74	0.73
Rich	UT	31	0.82	0.82	0.67	0.61	0.73
Slope	ND	36	0.66	0.88	0.71	0.69	0.74
Diamond	UT	27	0.79	0.87	0.58	0.70	0.74
Riddle	ID	25	0.78	0.72	0.69	0.76	0.74
Box Elder	UT	31	0.82	0.81	0.60	0.75	0.75
Owyhee	OR	25	0.78	0.69	0.67	0.84	0.75
Nye	NV	23	0.79	0.81	0.71	0.67	0.75
Middle Park	CO	21	0.87	0.85	0.57	0.71	0.75
Magic Valley	ID	31	0.76	0.76	0.71	0.78	0.75
Sheldon	NV	23	0.81	0.72	0.68	0.81	0.76
Humboldt	NV	24	0.80	0.73	0.71	0.79	0.76
Kemmerer	WY	21	0.84	0.80	0.70	0.70	0.76
Alberta	AB	36	0.77	0.91	0.67	0.69	0.76
Whitehorse	OR	18	0.81	0.74	0.75	0.74	0.76
Cold Springs	CO	30	0.84	0.75	0.69	0.77	0.76
Valley	MT	29	0.66	0.91	0.76	0.72	0.76
Beattys Butte	OR	24	0.75	0.74	0.77	0.79	0.76
Eagle	CO	26	0.80	0.84	0.64	0.77	0.76
Curlew Valley	ID	19	0.87	0.78	0.75	0.70	0.78

Table S2.3 continued

Steens	OR	22	0.79	0.73	0.78	0.80	0.78
Bowman	ND	24	0.69	0.87	0.79	0.75	0.78
Weston	WY	20	0.70	0.84	0.78	0.78	0.78
Blue Mountain	CO	25	0.83	0.84	0.65	0.80	0.78
Farson	WY	25	0.87	0.80	0.64	0.81	0.78
Rosebud	MT	25	0.78	0.90	0.73	0.71	0.78
Fergus	MT	30	0.76	0.88	0.78	0.72	0.79
Rawlins	WY	20	0.85	0.84	0.73	0.74	0.79
Medicine Lodge	ID	36	0.85	0.86	0.73	0.72	0.79
Phillips	MT	19	0.80	0.93	0.73	0.74	0.80
Beaverhead	MT	19	0.88	0.87	0.75	0.73	0.81
Elko	NV	22	0.85	0.85	0.75	0.81	0.82

[a] Lyon/Mono is synonymous with Bi-State area

[b] Expected heterozygosity in the Bi-State area reported by Oyler-McCance et al. (2005)

