

**POPULATION STRUCTURE OF GREATER SAGE-GROUSE IN NORTHEASTERN  
CALIFORNIA: IMPLICATIONS FOR CONSERVATION IN A DECLINING  
PERIPHERAL POPULATION**

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### **AUTHORIZATION TO SUBMIT DISSERTATION**

This dissertation of Dawn Davis, submitted for the degree of Doctor of Philosophy with a major in Natural Resources and titled “Population Structure of Greater Sage-Grouse in Northeastern California: Implications for Conservation in a Declining Peripheral Population,” has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

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## ABSTRACT

Long-term population declines and habitat loss and fragmentation have increased concern over the status of greater sage-grouse (*Centrocercus urophasianus*) throughout the geographic range of the species. Although demographic parameters have been well documented for this species, understanding greater sage-grouse demography and reproductive ecology, and identifying variation in survival rates is essential for recognizing mechanisms for population declines and planning effective conservation and management. In this study, I examined demographic parameters and factors influencing nest survival of female greater sage-grouse in northeastern California. Additionally, I used known-fate models in program MARK to examine survival of broods to 10 weeks of age and bi-weekly survival rates of female greater sage-grouse over an 8-month period (Mar-Oct, 2007-2009). The nest survival rate, assuming a 28-d exposure period, was 50% and was positively associated with grass height ( $\beta = 0.35, 0.22 \text{ SE}$ ). Females that nested under vegetation other than sagebrush (*Artemisia* spp.) had higher nest survival probabilities. Nest success was dependent upon female age, with adults ( $S_{77\text{-d nesting season}} = 0.59, 95\% \text{ CI} = 0.441\text{-}0.744$ ) more likely to nest successfully than yearlings ( $S_{77\text{-day nesting season}} = 0.31, 95\% \text{ CI} = 0.134\text{-}0.652$ ). Brood survival to 10 weeks was 50% ( $\text{SE} = 0.09$ ). Based on model-averaged estimates, the overall 8-month survival (breeding season through autumn migration) for female sage-grouse was 53% ( $\text{SE} = 0.09$ ) with most deaths occurring in the spring and autumn. Mortalities during spring coincided with nest initiation and losses during incubation, and following hatch when successfully nesting females were tending chicks. Mortalities in September coincided with dispersal and autumn migration. Survival estimates during the breeding season were

higher among known failed nesters ( $S = 0.69$ ,  $SE = 0.10$ ) than those females that nested successfully ( $S = 0.53$ ,  $SE = 0.09$ ), suggesting female greater sage-grouse were exposed to greater mortality risk during incubation and brood-rearing periods. Increased mortality risk during the breeding season can have a major impact on greater sage-grouse demography. Thus, conservation and management efforts should focus on enhancing greater sage-grouse survival during the breeding and brood-rearing season.

To gain insight into greater sage-grouse spatial ecology and to elucidate home range dynamics of this species, I examined diurnal space use and seasonal movement patterns of radiomarked greater sage-grouse. I collected a total of 3,072 diurnal locations from 132 greater sage-grouse radiomarked between 2007-2009. Greater sage-grouse in my study used relatively large areas and exhibited wide-ranging seasonal movements. Although most female greater sage-grouse in northeastern California sought suitable nesting habitat within a relatively small area (within 5 km of a lek site), 29% of females nested >5 km from an occupied lek site, of which 62% nested successfully. Therefore, my results suggest the proportion of nesting females located >5 km from a lek is important for population viability in northeastern California. Moreover, the annual range of greater sage-grouse in northeastern California indicates that conserving habitat within 5 km of active lek sites is insufficient to sustain long-term population persistence. Consequently, larger areas of habitat are needed to conserve greater sage-grouse in northeastern California to accommodate seasonal movements, annual variation in habitat requirements, and to maintain connectivity among leks.

