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RESEARCH ARTICLE

Genetic structure of Greater Sage-Grouse (*Centrocercus urophasianus*) in a declining, peripheral population

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ABSTRACT

Loss of suitable habitat and subsequent fragmentation of populations are recognized as important factors in the decline and extinction of many species because they result in smaller, more isolated populations with reduced genetic diversity. The Greater Sage-Grouse (*Centrocercus urophasianus*), having declined in distribution and abundance throughout its range, is a candidate species under the U.S. Endangered Species Act and a species of special concern in California. Because the relationships between dispersal, gene flow, and genetic structure are interrelated and affect the long-term persistence of Greater Sage-Grouse, we assessed the genetic structure and patterns of dispersal among Greater Sage-Grouse in a declining, peripheral population in northeastern California. We genotyped 19 microsatellite loci from 167 individuals from 13 leks and 20 individuals captured off lek. Greater Sage-Grouse in northeastern California appear to maintain gene flow and genetic diversity across the sampled region. Despite population declines and habitat loss, leks were not genetically differentiated. Our results showed significant isolation-by-distance among males, which suggests that male Greater Sage-Grouse are more philopatric than females. Spatial autocorrelation analysis revealed stronger spatial structuring for males than for females. Results from the corrected assignment index also confirmed female-biased dispersal, although differences between sexes were not significant. While more research is needed on the proximate and ultimate causes behind the patterns we observed, our results serve as an important step toward understanding genetic structure and patterns of sex-biased dispersal in Greater Sage-Grouse occupying the periphery of the species' geographic distribution.

Keywords: Centrocercus urophasianus, genetic structure, Greater Sage-Grouse, dispersal, isolation-by-distance

Estructura genética de *Centrocercus urophasianus* en una población periférica en disminución

RESUMEN

Se reconoce que la pérdida de hábitat adecuado y la subsiguiente fragmentación de las poblaciones son factores importantes en la disminución y extinción de muchas especies, ya que dan como resultado poblaciones más pequeñas y aisladas, con una diversidad genética reducida. La distribución y la abundancia de *Centrocercus urophasianus* han disminuido a través de su rango y como resultado la especie es considerada como especie candidato bajo la Ley de Especies Amenazadas de EEUU, y es considerada como especie de atención especial en California. Debido a que las relaciones entre dispersión, flujo génico y estructura genética están interrelacionadas y afectan la persistencia a largo plazo de *C. urophasianus*, evaluamos la estructura genética y los patrones de dispersión de los individuos de *C. urophasianus* en una población periférica en disminución en el noreste de California. Tipificamos el genotipo de 19 loci microsatelitales de 167 individuos provenientes de 13 asambleas de cortejo y de 20 individuos capturados afuera de las asambleas de cortejo. Los individuos de *C. urophasianus* en el noreste de California parecen mantener el flujo génico y la diversidad genética a lo largo de la región de muestreo. A pesar de la disminución poblacional y la pérdida de hábitat, las asambleas de cortejo no se diferenciaron genéticamente. Nuestros resultados mostraron un aislamiento por distancia significativo entre los machos, sugiriendo que los machos de *C. urophasianus* son más filantrópicos que las hembras. Los análisis de autocorrelación espacial revelaron una estructuración espacial más fuerte para los machos que para las hembras. Los resultados del índice corregido de asignación también confirmaron una dispersión sesgada de las hembras, aunque las diferencias entre sexos no fueron significativas. Se necesitan investigaciones adicionales sobre las causas directas e indirectas detrás de los patrones que observamos; sin embargo, nuestros resultados son un paso importante hacia el entendimiento de la estructura genética y los patrones de dispersión sesgados por sexo de los individuos de *C. urophasianus* que ocupan la periferia de la distribución geográfica de la especie.

Palabras clave: aislamiento por distancia, *Centrocercus urophasianus*, dispersión, estructura genética

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INTRODUCTION

Loss of suitable habitat and subsequent fragmentation of populations are recognized as important factors in the decline and extinction of many species because they result in smaller, more isolated populations with reduced genetic diversity (Frankham et al. 2002). One potential consequence of habitat fragmentation is decreased genetic variation in isolated populations, which are often marked by a reduction in fitness, loss of heterozygosity, and reduced allelic variation (Nei et al. 1975, Allendorf 1986). The consequences of small, isolated populations are particularly important in populations on the fringe of a species' distribution. Peripheral populations exhibit lower genetic variation than populations from the core of the species' distribution because they are subject to colonization and founder effects, which increase the potential for genetic drift and inbreeding depression (Lesica and Allendorf 1995).

Historically, the range of Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") closely paralleled the distribution of sagebrush (*Artemisia* spp.) ecosystems of western North America (Beetle 1960, Schroeder et al. 2004). However, sage-grouse populations have declined throughout much of the species' range (Connelly and Braun 1997, Braun 1998, Schroeder et al. 2004), mainly as a result of alterations in habitats (Crawford et al. 2004) and anthropogenic habitat loss and fragmentation (Braun 1986, Lyon and Anderson 2003, Johnson et al. 2011, Knick and Hanser 2011, Wisdom et al. 2011). In response to its declining abundance and distribution, the sage-grouse was listed as "warranted but precluded" under the U.S. Endangered Species Act, and it remains a candidate for federal listing (U.S. Department of Interior 2010; 75FR:13910–14014).

Sage-grouse occupy the western edge of their distribution in northeastern California, USA. Although little published information is available on sage-grouse population trends in northeastern California (Garton et al. 2011), invasions of western juniper (*Juniperus occidentalis*) and exotic annual grasses such as cheatgrass (*Bromus tectorum*) and medusahead rye (*Taeniatherum caput-medusa*) have resulted in loss and degradation of sagebrush communities and are considered the primary reason for the population decline and range contraction of sage-grouse in northeastern California (Davis 2012) over the past 35 yr (Connelly et al. 2004, Schroeder et al. 2004, Shuford and Gardali 2008). Furthermore, results from an analysis of factors associated with extirpation of sage-grouse suggest that populations in northeastern California have a higher risk of extinction than larger populations within the core of the species' distribution (Wisdom et al. 2011).

Populations that have undergone large decreases in size, such as sage-grouse in northeastern California, are more likely to lose genetic variation (Nei et al. 1975, Maruyama and Fuerst 1985). Although not documented in sage-grouse populations in northeastern California, a loss in genetic diversity could be associated with inbreeding and a reduction in fitness (Westemeier et al. 1998, Bouzat et al. 2009). Resistance to disease and the ability of populations to respond to stochastic events might also decrease with the loss of genetic variation (Lacy 1997). Thus, loss of genetic variation could negatively affect the long-term viability of sage-grouse populations in northeastern California.

Microsatellite loci can provide measures of genetic variation within sage-grouse populations in northeastern California relevant to our understanding of population genetic structure and gene flow. Measures of genetic variation allow evaluation of the degree to which small and scattered populations have lost genetic diversity. Although management of wildlife species has traditionally been based on demographic data, the use of molecular markers has been increasingly accepted as a tool for describing dispersal and to complement demographic studies (DeWoody 2005, DeYoung and Honeycutt 2005). Dispersal is of particular interest in conservation genetics because it results in gene flow. Gene flow not only affects the rate of genetic drift and the expression of deleterious alleles, it shapes the genetic structure of populations (Hanski and Gilpin 1997, Frankham et al. 2002).