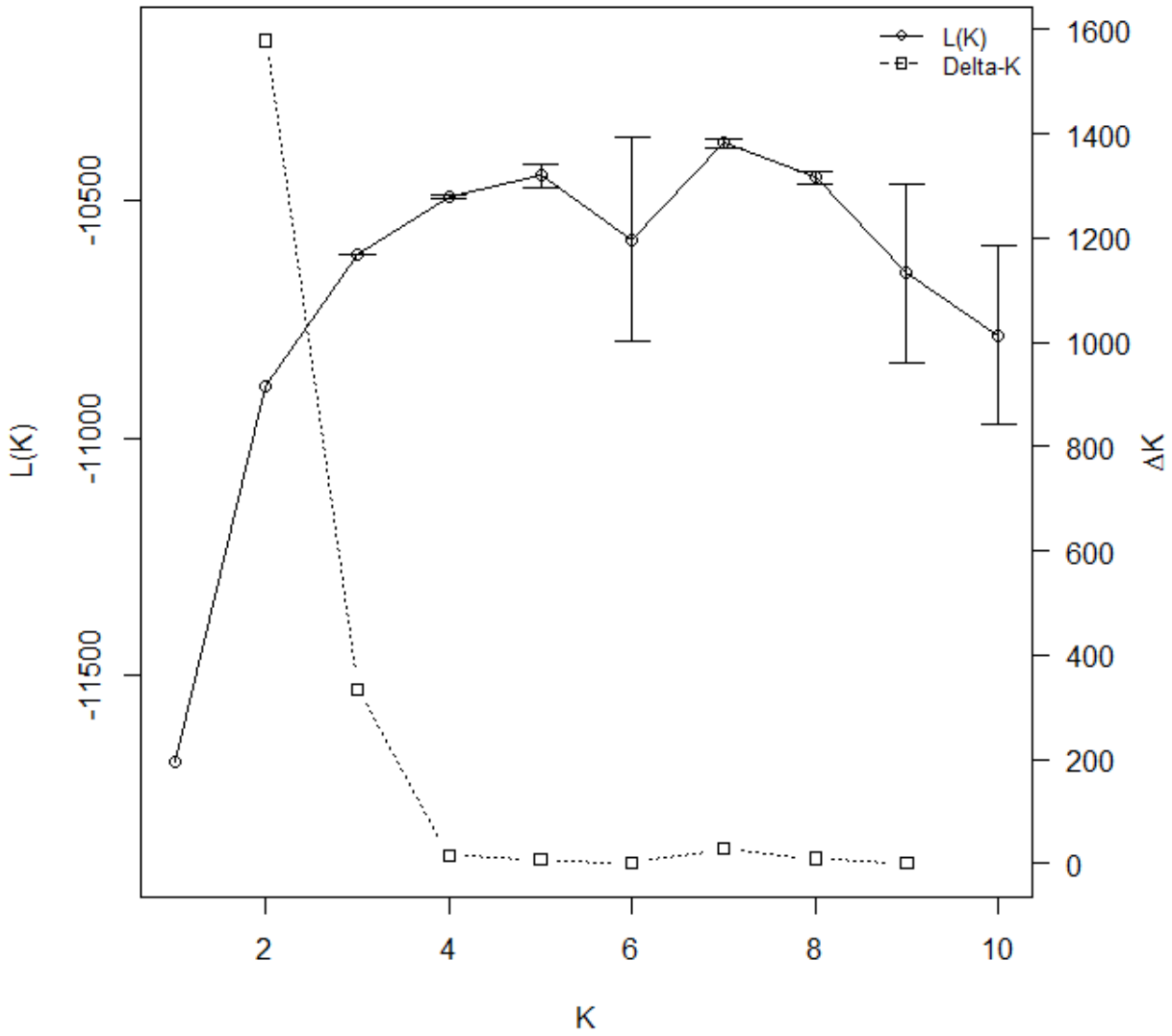

Fig. S2.1 The mean log likelihood of K (L(K)) and rate of change for the log likelihood of K (ΔK) using K = 1-10 for the STRUCTURE analysis containing all greater sage-grouse samples collected from a known lek of origin in Mono County, California between 2007 – 2012

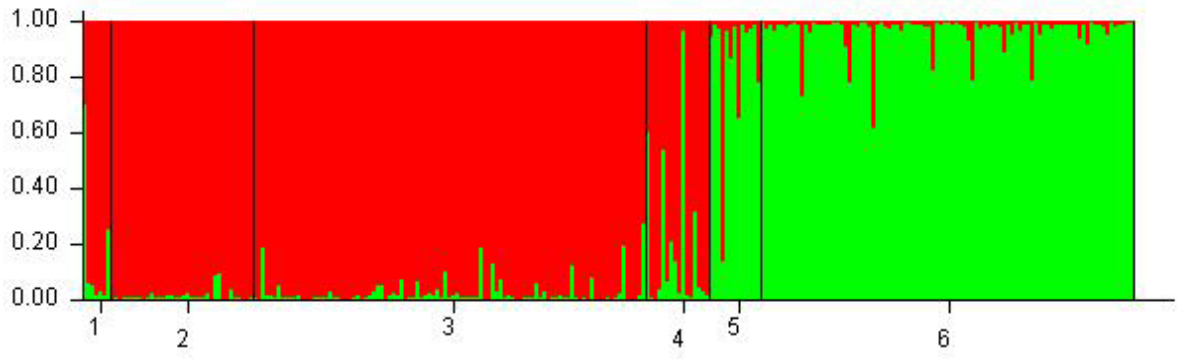

Fig. S2.2 STRUCTURE plot of K = 2 for all greater sage-grouse samples collected from a known lek of origin in the 1) Jackass, 2) Wheeler-Burcham, 3) Bodie Hills, 4) Parker, 5) Granite Mountain, and 6) Long Valley subareas of Mono County, California between 2007-2012. Each bar represents a unique individual and different colors indicate the proportion of ancestry belonging to each of the 2 clusters