To evaluate the population genetic structure of greater sage-grouse a total of 167 blood samples collected from birds captured on 13 known, active leks and 20 blood samples from birds captured off-lek during the autumn were genotyped at 19 microsatellite loci. Although greater sage-grouse populations are declining and have lost a significant portion of their range in northeastern California, the species in my study exhibited high genetic diversity. I observed no population structure and despite population declines and habitat loss, leks in northeastern California were not differentiated. My results showed significant isolation-by-distance among males, suggesting that male greater sage-grouse are the more philopatric sex and females have a greater predisposition to disperse. Furthermore, spatial autocorrelation analysis revealed stronger spatial structuring for males than for females. The results from the corrected Assignment Index (A<sub>IC</sub>) also confirmed female-biased dispersal, although difference between genders was not significant. Although greater sage-grouse in northeastern California have maintained gene flow across the sampled region and have tolerated some degree of habitat fragmentation and deterioration without losing genetic diversity, continued habitat loss could result in small, isolated greater sage-grouse populations at risk of losing genetic variation. Thus, improving habitat quality and connectivity of greater sage-grouse habitats in northeastern California is critical for maintaining gene flow and is important for the long-term persistence of greater sage-grouse occurring on the geographic periphery of the species' distribution.

Understanding habitat selection across multiple scales and identifying the environmental variables that influence the geographic distribution of greater sage-grouse breeding habitats (i.e., nesting and brood-rearing) is critical for conservation planning and

long-term population persistence. Accordingly, I used a 2-step approach to identify nesting and brood-rearing habitat for the species in northeastern California. First, I used spatial autoregressive models to examine local scale habitat characteristics to describe the distribution of nest sites and brood-rearing locations. Second, I used Geographic Information System analysis and maximum entropy techniques to develop a spatially explicit model to identify nesting and brood-rearing habitat at a landscape scale. At the local scale, females selected sagebrush landcover types with increased grass height and visual obstruction for nesting. The amount of sagebrush canopy cover was also important in explaining greater sage-grouse brood habitat use. The primary difference between brood-rearing locations within sagebrush-dominated habitats and paired random locations was grass height and visual obscurity in the surrounding sagebrush-steppe community. My landscape scale model indicated that greater sage-grouse nesting and brood-rearing habitat were limited across my study area. Loss and degradation of existing sagebrush habitats and conversion of large tracts of sagebrush to other vegetation, such as annual grasslands and juniper (*Juniperus occidentalis*) woodlands, in northeastern California will likely result in declining greater sage-grouse populations because of reduced nesting success and decreased productivity. Given the limited amount of suitable nesting and brood-rearing habitat, my results suggest conservation efforts focused on these scarce resources will be important for effective management of breeding habitat for greater sage-grouse in northeastern California.

Exploring how greater sage-grouse move in response to the spatial structure of their environment is a crucial step toward understanding the influence of landscape structure on dispersal and seasonal movement patterns. I used a habitat suitability model developed from

presence-only data to predict the annual geographic distribution of greater sage-grouse within my study area. I then incorporated habitat suitability modeling into a least-cost path analysis to assess landscape connectivity for greater sage-grouse and to identify potential dispersal corridors that will facilitate movement of greater sage-grouse between adjacent leks. My results show that greater sage-grouse were closely associated with high quality habitat patches and that the geographic distribution of greater sage-grouse habitat was strongly affected by topographic complexity. An analysis of lek connectivity indicated that movement corridors between adjacent leks exceeded the dispersal capability of greater sage-grouse, resulting in dispersal routes too long to promote connectivity. Functional connectivity between adjacent leks was likely altered by invasive annual grass species, such as cheatgrass (*Bromus tectorum*) and medusahead rye (*Taeiatherum caput-medusa*), and juniper encroachment. Thus, the spatial structure of the greater sage-grouse population in northeastern California might not be conducive to long-term persistence. To ensure landscape connectivity, maintenance of large tracts of contiguous sagebrush is critical to sustain demographic and genetic exchange among greater sage-grouse populations occurring on the western periphery of the species geographic range.