Ideally, methods that integrate genetic and demographic data will enhance our understanding of the role of dispersal in sage-grouse population structure. However, traditional demographic studies (e.g., mark–recapture and telemetry studies) are spatially and temporally restricted, with limited ability to detect long-distance dispersal among populations (Koenig et al. 1996), which leads to discrepancies between genetic and demographic estimates of dispersal distances. While direct measures of movement provide data on the within-population component of dispersal, indirect measures of genetic variation within and among populations can be used to infer long-term patterns of gene flow. Therefore, genetic-based estimates provide information about dispersal integrated over larger spatial and temporal scales than can be obtained from behavioral data.

Several studies have documented significant population genetic structure of sage-grouse occupying fragmented landscapes (e.g., Oyler-McCance et al. 2005, 2015, Bush et al. 2011, Schulwitz et al. 2014). Sage-grouse in northeastern California have experienced similar isolation and reduction in population size resulting from habitat loss (Davis 2012), which appears to have split sage-grouse populations into smaller, loosely connected lek complexes where connectivity is unknown. At current population levels and distribution, our expectation was that move-

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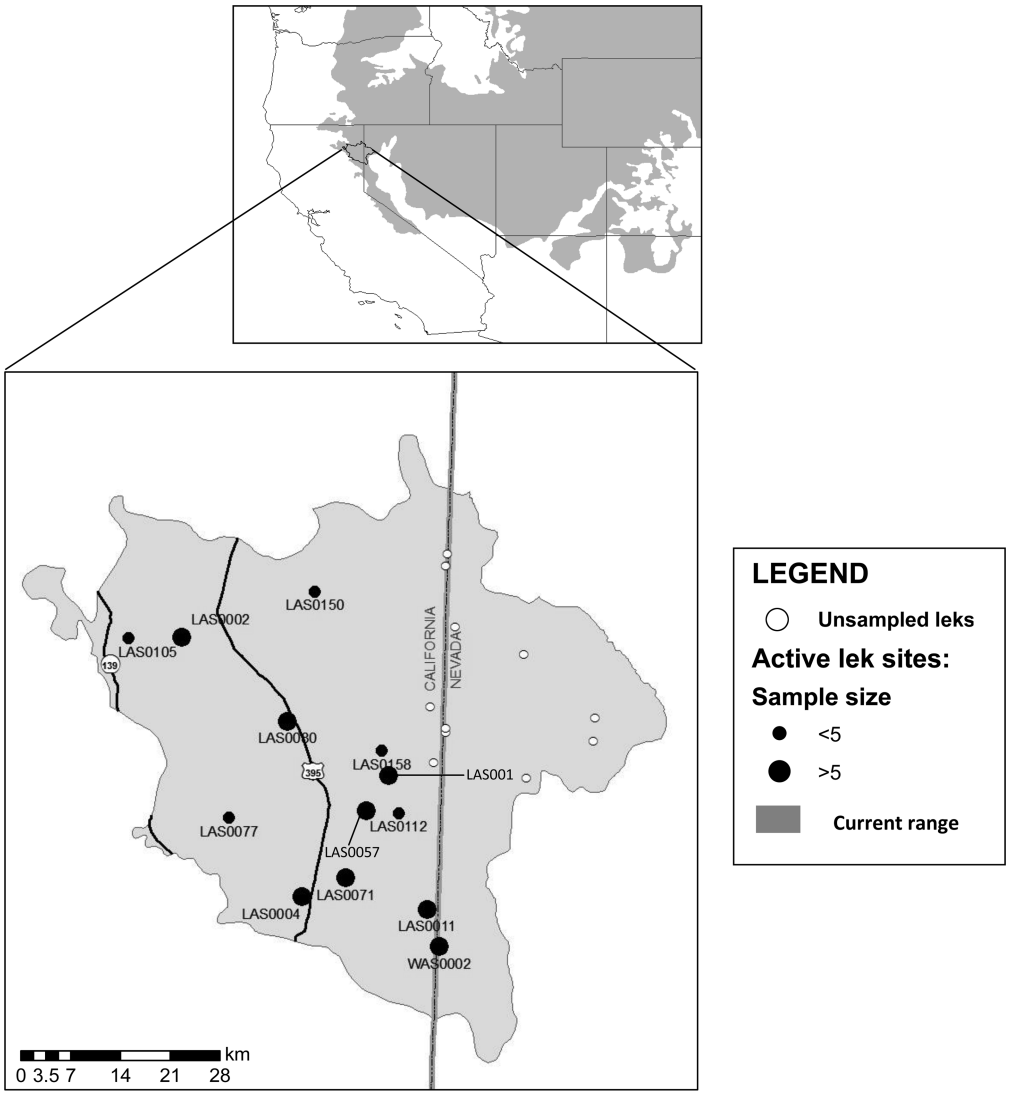


FIGURE 1. Sampled Greater Sage-Grouse leks (black circles; $n = 13$) in northeastern California, USA. Leks LAS0105 and LAS0150 each contained <5 males in 2007, became inactive in 2008, and remained abandoned through 2009.

ment between leks would be necessary to facilitate population persistence and genetic variability.

A range-wide genetic survey of sage-grouse found that gene flow is likely limited to movements by sage-grouse between geographically adjacent populations and not likely the result of long-distance movements of individuals between non-neighboring populations (Oyler-McCance et al. 2005). However, the connectivity of habitats suitable for sage-grouse has not been studied in northeastern California, and little is known about the population genetic structure or how sage-grouse respond to habitat fragmentation. Because dispersal, gene flow, and genetic structure are interrelated and affect the long-term persistence of sage-grouse, the objective of our study was to examine the genetic structure in this population. Specifically, we address the following questions: (1) What is the population genetic structure of sage-grouse in northeastern California? (2) What is the degree (if any) of sex-specific relatedness within leks? (3) Is there evidence for any sex-specific differences in dispersal?

METHODS

Study Area

We assessed population genetic structure in a 466,703-ha region of sagebrush-steppe habitat that included portions of the Buffalo-Skedaddle Population Management Unit (PMU) in northeastern California, extending east to the Nevada border (Figure 1). The predominant sagebrush types included Wyoming big sagebrush (*A. tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), and little sagebrush (*A. arbuscula*). Slightly more than 46% of

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TABLE 1. Location of Greater Sage-Grouse genetic samples collected in northeastern California, USA, 2007–2009. "Autumn capture" refers to samples collected off lek, which could not be assigned to any lek site. Data for these individuals were not used in any lek-specific analysis.