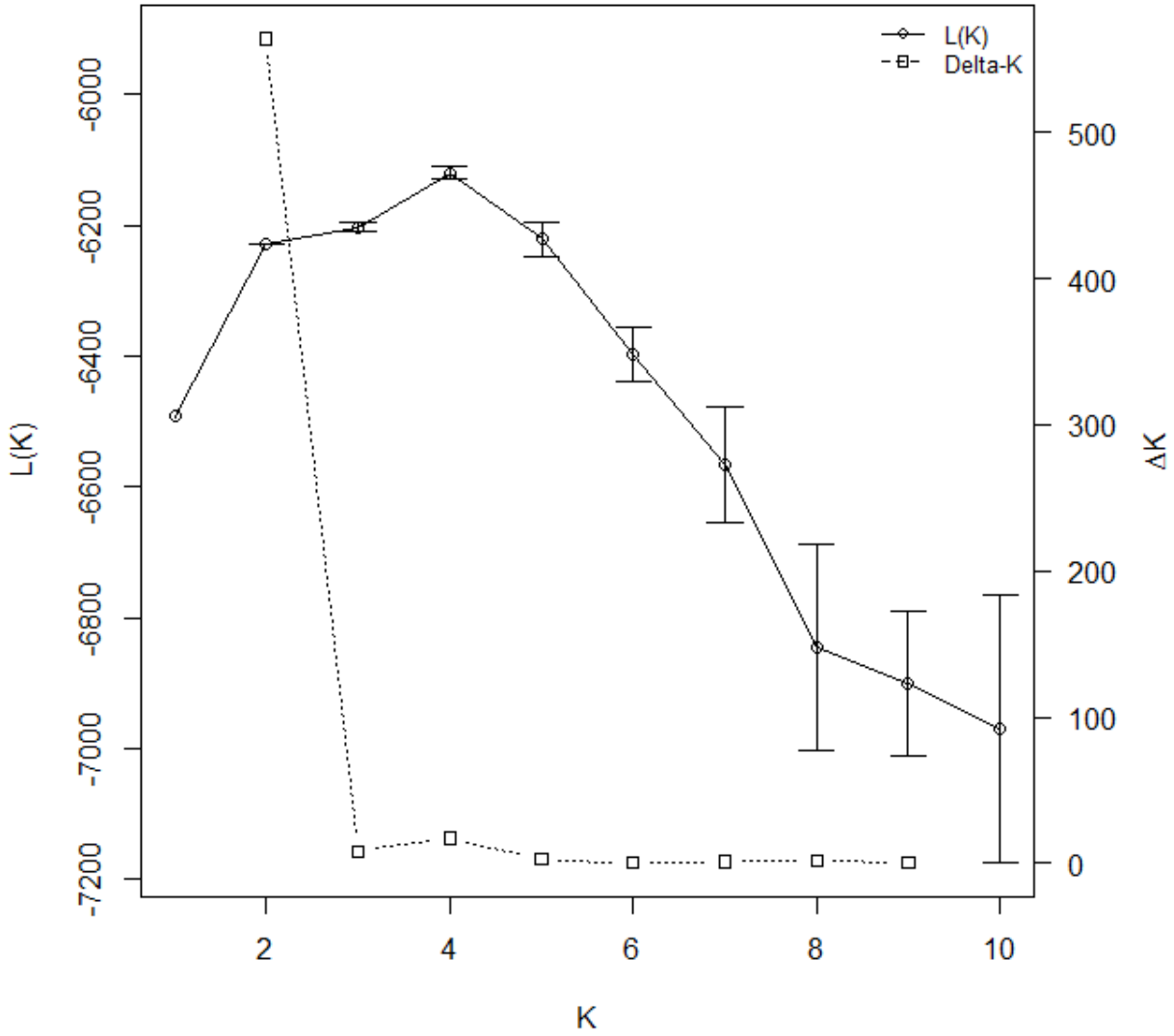

Fig. S2.3 The mean log likelihood of K (L(K)) and rate of change in the log likelihood of K (ΔK) using K = 1-10 for the STRUCTURE analysis of greater sage-grouse from Mono County, California assigned to Cluster 2.1. Cluster 2.1 includes samples from the Jackass, Wheeler-Burcham, Bodie Hills, and Parker subareas collected between 2007-2012