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## CHAPTER 1. DISSERTATION INTRODUCTION

Historically, the range of greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) closely paralleled the distribution of sagebrush (*Artemisia* spp.) ecosystems (Beetle 1960, Autenrieth 1981), however, populations have declined throughout much of their range (Connelly and Braun 1997, Braun 1998, Schroeder et al. 2004). Alteration of sage-grouse habitats by expanding agriculture and urban development, sagebrush control programs, over-utilization of rangelands by domestic livestock, altered fire regimes, and prolonged drought throughout the sagebrush-steppe in the 1930s and again in the late 1980s and early 1990s have contributed to the decline in sage-grouse numbers (Crawford et al. 2004). Recent research has shown sage-grouse are sensitive to habitat fragmentation caused by anthropogenic features (Braun 1986, Lyon and Anderson 2003, Connelly et al. 2004, Aldridge 2005, Johnson et al. 2011, Knick and Hanser 2011, Wisdom et al. 2011) and human activity can affect sage-grouse habitat selection (Aldridge and Boyce 2007, Doherty et al. 2010). Global climate change also poses a significant threat to sage-grouse through a variety of mechanisms. In particular, global climate change models predict more variable and extreme weather events, higher temperatures, drier summer soil conditions, and wetter winters (Miller et al. 2011). Though research demonstrating how sage-grouse will respond to these regional anthropogenic-driven climatic shifts is lacking, models predict climate change and associated consequences will likely interact, and potentially magnify the consequences of, limiting factors such as disease (Walker and Naugle 2011) and habitat loss and degradation, which are already impacting sage-grouse across the species' geographic distribution (e.g., see USDI 2010, 75FR:13910-14014).

In California, 2 sage-grouse populations occupy the western periphery of the species' range: Lassen and Modoc counties in northeastern California and a genetically unique and relatively isolated population (Benedict et al. 2003) in Mono County to the south. Although little published information is available on sage-grouse population trends in California (Garton et al. 2011), sage-grouse have lost a significant portion of their range in northeastern California over the past 35 years (Connelly et al. 2004, Schroeder et al. 2004, Shuford and Gardali 2008), particularly in the most northern portion of their range in Modoc County. Invasion 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 habitats and are considered the primary reason for the decline in sage-grouse populations in northeastern California (S. C. Gardner, personal communication).

Continued habitat loss and fragmentation will likely result in small, isolated sage-grouse populations at risk of losing genetic variation. Genetic diversity is necessary for a population to respond to environmental change, thus, loss of genetic variation could jeopardize the persistence of fragmented sage-grouse populations (Shaffer 1981). Recent genetic work on sage-grouse populations has demonstrated that birds in Mono County are genetically unique, suggesting that they have no interchange with other sage-grouse populations and that they likely have been isolated for thousands of years (Benedict et al. 2003, Oyler-McCance et al. 2005). Additional genetic analyses of northern sage-grouse populations would permit evaluation of the degree (if any) to which sage-grouse populations in northeastern California have experienced a loss of genetic diversity.

The long-term viability of sage-grouse populations also depends on the effects of landscape level habitat stability on dispersal rates and distances (Dale 2001). Grouse populations are particularly vulnerable to fragmentation of native rangelands (Woodward et al. 2001, Fuhlendorf et al. 2002, Schroeder and Robb 2003) and the ability of sage-grouse to move among suitable patches of habitat depends not only on the juxtaposition of such patches but also on the dispersal behavior of the species (Fahrig and Merriam 1994). Data on natal dispersal distances are important for understanding the genetic structure of populations and the effects of habitat fragmentation on metapopulation dynamics (Caizergues and Ellison 2002). Research conducted on sage-grouse populations threatened by habitat fragmentation traditionally reported on habitat use, breeding success, and survival (Homer et al. 1993, Schroeder 1997), however, few studies (e.g., Shepherd et al. 2011) have documented the relationship between seasonal movement patterns and changes in landscape structure and little is known about the genetic effects of habitat fragmentation on sage-grouse populations.

Populations that have undergone large reductions in numbers, such as sage-grouse in California, are likely to lose genetic variation (Nei et al. 1975, Maruyama and Fuerst 1985). Although no deleterious effects to demographic rates have been documented in California sage-grouse populations (CDFG, unpublished data), a loss in genetic diversity might be associated with inbreeding and a reduction in reproductive fitness (Bouzat et al. 1998a, b; Johnson et al. 2003, Johnson et al. 2004). 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 impact the long-term viability of sage-grouse populations in California.