Lek	Mean number of males lek^{-1} (2007–2009)	Number of genetic samples		
		Female	Male	Total
LAS0077	23	1	0	1
LAS0004	21	9	12	21
LAS0071	44	14	14	28
LAS0011	43	3	13	16
WAS0002	64	8	14	22
LAS0080	15	11	9	20
LAS0012	15	1	0	1
LAS0057	21	11	13	24
LAS0001	23	3	3	6
LAS0158	25	1	1	2
LAS0105	4	1	0	1
LAS0002	41	4	20	24
LAS0150	2	1	0	1
Autumn capture	NA	20	0	20
Total		88	99	187

potential sagebrush habitat within our study area had a high percentage of cheatgrass or western juniper invasion. Approximately 19% of the sagebrush ecosystem within our study area had crossed the threshold to being dominated by cheatgrass or juniper woodlands (Armentrout and Hall 2005). The study area was predominantly public lands (>60%) administered by the Bureau of Land Management; the primary land use was domestic livestock grazing, including both sheep and cattle. Other land uses included agricultural crops, primarily irrigated alfalfa (*Medicago* spp.).

Tissue Collection

We captured sage-grouse opportunistically, on or near leks, using spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) from March through April 2007–2009 (Table 1). We classified sex and age of captured birds by plumage characteristics (Crunden 1963, Dalke et al. 1963). We collected blood samples from 167 sage-grouse (99 males, 68 females) captured on 13 known, active lek sites within the Buffalo-Skedaddle PMU (Figure 1). Two of 13 leks (LAS0105, LAS0150) were inactive by 2008 and remained abandoned through 2009.

We collected ~3 drops of blood from a clipped hallux nail and then stored the sample in Queen's lysis buffer (Seutin et al. 1991) or a microfuge tube previously coated with EDTA (Oyler-McCance et al. 1999). When possible, approximately equal numbers of males and females were sampled at each lek. Additional sage-grouse ($n = 20$) were captured off lek during the late summer and autumn of 2007 and 2008. Because sampling juveniles can reduce the ability of genetic tests to detect sex-biased dispersal (Prugnolle and de Meeus 2002), we included only yearling and adult birds in our analyses.

Capture locations spanned the breadth of our study area, and we attempted to acquire a random sample of individuals for the entire area. We do not suggest that leks represent separate populations. Rather, as a consequence of their lek mating system, we consider lek sites well suited to accurately represent unique sample groups (e.g., Row et al. 2015). Thus, for the purposes of our analyses, we assumed that the distribution of lek sites we sampled was a representative sample of the breeding population in northeastern California. All birds sampled off lek ($n = 20$) were assigned an "unknown" lek status. Samples from birds captured off lek were retained in population-level estimates of genetic diversity (i.e. when all leks were analyzed together) but were not used in any lek-specific analyses, including spatial autocorrelation analysis. We included leks with low samples sizes ($n < 5$ individuals sampled) in population-level estimates of genetic diversity, but only data from leks with ≥5 individuals sampled ($n = 8$ leks) were retained for lek-specific analysis. There was no evidence to suggest that significant changes to demographic parameters (e.g., nest initiation rate, apparent nest success, clutch size, renesting rate, brood success, and survival) occurred during the 3-yr sampling period (Davis 2012), which could potentially alter allele frequency, so samples were combined across all years. Individual sage-grouse were marked with a numbered aluminum leg band at capture to ensure that blood samples collected across different years did not include duplicate samples.

DNA Extraction and Microsatellite Genotyping

DNA was extracted using DNeasy Tissue Kits (Qiagen, Germantown, MD, USA), following manufacturer's protocols and incorporating modifications from Bush et al. (2005). We genotyped individuals at 19 polymorphic microsatellite loci originally developed for the Domestic Chicken (*Gallus gallus*; ADL230; Cheng et al. 1995), Wild Turkey (*Meleagris gallopavo*; RHT0094; Burt et al. 2003), sage-grouse (SGCA9-2, SGCA5; Taylor et al. 2003), and other grouse species, including Eurasian Capercaillie (*Tetrao urogallus*; TUT3, TUT4, TUD1, TUD3, TUD4; Segelbacher et al. 2000), Black Grouse (*T. tetrix*; BG6, BG14, BG15, BG16 [Piertney and Höglund 2001]; TTD1, TTD2, TTD6, TTT1 [Caizergues et al. 2001]; TTT3 [Caizergues et al. 2003b]), and Red Grouse (*Lagopus lagopus scoticus*; LLSD8; Piertney and Dallas 1997).

We divided the polymerase chain reactions (PCRs) into 3 multiplex panels using the Qiagen Multiplex PCR kit (7-μL total volume) containing 119 ng μL of DNA as described by Thompson (2012). Multiplex 1 consisted of primers ADL230, BG14, BG15, BG16, LLSD8, SGCA5, and SGCA9-2. Multiplex 2 consisted of primers TUD1, TUD3, TUD4, TUT3, and TUT4. Multiplex 3 consisted of primers

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BG6, RHT0094, TTD1, TTD2, TTD6, TTT1, and TTT3. Cycling was performed using a PTC-240 DNA Engine Tetrad 2 Peltier Thermal Cycler, following Thompson (2012): initial denaturation of 95°C for 15 min, followed by 11 cycles touchdown at 94°C for 30 s, annealing while stepping down from 60°C to 47°C for 90 s, elongation at 72°C for 1 min, followed by 27 cycles of denaturing (20 and 31 cycles for Multiplexes 2 and 3, respectively) at 94°C for 30 s, 45°C (annealing at 47°C and 55°C for Multiplexes 2 and 3, respectively) for 90 s, and 72°C for 60 s, and a final 60-min elongation at 60°C. Amplification products were run against an LIZ 500 size standard on an ABI 3130xl automated sequencer (Applied Biosystems, Foster City, California). We used GENEMAPPER version 3.7 (Applied Biosystems), followed by visual inspection and verification, to genotype all samples. Genotyping errors (e.g., the presence of null alleles, scoring errors due to stuttering, and allelic dropout) were checked across all loci using Micro-Checker version 2.2.3 (van Oosterhout et al. 2004).

Genetic Diversity, Differentiation, and Gene Flow

To investigate genetic diversity within and between lek sites, we calculated expected (H_E) and observed (H_O) heterozygosity for each locus and tested for deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium using GENEPOP (Raymond and Rousset 1995; http://wbiomed.curtin.edu.au/genepop/). The significance level was adjusted for the number of comparisons with Bonferroni (Dunn-Šidák) techniques (Ury 1976). Genetic variability at each lek site was assessed using allele frequency data from which the number of alleles per locus (A) and the inbreeding coefficient (F_{IS}) were calculated using GenAlEx version 6.3 (Peakall and Smouse 2006); and allelic richness (AR), which corrects for sample-size differences, was determined using FSTAT version 2.9.3 (Goudet 2001). We calculated F_{ST} using Weir and Cockerham's (1984) estimator. To investigate population genetic structure, pairwise F_{ST} estimates (Weir and Cockerham 1984) were obtained from GENEPOP. To assess genetic variability among leks, we compared AR, H_O, F_{IS}, and F_{ST} in FSTAT using 1,000 permutations and 2-sided tests.