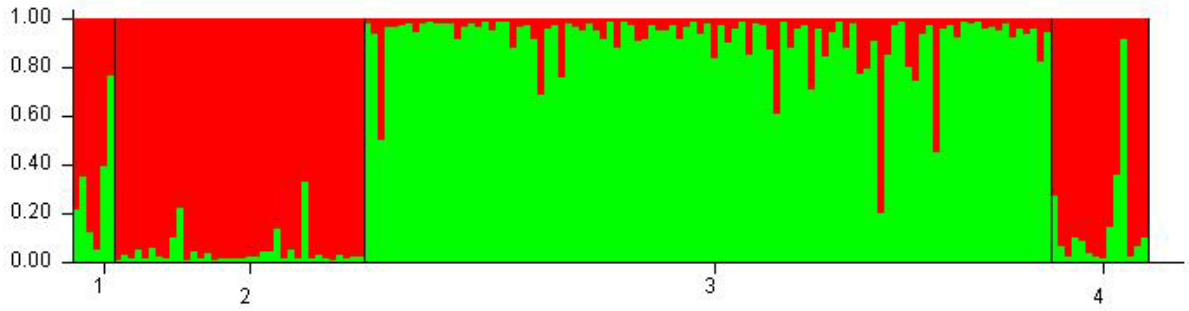

Fig. S2.4 STRUCTURE plot of K = 2 for greater sage-grouse assigned to Cluster 2.1, which includes samples from the 1) Jackass, 2) Wheeler-Burcham, 3) Bodie Hills, and 4) Parker subareas of Mono County, California collected between 2007-2012. Each bar represents a unique individual and different colors indicate the proportion of ancestry belonging to each of the 2 clusters. Cluster 3.1 (shown in green) includes mostly birds from the Bodie Hills and Cluster 3.2 (shown in red) includes mostly birds from Jackass, Wheeler-Burcham, and Parker

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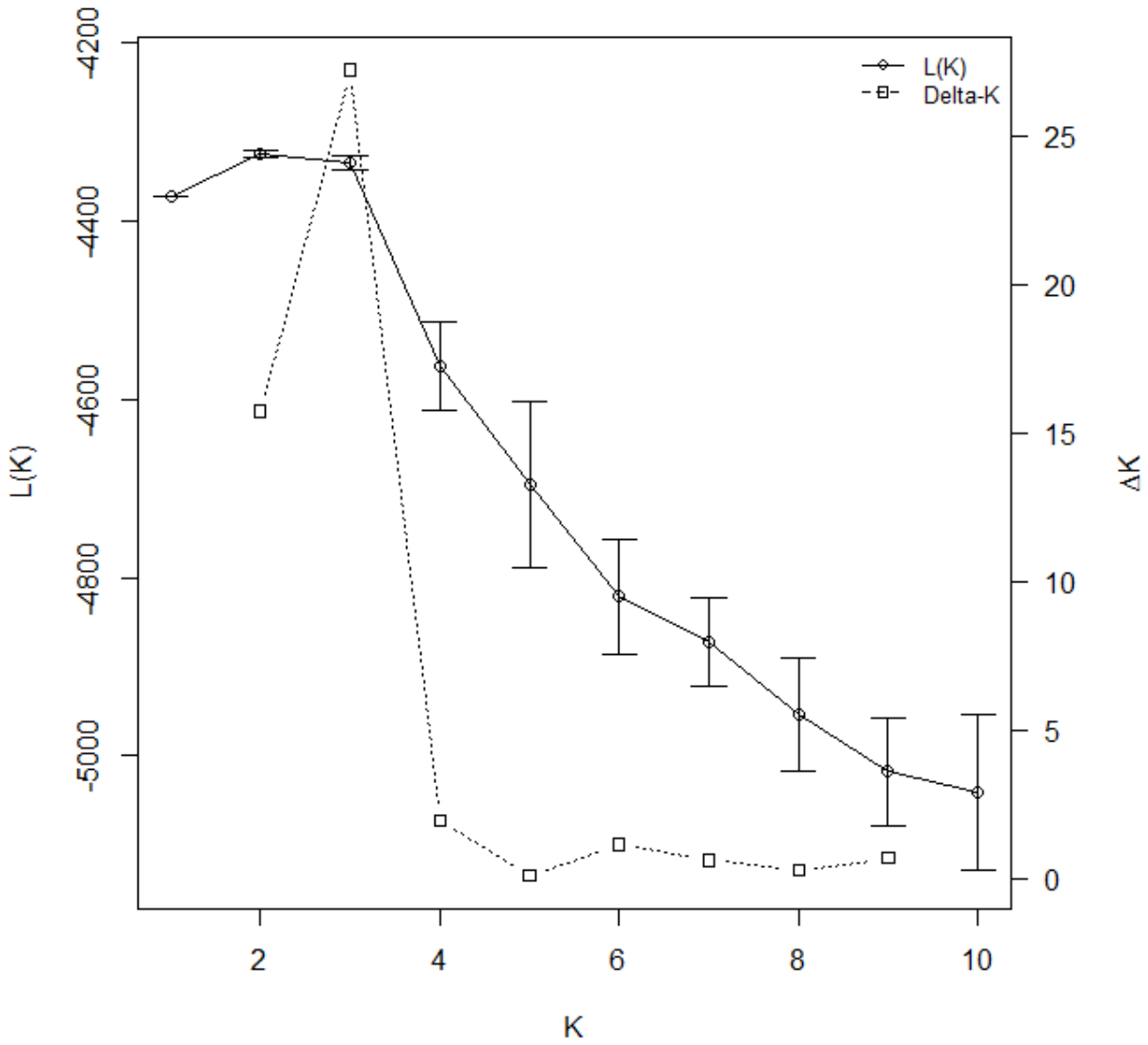