Knowledge of dispersal is critical for understanding how sage-grouse populations expand and how this process can be augmented by relocation and re-introduction of sage-grouse into unoccupied habitats. In addition, statistical analysis of microsatellite loci will provide measures of genetic variation within sage-grouse populations. Measures of genetic variation would permit evaluation of the degree to which sparse and scattered populations in northeastern California have experienced a loss of genetic diversity through processes such as genetic drift or inbreeding depression. Further, assessing the genetic variation of sage-grouse populations will assist managers in evaluating whether translocating birds from populations within California or supplementing California populations with birds from populations with higher genetic variability outside California (genetic introgression) is necessary. This would have practical management implications when making recommendations for conservation efforts, particularly when assessing landscape level habitat change and its effects on sage-grouse population dynamics. Thus, the goal of my study was to develop a landscape level, habitat-based approach to assess sage-grouse viability in northeastern California. Specifically, the objectives of this study were to adopt a hierarchical framework (e.g., Haufler et al. 2002), which identifies the different ecological and demographic processes operating at 3 different levels: the individual or species level, the genetic level, and the ecosystem or landscape level.

Although demographic parameters have been well documented for this species, understanding sage-grouse demography and reproductive ecology, and identifying variation in survival rates are essential for recognizing mechanisms for population declines and planning effective conservation and management. In Chapter 2 of this dissertation, I

examined demographic parameters and factors influencing nest survival of female sage-grouse in northeastern California. Additionally, I used known-fate models in program MARK (White and Burnham 1999) to ascertain brood survival for broods to 10 weeks of age and bi-weekly survival rates of female sage-grouse over an 8-month period (Mar-Oct, 2007-2009), which included the breeding season through autumn migration.

An accurate analysis and depiction of animal space use provides insights into a species' behavior and its needs in terms of habitat size, shape, and juxtaposition. This is especially true for sage-grouse, a candidate species under the United States Endangered Species Act (USDI 2010, 75FR:13910-14014) and a bird species of special concern in California (Remsen 1978, CDFG 1992). Thus, to gain insight into sage-grouse spatial ecology and to elucidate home range dynamics of this species, in Chapter 3, I investigated diurnal space use and seasonal movement patterns of sage-grouse within my study area.

Reports of local and range-wide declines in sage-grouse populations have traditionally focused attention on demographic factors influencing the distribution and abundance of sage-grouse (Braun 1998, Connelly et al. 2004). These declines are generally attributed to habitat loss and fragmentation, yet, little is known about the genetic structure of sage-grouse populations. In northeastern California, it appears that loss and fragmentation of sagebrush habitat have split sage-grouse populations into smaller, loosely connected lek complexes where connectivity is unknown. At the current population level and spatial distribution, movement between leks is necessary to facilitate population persistence and genetic variability. However, information on whether leks in northeastern California are interconnected by gene flow is lacking. Therefore, in Chapter 4, I assessed the genetic

structure of sage-grouse within my study area and in Chapter 5, I used molecular data to identify the patterns of dispersal among sage-grouse in northeastern California.

Understanding habitat selection across multiple scales and identifying the environmental variables that influence the geographic distribution of sage-grouse breeding habitats (i.e., nesting and brood-rearing) is critical for conservation planning and long-term population persistence. In Chapter 6, I used a 2-step approach to identify nesting and brood-rearing habitat for sage-grouse in northeastern California. First, I used spatial autoregressive models to examine local scale habitat characteristics to describe the distribution of nest sites and brood-rearing locations in northeastern California. Then, I used Geographic Information System analysis and maximum entropy techniques to develop a spatially explicit model to identify nesting and brood-rearing habitat at a landscape scale. Lastly, in Chapter 7, I used a habitat suitability model developed from presence-only data to predict the annual geographic distribution of sage-grouse in northeastern California. I then incorporated habitat suitability modeling into a least-cost path analysis to assess landscape connectivity for sage-grouse in my study area and to identify potential dispersal corridors that will facilitate movement of sage-grouse between adjacent leks.