To investigate spatial genetic structure within northeastern California, we used the Bayesian program STRUCTURE version 2.3.3 (Pritchard et al. 2000), which infers the optimal number of genetic clusters (K) from the multilocus genotypes without prior population information. We performed 10 independent simulations for different values of K (1–13) with 100,000 burn-in iterations and 1 million data repetitions, using no prior information and assuming an admixture model. We assessed the most likely number of clusters by estimating the log probability of the data $\Pr(X|K)$, from the 10 independent runs against K to identify the most likely number of true populations from our dataset (Pritchard et al. 2000).

Relatedness

We computed the average within-lek relatedness (R) for males and females separately in SPAGEDI version 1.1 (Hardy and Vekemans 2002), using the relationship coefficient of Queller and Goodnight (1989). All birds belonged to a single population ($K = 1$); therefore, we used allelic frequencies from the overall population for all analyses. Standard errors of the mean coefficients of relatedness estimates were generated by using jackknife procedures over all loci (Hardy and Vekemans 2002). To assess whether males and females were more related than expected by chance, we compared sample means to a null expectation of zero, using a 1-sample t-test (e.g., Gibson et al. 2005). To evaluate whether genetic relatedness was related to geographic distance, we tested for correlations between the pairwise genetic relatedness among lek sites and Euclidean distance, using a Mantel test (Mantel 1967).

Sex-biased Dispersal

We used 3 approaches to assess patterns of dispersal in northeastern California. First, we assessed isolation-by-distance (IBD) of males and females separately to identify sex-specific differences in dispersal. We calculated the straight-line Euclidean distance from the geographic coordinates between known, active lek sites within our study area. To test for IBD across the sampled region, we used a Mantel test (Mantel 1967) in R-PACKAGE version 4.0 (Casgrain and Legendre 2001). The patterns of IBD were analyzed by regressing pairwise estimates of $F_{ST}/(1 - F_{ST})$ against the natural logarithm of the Euclidean distance (ln km) between active lek sites (Rousset 1997). Only data from leks with samples of >5 individuals ($n = 8$ leks) were retained for all lek-to-lek analyses.

Second, we analyzed spatial genetic structure at the individual level, using a spatial autocorrelation analysis (Smouse and Peakall 1999, Peakall et al. 2003) as incorporated in GenAlEx version 6.3 (Peakall and Smouse 2006). With this method, different rates of dispersal by males and females are expected to result in stronger spatial autocorrelation among individuals of the more philopatric sex (e.g., Peakall et al. 2003). We conducted these analyses by calculating pairwise squared genetic distance and geographic matrices, which were used to generate an autocorrelation coefficient (r) for each distance class, presented as a correlogram. The autocorrelation coefficient ranges from 1 (positive autocorrelation) to −1 (negative autocorrelation), with an r value of zero indicating no spatial genetic structure. The geographic distances were calculated as the straight-line Euclidian distance between known, active lek sites.

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TABLE 2. Summary of the average genetic variability (H_O = observed heterozygosity, H_E = expected heterozygosity, A = number of alleles locus^{-1}, AR = allelic richness, F_{IS} = inbreeding coefficient, and R = average relatedness) by locus for Greater Sage-Grouse in northeastern California, USA, 2007–2009.

Locus	H_O	H_E	A	AR	F_{IS}	R
ADL230	0.701	0.741	8	7.794	0.057	−0.0054
BG14	0.791	0.865	13	12.956	0.087	−0.0054
BG15	0.615	0.604	7	6.993	−0.016	−0.0054
BG16	0.763	0.797	8	7.812	0.045	−0.0054
LLSD8	0.790	0.829	10	9.962	0.051	−0.0064
SGCA5	0.701	0.755	8	7.992	0.075	−0.0054
SGCA9-2	0.481	0.816	13	12.756	0.413	−0.0054
TUD1	0.523	0.670	8	8	0.222	−0.0067
TUD3	0.536	0.836	15	14.938	0.362	−0.0055
TUD4	0.838	0.820	16	15.769	−0.02	−0.0054
TUT3	0.685	0.701	7	6.967	0.026	−0.0055
TUT4	0.585	0.799	8	7.987	0.27	−0.0059
BG6	0.856	0.872	14	13.974	0.021	−0.0066
RHT0094	0.284	0.338	7	6.776	0.163	−0.006
TTD1	0.353	0.383	4	4	0.08	−0.006
TTD2	0.724	0.802	15	14.471	0.1	−0.0058
TTD6	0.705	0.777	12	11.902	0.096	−0.0061
TTT1	0.632	0.802	9	8.83	0.215	−0.0055
TTT3	0.681	0.796	10	9.882	0.147	−0.0063
Global mean [a]	0.644	0.737	10.11	9.997	0.126	−0.0058

[a] All leks were analyzed together for global (i.e. population-level) estimates of genetic variation.

We performed separate spatial autocorrelation analyses for males and females. Distance classes for male and female sage-grouse differed considerably in scale, and geographic distances of <20 km contained no observations of female sage-grouse (see Figure 5B). Therefore, we divided spatial distances used to assess patterns of dispersal into discrete distance classes for males (5 km) and females (20 km) separately. For each analysis, we used 1,000 permutations to test the hypothesis of no spatial genetic structure ($r = 0$) and 1,000 bootstraps to estimate 95% confidence intervals for the autocorrelation coefficient for a given geographic distance (Peakall et al. 2003). Statistical significance of the genetic autocorrelation coefficient was inferred if male or female r values fell outside the bootstrap confidence interval of the permuted data (Peakall and Smouse 2006).

Third, we calculated a separate corrected assignment index (AI) for male and female sage-grouse using the approach by Favre et al. (1997). The corrected AI calculates the probability that a genotype originated in the population (lek) from which it was sampled (Favre et al. 1997, Waser and Strobeck 1998). A negative corrected AI value indicates dispersal, whereas a positive corrected AI value implies philopatry (Mossman and Waser 1999). We tested the mean corrected AI for males versus females with a Mann-Whitney U-test (Mann and Whiney 1947).

RESULTS

Genetic Diversity, Differentiation, and Gene Flow

Sixteen of 19 loci deviated from HWE at the population level after the significance level was adjusted for multiple comparisons ($\alpha = 0.002696$). At the lek level, 9 of 247 comparisons deviated from HWE ($\alpha = 0.000337$). Five of 171 comparisons at the population level were in linkage disequilibrium, but we did not detect linkage disequilibrium between loci at the lek level after corrections for multiple comparisons. The patterns of Hardy-Weinberg and linkage disequilibrium we observed at the population level were likely a consequence of genetic substructure—occurring, in part, because of a lek mating system and potential relatedness within leks (Bush et al. 2010). Linkage disequilibrium has also been found to be linked with levels of genetic diversity and elevated levels of population structure (Li and Merilä 2011), both of which would be reflected at the lek level. Two loci (SGCA9-2 and TUD3) were out of HWE because of heterozygote deficiencies. However, there was no evidence that any locus was out of equilibrium consistently, and Micro-Checker found that the frequency of allelic dropout and null alleles was low. No loci were in disequilibrium at the lek level after adjusting for the number of comparisons ($\alpha = 0.000337$). We observed no evidence of physical linkage among loci, and there were no significant differences between the results when the tests were run with and without SGCA9-2and TUD3 (Bush et al. 2010, 2011); therefore, all loci were considered unlinked and retained for analysis.