Fig. S2.5 The mean log likelihood of K (L(K)) and rate of change in the log likelihood of K (ΔK) using K = 1-10 for the STRUCTURE analysis of greater sage-grouse from Mono County, California assigned to Cluster 2.2. Cluster 2.2 primarily includes samples from the Granite Mountain and Long Valley subareas collected between 2007-2012

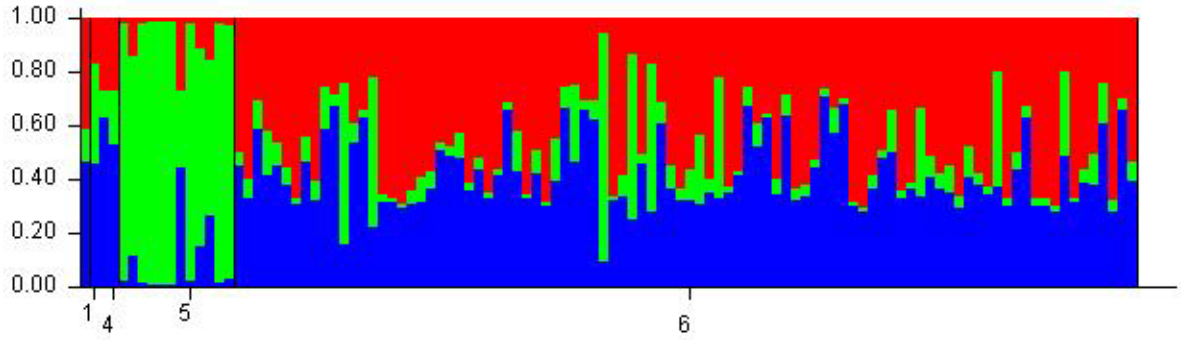

Fig. S2.6 STRUCTURE plot of K = 3 for greater sage-grouse assigned to Cluster 2.2 which includes samples from the 1) Jackass, 4) Parker, 5) Granite Mountain, and 6) Long Valley subareas of Mono County, California collected between 2007-2012. Each bar represents a unique individual and different colors indicate the proportion of ancestry belonging to each of the 3 clusters