## **LITERATURE CITED**

- Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. *Ecological Applications* 17:508–526.
- Autenrieth, R. E. 1981. Sage grouse management in Idaho. Idaho Department of Fish and Game. Wildlife Bulletin 9.

- Beetle, A. A. 1960. A study of sagebrush. The section Tridentata of *Artemisia*. University of Wyoming Agricultural Experiment Station Bulletin 368.
- Benedict, N. G., S. J. Oyler-McCance, S. E. Taylor, C. E. Braun, and T. W. Quinn. 2003. Evaluation of the eastern (*Centrocercus urophasianus urophasianus*) and western (*C. u. phaios*) subspecies of sage-grouse using mitochondrial control-region sequence data. *Conservation Genetics* 4:301-310.
- Bouzat, J. L., H. H. Cheng, H. A. Lewin, R. I. Westemeier, J. D. Brawn, and K. N. Paige. 1998a. Genetic evaluation of a demographic bottleneck in the greater prairie-chicken. *Conservation Biology* 12:836-849.
- Bouzat, J. L., H. A. Lewin, and K. N. Paige. 1998b. The ghost of genetic diversity past: historical DNA analysis of the greater prairie-chicken. *American Naturalist* 152:1-6.
- Braun, C. E. 1986. Changes in sage grouse lek counts with advent of surface coal mining. *Proceedings of Issues and Techniques in the Management of Impacted Western Wildlife* 2:227-231.
- Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? *Proceedings of the Western Association State Fish and Game Wildlife Agencies* 78:139-156.
- Caizergues, A., and L. N. Ellison. 2002. Natal dispersal and its consequences in black grouse *Tetrao tetrix*. *Ibis* 144:478-487.
- California Department of Fish and Game (CDFG). 1992. Bird species of special concern. Unpublished list, July 1992. California Department of Fish and Game, Sacramento, California, USA.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished report, Cheyenne, Wyoming, USA.
- Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosely, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. *Journal of Range Management* 57:2-19.
- Dale, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small isolated bird populations. *Oikos* 92:344-356.



- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. *Journal of Wildlife Management* 74:1544-1553.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50-59.
- Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie Jr., and J. S. Shackford. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. *Landscape Ecology* 17:617-628.
- Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and S. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pages 293-381 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Haufler, J. B., R. K. Baydack, H. Campa III, B. J. Kernohan, C. Miller, L. J. O'Neil, and L. Waits. 2002. Performance measures for ecosystem management and ecological sustainability. *Wildlife Society Technical Review* 02-1.
- Homer, C. G., T. C. Edwards, R. D. Ramsey, and K. P. Price. 1993. Use of remote sensing methods in modeling sage grouse winter habitat. *Journal of Wildlife Management* 57:78-84.
- Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997-2007. Pages 407-450 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Johnson, J. A., M. R. Bellinger, J. E. Toepfer, and P. Dunn 2004. Temporal changes in allele frequencies and low effective population size in greater prairie-chickens. *Molecular Ecology* 13:2617-2630.
- Johnson, J. A., J. E. Toepfer, and P. O. Dunn. 2003. Contrasting patterns of mitochondrial and microsatellite population structure in fragmented populations of greater prairie-chickens. *Molecular Ecology* 12:3335-3347.
- Knick, S. T., and S. E. Hanser. 2011. Connecting pattern and process in greater sage-grouse populations and sagebrush landscapes. Pages 383-405 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape*

- species and its habitats. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Lacy, R. C. 1997. Importance of genetic variation to the viability of mammalian populations. *Journal of Mammalogy* 78:320-335.
- Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:486-491.
- Maruyama, T., and P. A. Fuerst. 1985. Number of alleles in a small population that was formed by a recent bottleneck. *Genetics* 111:675-689.
- Miller, R. F., S. T. Knick, D. A. Pyke, C W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145-184 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29:1-10.
- Oyler-McCance, S. J., S. E. Taylor, and T. W. Quinn. 2005. A multilocus population genetic survey of the greater sage-grouse across their range. *Molecular Ecology* 14:1293-1310.
- Remsen, J. V., Jr. 1978. Bird species of special concern in California: an annotated list of declining or vulnerable bird species. Nongame Wildlife Investigations, Wildlife Management Branch Administration Report 78-1, California Department of Fish and Game, Sacramento, California, USA.
- Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. *Condor* 99:933-941.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. *Condor* 106:363-376.
- Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. *Wildlife Biology* 9:291-299.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *Biosciences*

31:131-134.