All 19 microsatellite loci were polymorphic (Table 2), and the number of alleles ranged from 4 (TTD1) to 16 (TUD4) at the population level. The lowest number of alleles was observed in the LAS0001 lek site (but the number of individuals analyzed was small; $n = 6$), and the highest number of alleles occurred in the LAS0071 and LAS0080 lek sites (Table 3). The only significant difference observed in measures of genetic diversity between lek sites was F_{IS} (i.e. the inbreeding coefficient, $P = 0.024$) between LAS0004 and LAS0011. Additionally, the inbreeding coefficient for the LAS0011 lek was 0.173, possibly indicating a departure from random mating at this site.

Overall genetic differentiation between leks observed in our study was low and ranged from 0.002 to 0.037. Pairwise F_{ST} comparisons among lek sites did not differ significantly from zero, and there were no significant differences among the 28 pairwise values, which suggests that gene flow occurs across the sampled region. Additionally, Bayesian analysis using STRUCTURE did not indicate the presence of substructure in this sample of sage-grouse ($K = 1$), suggesting that sage-grouse in northeastern California are a single population.

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TABLE 3. Genetic diversity estimates and mean allelic patterns of Greater Sage-Grouse leks in northeastern California, USA, 2007–2009 (n = number of individuals analyzed, H_O = mean observed heterozygosity, H_E = mean expected heterozygosity, A = number of alleles per locus, AR = allelic richness, F_{IS} = inbreeding coefficient, R = average relatedness; "private alleles" are alleles that are unique to a single lek).

Lek	n	H_O	H_E	A	AR	F_{IS}	R	Number of private alleles
LAS0071	28	0.659	0.703	7.211	3.938	0.078	0.0317	0.263
LAS0004	21	0.670	0.712	6.737	4.022	0.091	0.0139	0.263
LAS0011	16	0.606	0.713	6.105	3.976	0.173	−0.0041	0.105
WAS0002	22	0.639	0.698	6.474	3.960	0.104	0.0401	0.316
LAS0057	24	0.651	0.708	6.526	4.005	0.093	0.0155	0
LAS0001	6	0.649	0.668	4.579	3.956	0.106	0.0006	0
LAS0080	20	0.672	0.721	7.263	4.157	0.090	−0.0027	0.105
LAS0002	24	0.642	0.713	6.579	3.985	0.126	0.0277	0.421

Relatedness

There was a significant negative relationship between lek-to-lek relatedness and geographic distance for all birds combined ($r = -0.656$, $P = 0.002$; Figure 2). To further assess lek genetic structure, we computed the mean coefficients of relatedness across all leks for males and females separately (Figure 3). Our results indicate that both males (mean ± SE = 0.011 ± 0.010, $t_{0.05(1),7} = 1.16$, $P = 0.28$) and females (mean ± SE = −0.012 ± 0.014, $t_{0.05(1),7} = -0.79$, $P = 0.45$) exhibited low average relatedness, which suggests that sage-grouse leks are largely assemblages of unrelated birds. For analyses by sex, we included leks with low sample sizes. Thus, variation in R within leks might be attributed to insufficient sample size (i.e. leks where <5 individuals were sampled).

Sex-biased Dispersal

We assessed IBD of males and females separately to identify sex-specific differences in dispersal (Figure 4). Isolation-by-distance was detected in males ($r = 0.656$, $P = 0.003$) but not females ($r = 0.029$, $P = 0.499$), which suggests that females disperse farther than males.

Spatial autocorrelation analysis revealed stronger spatial structuring for males than for females. Maximum distance

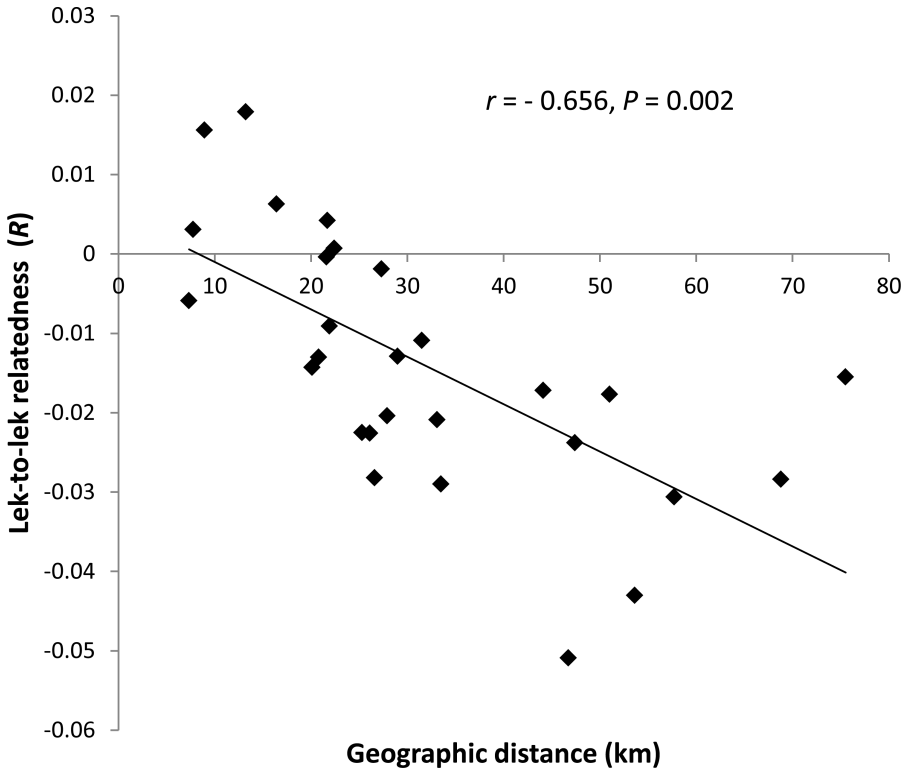


FIGURE 2. Average lek-to-lek relatedness versus geographic distance between Greater Sage-Grouse leks in northeastern California, USA, 2007–2009.