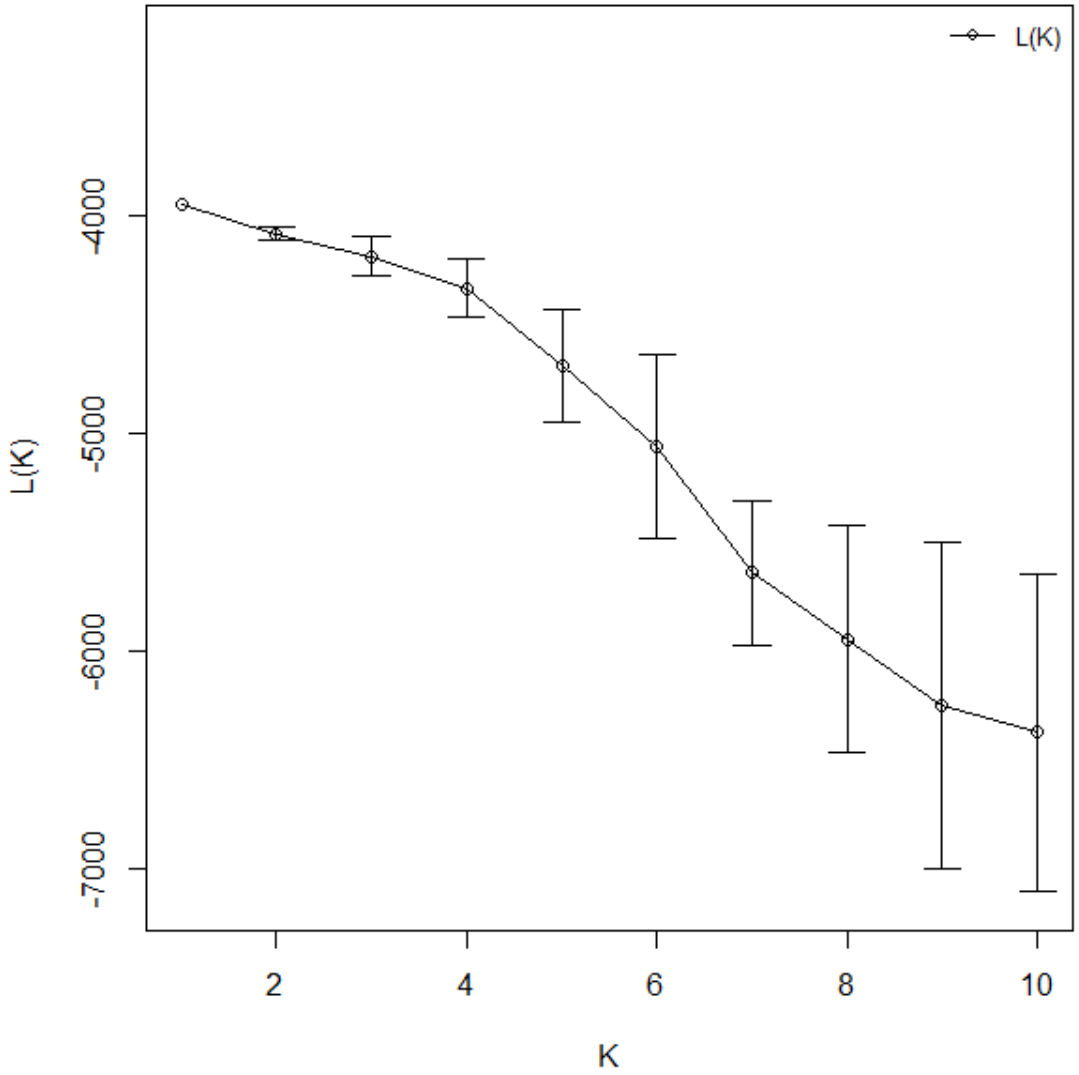

Fig. S2.7 The mean log likelihood of K (L(K)) using K = 1-10 for the STRUCTURE analysis of greater sage-grouse from Mono County, California assigned to Cluster 3.1. Cluster 3.1 primarily includes samples from the Bodie Hills subarea collected between 2007-2012