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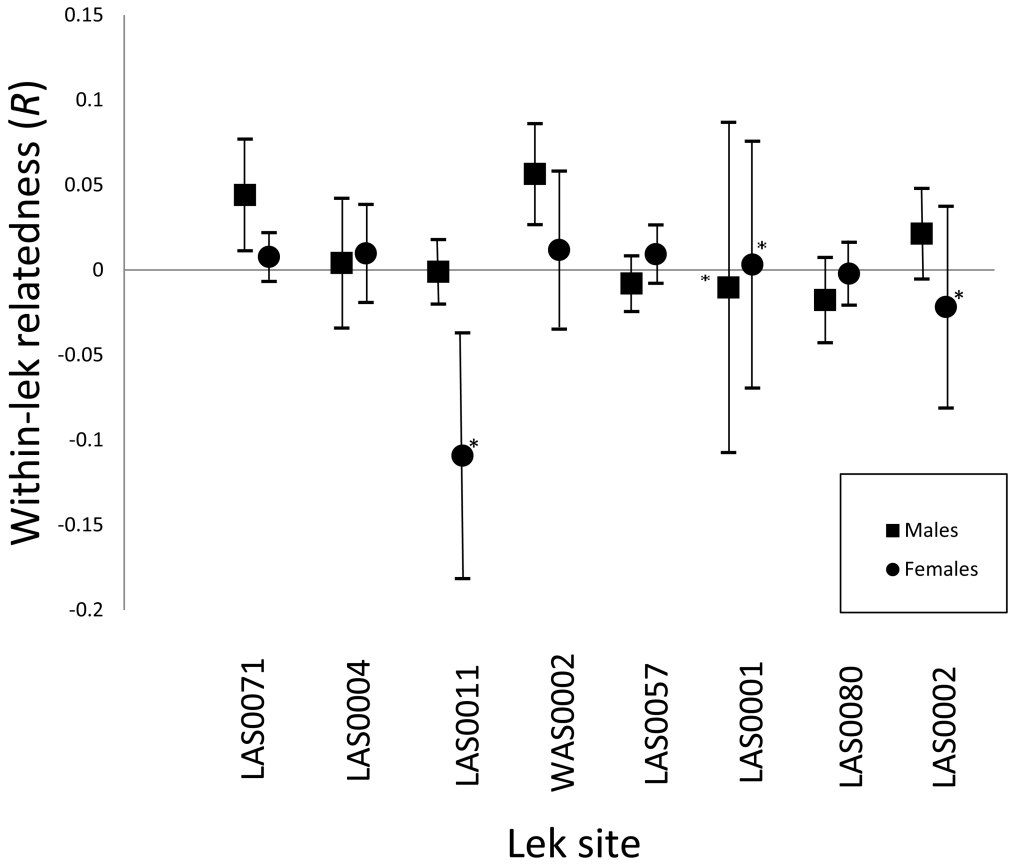


FIGURE 3. Average within-lek relatedness (*R*) for Greater Sage-Grouse leks in northeastern California, USA, 2007–2009. Within individual leks, variation in *R* might be attributed to insufficient sample size (i.e. leks where <5 individuals were sampled, denoted by asterisk). Bars indicate SE.

between known, active lek sites in our sampled region was 82 km (mean = 34.8 km ± 18.4 [SD], range: 4.6–82.1 km). Spatial autocorrelation analysis of male sage-grouse resulted in significant, positive autocorrelation coefficients within the 15-, 35-, and 75-km distances classes. This suggests that males were more genetically similar than females at distances of <35 km (Figure 5A). However, patterns of genetic structure were similar between the sexes at distances of 75–80 km. Although females had significant genetic similarities at the 80-km distance class, we failed to detect spatial genetic structure at shorter distance classes (Figure 5B).

Female-biased dispersal was also evident from the mean AI values of sage-grouse sampled from our study area. Although a significant difference between male and female sage-grouse was not detected ($P = 0.698$), males sampled across the study region had a positive mean corrected AI (0.144) in contrast to the negative mean corrected AI for females (–0.123). Negative corrected AI values indicate genotypes less likely than average to occur in the sample (i.e. it characterizes individuals with a higher probability of being immigrants). A positive corrected AI value indicates a genotype more likely than average to occur in a sample and characterizes individuals with lower probability of being immigrants (Mossman and Waser 1999). Moreover, females had proportionally more negative corrected AI values, although the variance between males and females was not significantly different, indicating a tendency toward higher dispersal in females.

DISCUSSION

Although sage-grouse are declining and have lost a significant portion of their range in northeastern California (Schroeder et al. 2004, Shuford and Gardali 2008), our estimates of genetic diversity were comparable to published studies within the core of the species' distribution in Montana, Wyoming, Nevada, Oregon, and Idaho, USA (Oyler-McCance et al. 2005). Previous investigations assessing the relative diversity of sage-grouse have typically used different microsatellite loci, making comparisons of genetic diversity values across the species' range difficult. Even though the number of common microsatellite markers has varied among studies, our estimates of

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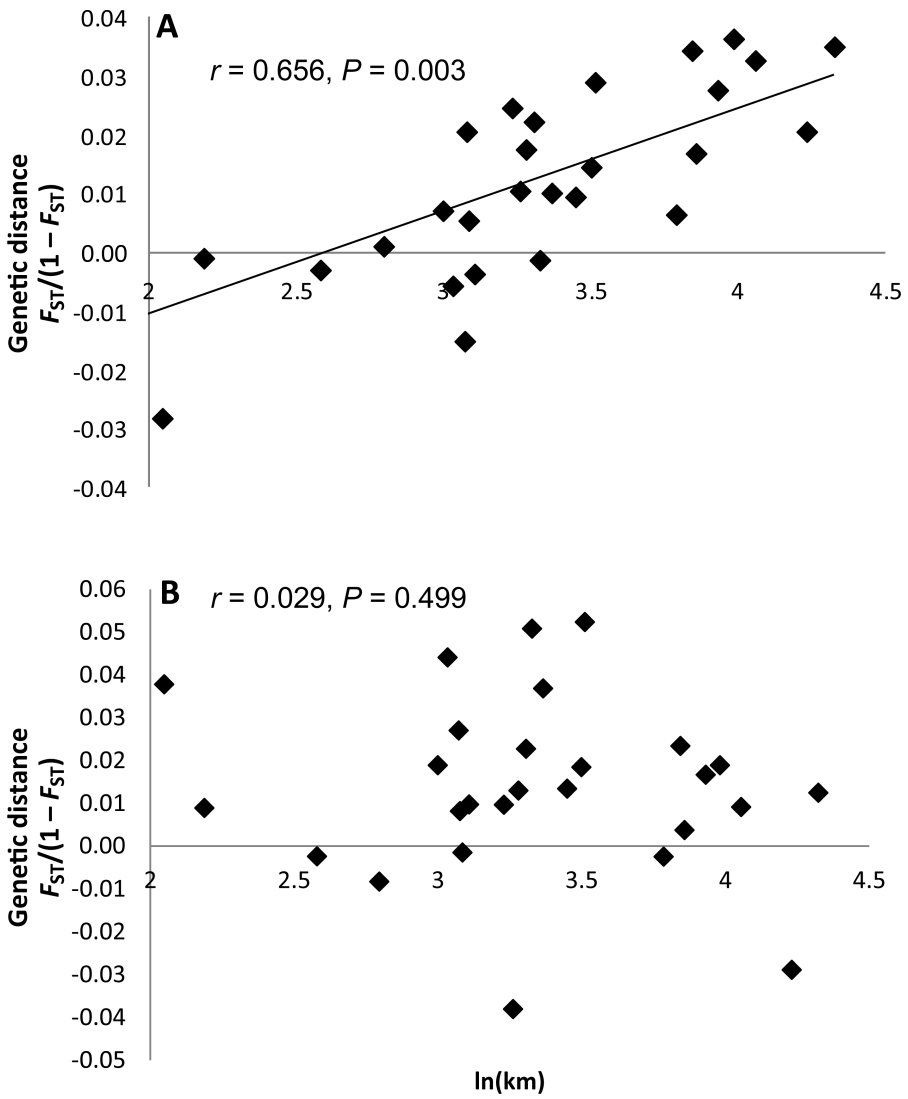


FIGURE 4. Analysis of isolation-by-distance for (**A**) males and (**B**) females, respectively. Genetic distances ($F_{ST}/(1 - F_{ST})$) are plotted against geographic distance for pairwise comparisons of 8 Greater Sage-Grouse leks in northeastern California, USA, 2007–2009.

heterozygosity suggest that sage-grouse in northeastern California had higher heterozyosity than a geographically isolated population in Mono County, California (Gibson et al. 2005, Tebbenkamp 2014; but see Semple et al. 2001, Oyler-McCance et al. 2014), and was comparable to levels reported in a peripheral population in southeastern Alberta, Canada (Bush et al. 2010).

We observed no major population subdivisions. Despite population declines and habitat loss, leks in northeastern California were not genetically differentiated. Bush et al. (2011) reported that sage-grouse occupying fragmented landscapes at the northern fringe of the species' range exhibited high genetic diversity, with no evidence that peripheral populations were genetically depauperate. By contrast, Schulwitz et al. (2014) found that sage-grouse populations in Jackson Hole and Gros Ventre were genetically isolated, with reduced genetic diversity compared to nearby populations in Wyoming and southeast Montana. Although habitat loss from anthropogenic activities was a contributing factor to genetic isolation in Jackson Hole (Schulwitz et al. 2014), the pattern of population differentiation observed suggests that landscape features, such as mountains that limit dispersal, could have been an important factor leading to genetic differentiation (Schulwitz et al. 2014, Row et al. 2015).

Identifying how landscape features and changes in landscape structure (i.e. loss of habitat quantity and quality, as well as fragmentation) influence gene flow and population connectivity is crucial for understanding whether contemporary genetic patterns are caused by extant landscapes or are a function of historical events. For species that have low dispersal capability (e.g., <10 km), it

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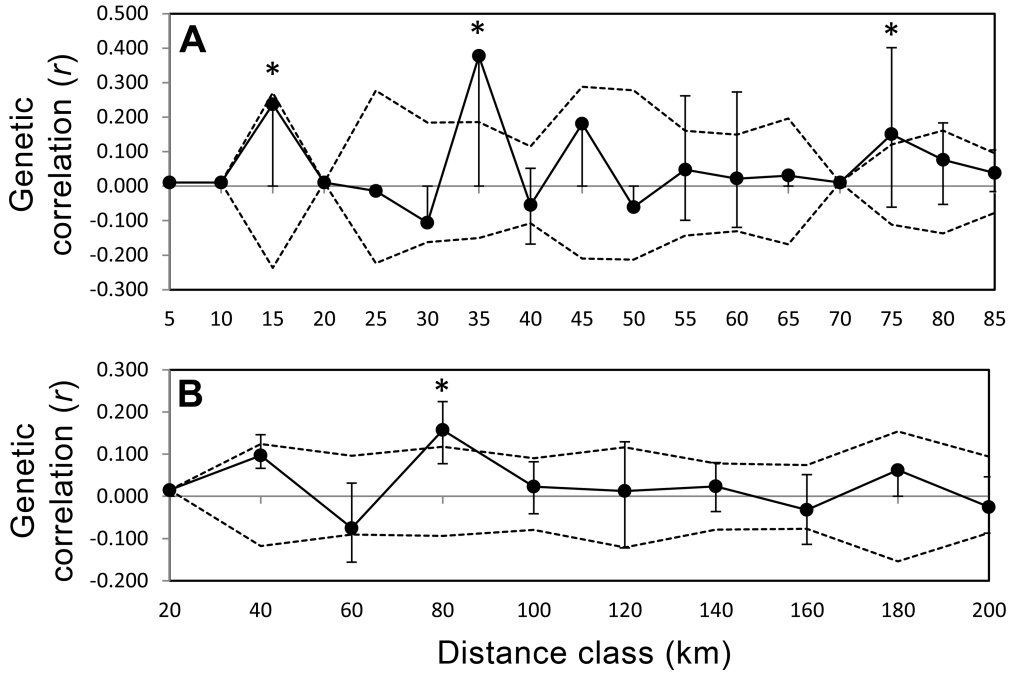


FIGURE 5. Spatial genetic structure of (**A**) male ($n = 99$) and (**B**) female ($n = 68$) Greater Sage-Grouse in northeastern California, USA, 2007–2009. The permutation 95% confidence interval (dashed lines) and the bootstrapped 95% confidence error bars are shown. Asterisks indicate significant positive spatial autocorrelation values. Geographic distances of <20 km contained no observations of females. Females sampled off lek ($n = 20$) were excluded.

will take longer for a barrier to be detected than for those with long-distance dispersal capability (Landguth et al. 2010). For example, results of simulation studies suggest that when dispersal capability is limited, organisms will retain a genetic signal from a past barrier for tens to hundreds of generations, compared to only 15 generations for populations of organisms with large dispersal capabilities (Landguth et al. 2010). This implies that genetic studies of species with low dispersal capability might not detect effects of landscape fragmentation for many generations, even if the landscape change has resulted in complete isolation of a previously connected population. Additionally, genetic data may not detect the effects of landscape changes if insufficient time has elapsed for the effects of the causal event to become detectable (Cushman et al. 2006), primarily because temporal lags are expected to occur between the time when the landscape is disturbed and the time when the effect of the disturbance can be detected with genetic data (Landguth et al. 2010, Miller et al. 2013).

Dispersal appears to be a critical demographic factor in maintaining genetically viable grouse populations (Caizergues et al. 2003a, 2003b, Johnson et al. 2004, Höglund et al. 2007, Segelbacher et al. 2008). Johnson et al. (2004) demonstrated that a change in the genetic structure of Greater Prairie-Chicken (*Tympanuchus cupido*) populations occurred within a relatively short period (<50 yr) and coincided with anthropogenic habitat deterioration and fragmentation. Reduced levels of gene flow resulting from habitat fragmentation and the loss or reduction of dispersal capabilities among subpopulations have been reported in other grouse species, including sage-grouse (Oyler-McCance et al. 1999, 2005), and could significantly affect the fitness and viability of remaining grouse populations (Bouzat et al. 1998a, 1998b, Segelbacher and Storch 2002, Caizergues et al. 2003b, Segelbacher et al. 2003, 2008, Johnson et al. 2004, Höglund et al. 2007). Areas that are not connected by direct movements might still experience high rates of gene flow. Genes can move over multiple generations, often connecting habitat patches separated by distances greater than an organism can move over a lifetime (Bohonak 1999). Using genetic analysis of microsatellite data, Bush (2009) reported dispersal distances of ≤316 km for sage-grouse in northern Montana. However, despite having a sufficient number of birds dispersing to maintain genetic diversity, Bush et al. (2011) cautioned that increased fragmentation would likely result in demographic declines in peripheral populations. Thus, accounting for landscape heterogeneity can contribute to our understanding of gene flow and population structure of sage-grouse in northeastern California.