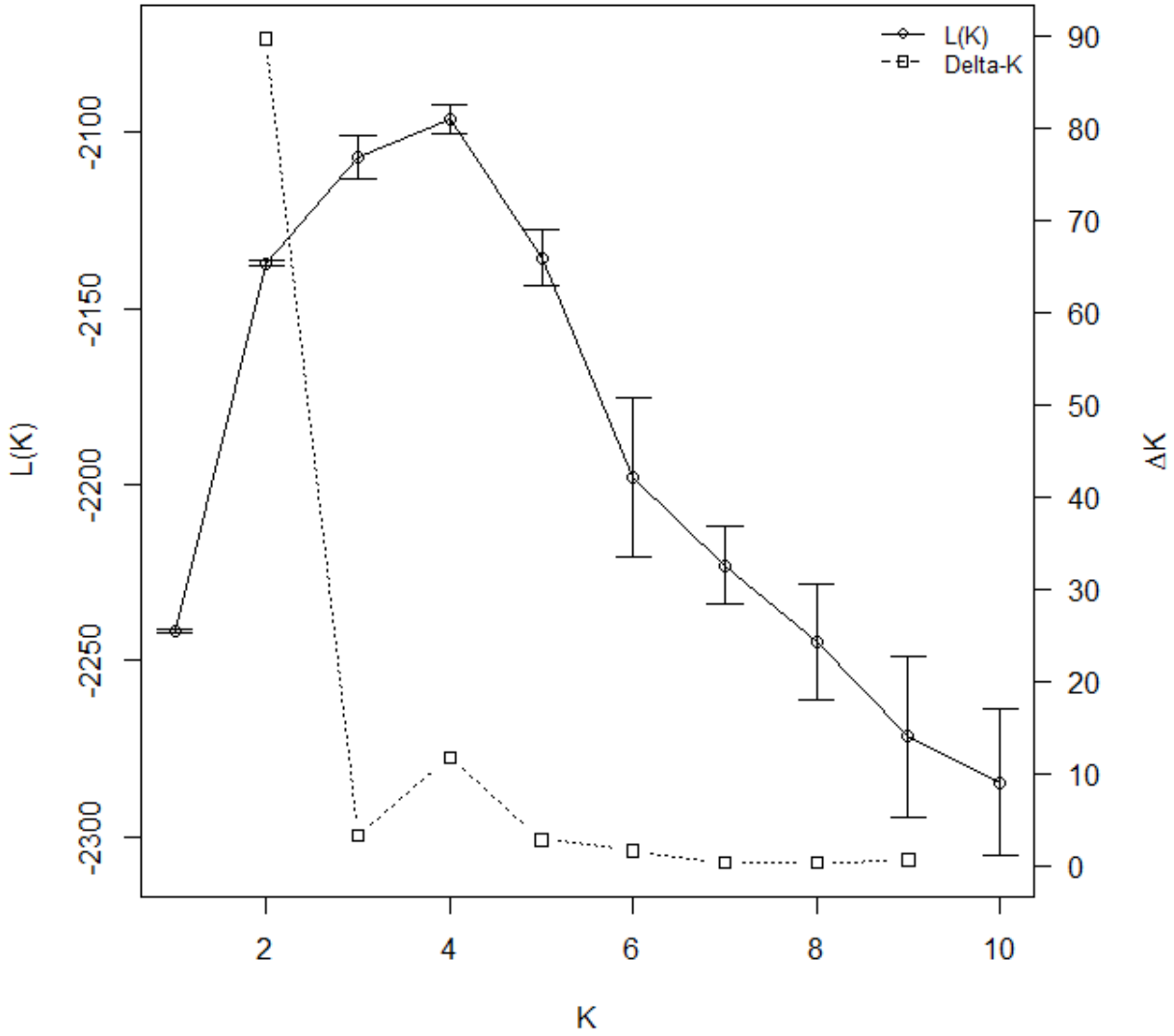

Fig. S2.8 The mean log likelihood of K (L(K)) and rate of change in the log likelihood of K (ΔK) using K = 1-10 for the STRUCTURE analysis of greater sage-grouse from Mono County, California assigned to Cluster 3.2. Cluster 3.2 primarily includes samples from the Jackass, Wheeler-Burcham, and Parker subareas collected between 2007-2012

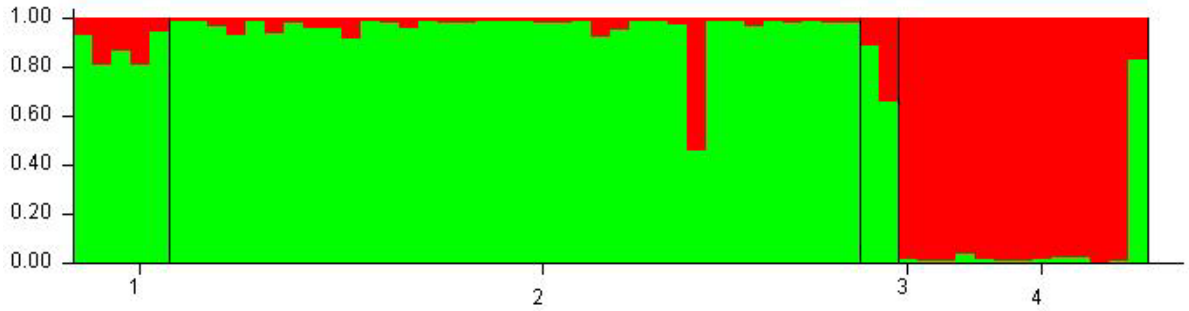

Fig. S2.9 STRUCTURE plot of K = 2 for greater sage-grouse from Mono County, California assigned to cluster 3.2, which included samples from the 1) Jackass, 2) Wheeler-Burcham, 3) Bodie Hills and 4) Parker subareas collected between 2007 – 2012. Each bar represents a unique individual and different colors indicate the proportion of ancestry belonging to each of the 2 clusters