A range-wide genetic survey of sage-grouse previously conducted by Oyler-McCance et al. (2005) assigned birds from northern California to clusters that included

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populations from northwestern Nevada and southeastern Oregon. Our results suggest that sage-grouse in northeastern California form a single genetic population; we hypothesize that high levels of genetic diversity are likely being maintained through gene flow between leks or from the adjacent northern Nevada population. While it is possible that gene flow from Nevada has helped maintain relatively high genetic diversity in northeastern California, it is not known whether sage-grouse currently disperse between the 2 regions. Therefore, the high genetic diversity we observed could indicate either that sage-grouse populations in northeastern California are connected by contemporary gene flow or that isolation from Nevada has occurred so recently that the effects on genetic structure are not yet detectable. We had no samples from Nevada to test either hypothesis.

Within-lek relatedness was low in northeastern California, which suggests that sage-grouse lek sites are largely assemblages of unrelated males and females. The overall pattern of relatedness that we observed was similar to that reported in other sage-grouse studies (Gibson et al. 2005, Bush et al. 2010, 2011) in which no patterns of kin structure at the lek level were observed. In addition, our results showed a significant negative relationship between lek relatedness and geographic distance (i.e. higher relatedness occurs at shorter geographic distances). This pattern is consistent with results of other studies that examined the effects of habitat fragmentation on the genetic structure of Cantabrian Capercaillie (*T. u. cantabricus*) occupying the periphery of their range in northern Spain (Alda et al. 2011, Vázquez et al. 2012) and has previously been demonstrated for Capercaillie in the Alps (Storch and Segelbacher 2000). Authors attributed the genetic structuring they observed, in part, to the limited natal dispersal of males (Regnaut et al. 2006) and other factors, such as habitat quality and configuration, that could reduce dispersal capabilities among subpopulations (Alda et al. 2011,Vázquez et al. 2012).

Male and female sage-grouse in our study displayed different patterns of gene flow across the sampled region, indicating higher rates of gene flow and longer dispersal distances in females. Male, but not female, sage-grouse showed significant IBD, which suggests that females are dispersing farther than males or, alternatively, that females are migrating beyond the spatial scale of our genetic sampling. Additionally, we detected significant spatial autocorrelation among males at shorter distance classes, but no such pattern was evident among females. This implies that females are more likely to disperse than males, which is consistent with the general pattern observed in birds (Greenwood 1980). Female-biased dispersal has been reported in other grouse species (e.g., Small and Rusch 1989, Giesen and Braun 1993, Caizergues and Ellison 2002, Caizergues et al. 2003a, Segelbacher et al. 2008).

Detection of sex-biased dispersal using assignment indices can be difficult unless the bias is extreme (e.g., at least 80:20; Goudet et al. 2002). In our study, the corrected AI confirmed female-biased dispersal, although differences between sexes were not statistically significant. However, previous studies (Favre et al. 1997, Mossman and Waser 1999) have also demonstrated that while the dispersing sex might have a negative skew in the frequency distribution of corrected AI values and a higher variance, the difference might not be significant. Exhaustive or large sampling efforts (e.g., the whole population) are necessary to detect sex-biased dispersal using assignment indices (Goudet et al. 2002). Thus, our failure to detect significant differences in mean corrected AI values between the sexes is likely a result of sample size. Moreover, leks in northeastern California were not highly differentiated from each other, indicating a high rate of gene flow across the sampled region and making it difficult to detect significant patterns of sex-biased dispersal using assignment indices. Whether the lack of significance in our results reflects the low power of assignment indices to assess differences in dispersal bias (Goudet et al. 2002), or a true lack of genetic differentiation between lek sites, is unknown.

Spatial autocorrelation analysis showed that significant spatial genetic structuring was detectable within distances of 15 km for males. However, no such pattern was evident in females at shorter distance classes (<80 km), which suggests that females (rather than males) appear to be dispersing longer distances, possibly maintaining genetic connectivity in this population. Results from our spatial autocorrelation analysis are commensurate with the patterns of IBD we observed. Collectively, these results reflect the approximate size of the area occupied by related individuals (i.e. "genetic patch size") and provide an indication of what scale of dispersal is taking place in northeastern California.

Knick and Hanser (2011) found that leks separated by distances greater than 13–18 km could be isolated by the decreased probability of dispersal from neighboring leks. Lek sites within our study area were considerably farther apart ($\text{Mean}_{\text{nearest neighbor}} = 10.9$ km; Davis 2012) than has been reported across the geographic range of sage-grouse (range: 1.1–4.0 km; Dalke et al. 1963, Wallestad 1975, Hanf et al. 1994). In north-central Washington, Schroeder and Robb (2003) speculated that large inter-lek distances (10.2 km), similar to those observed in our study, and substantial population declines were associated with habitat fragmentation. Despite documentation of extensive seasonal movements in this species (Fedy et al. 2012, Tack et al. 2012, Davis et al. 2014), the dispersal capabilities of sage-grouse have been shown to be low (e.g., median natal dispersal distance = 8.8 km for females and 7.4 km for males [Dunn and Braun 1985]; and 3.8 ± 1.3 km and 2.7 ± 0.3 km for males and females, respectively [Thompson

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2012]). Although the straight-line Euclidian distance between leks in northeastern California are within the reported range of interseasonal movements of sage-grouse (e.g., Fedy et al. 2012, Davis et al. 2014), it is not known whether effective dispersal (i.e. dispersal that results in gene flow) is occurring between adjacent leks within our study area. If leks become isolated, movement between occupied habitat patches could be challenging in northeastern California unless remnant habitat patches are large enough to support dispersal corridors or stepping-stones between leks and/or existing sage-grouse habitats. Consequently, sage-grouse populations in northeastern California, which occupy increasingly disjunct portions of the occupied range, have a higher risk of extinction than larger, core populations (Wisdom et al. 2011).

Although sage-grouse in northeastern California have maintained gene flow across the sampled region, continued habitat loss will likely result in small, isolated sage-grouse subpopulations at risk of losing genetic variation. Our results suggest that sage-grouse have tolerated some degree of habitat deterioration and fragmentation without losing genetic diversity, but it is unclear whether sage-grouse populations in northeastern California are connected by contemporary gene flow or if isolation from the core of the species' geographic range has occurred so recently that the effects on genetic structure are not yet detectable. Genetic diversity is necessary for a population to respond to environmental change; therefore, loss of genetic variation could jeopardize the persistence of fragmented sage-grouse populations (Shaffer 1981).

Habitat fragmentation is an ongoing process and, unless connectivity among leks is preserved, sage-grouse in northeastern California are likely to become more isolated—which, ultimately, will negatively affect gene flow and genetic diversity. Maintaining and improving habitat quality and connectivity of sage-grouse habitats in northeastern California is critical for maintaining gene flow and will be important for the long-term persistence of sage-grouse populations. To sustain sage-grouse in northeastern California, conservation measures should focus on securing connectivity between spatially discrete leks by enhancing existing habitat patches and preventing future habitat loss and fragmentation. Thus, future conservation actions for sage-grouse must consider the processes and patterns of gene flow operating at landscape scales to ensure the persistence of this species in northeastern California.

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