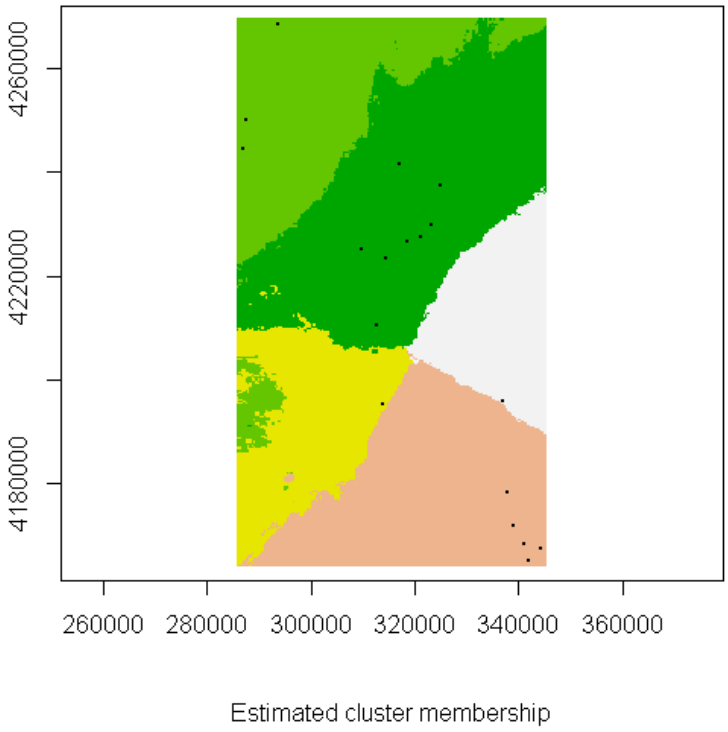

Fig. S2.10 GENELAND map of population membership illustrating genetic subdivision for greater sage-grouse in Mono County, California with black dots representing leks sampled between 2007–2012 and different colored polygons representing the different genetic clusters for K = 5. The populations are as follows: 1) Fales (Jackass and Wheeler-Burcham subareas) = light green, 2) Bodie Hills = dark green, 3) Granite Mountain = beige, 4) Parker = yellow, and 5) Long Valley = salmon

Appendix B: Animal Care and Use Protocol

Reese. Kerry
From: campusvet@uidaho.edu
Sent: Thursday, February 25,20101:37 PM
To: Reese, Kerry
Cc: Office of Sponsored Programs Univ of Idaho - Post Award; West, Michael; Austin, Marilyn
Subject: Protocol 2010-35 - Population Dynamics, Habitat Use and Dispersal of Greater Sage-Grouse in California - an Extension to Investigate Spatial GenetiCS of the Mono Population

University of Idaho
Animal Care and Use Committee

Date: Thursday, February 25,2010
To: Kerry Reese
From: University of Idaho
Re: Protocol 2010-35
Population Dynamics, Habitat Use and Dispersal of Greater Sage-Grouse in California - an Extension to Investigate Spatial Genetics of the Mono Population

Your animal care and use protocol for the project shown above was reviewed by the University ofIdaho on Thursday, February 25, 2010.

> This protocol was originally submitted for review on: Thursday, January 07, 2010
> The original approval date for this protocol is: Thursday, February 25,2010
> This approval will remain in affect until: Friday, February 25,2011
> The protocol may be continued by annual updates until: Monday, February 25, 2013

Federal laws and guidelines require that institutional animal care and use committees review ongoing projects annually. For the first two years after initial approval of the protocol you will be asked to submit an annual update form describing any changes in procedures or personnel. The committee may, at its discretion, extend approval for the project in yearly increments until the third anniversary of the original approval of the project. At that time, the protocol must be replaced by an entirely new submission.

Brad Williams, DVM
Campus Veterinarian
University of Idaho
208-885-8958