- Shepherd, J. F., K. P. Reese, and J. W. Connelly. 2011. Landscape fragmentation and non-breeding greater sage-grouse. Pages 77-88 in B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. Studies in Avian Biology (no. 39), University of California Press, Berkeley, California, USA.
- Shuford, W. D., and Gardali, T. 2008. California Bird Species of Special Concern: A ranked assessment of species, subspecies, and distinct populations of birds of immediate conservation concern in California. Studies of Western Birds 1. Western Field Ornithologists, Camarillo, California, and California Department of Fish and Game, Sacramento, California, USA.
- United States Department of Interior (USDI). 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 75:13910-14014 (23 March 2010).
- Walker, B. L., and D. E. Naugle. 2011. West Nile virus ecology in sagebrush habitat and impacts on greater sage-grouse populations. Pages 127-142 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.
- Wisdom, M. J., C. W. Meinke, S. T. Knick, and M. A. Schroeder. 2011. Factors associated with extirpation of sage-grouse. Pages 451-472 in Knick, S. T., and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Woodward, A. J. W., S. D. Fuhlendorf, D. M. Leslie Jr., and J. Shackford. 2001. Influence of landscape composition and change on lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations. American Midland Naturalist 145:261-274.

## CHAPTER 2. DEMOGRAPHY, REPRODUCTIVE ECOLOGY, AND VARIATION IN SURVIVAL OF GREATER SAGE-GROUSE IN NORTHEASTERN CALIFORNIA

**ABSTRACT** – Long-term population declines and habitat loss and fragmentation have increased concern over the status of greater sage-grouse (*Centrocercus urophasianus*) throughout the geographic range of the species. Although demographic parameters are well documented for this species, understanding greater sage-grouse demography and reproductive ecology, and identifying variation in survival rates is essential for recognizing mechanisms for population declines and planning effective conservation and management. In this study, I examined demographic parameters and factors influencing nest survival of female greater sage-grouse in northeastern California. Additionally, I used known-fate models in program MARK to examine brood survival for broods to 10 weeks of age and bi-weekly survival rates of female greater sage-grouse over an 8-month period (Mar-Oct, 2007-2009). Nest survival rate, assuming a 28-d exposure period, was 50% and was positively associated with grass height ( $\beta = 0.35, 0.22 \text{ SE}$ ). Females that nested under vegetation other than sagebrush (*Artemisia* spp.) had increased nest survival probabilities. Nest success was dependent upon female age and adults ( $S_{77\text{-d nesting season}} = 0.59, 95\% \text{ CI} = 0.441\text{-}0.744$ ) were more likely to nest successfully than yearling females ( $S_{77\text{-d nesting season}} = 0.31, 95\% \text{ CI} = 0.134\text{-}0.652$ ). Brood survival to 10 weeks was 50% ( $\text{SE} = 0.09$ ). Based on model-averaged estimates, the overall 8-month survival (breeding season through autumn migration) for female sage-grouse was 53% ( $\text{SE} = 0.09$ ) with most deaths occurring in spring and autumn. Mortalities during spring coincided with nest initiation, incubation, and following hatch

when successfully nesting females were tending chicks. Mortalities in September coincided with dispersal and autumn migration. The survival estimate during the breeding season was higher among known failed nesters ( $S = 0.69$ ,  $SE = 0.10$ ) than those females that nested successfully ( $S = 0.53$ ,  $SE = 0.09$ ), suggesting that female greater sage-grouse were exposed to greater mortality risk during incubation and brood-rearing periods. Greater mortality risk during the breeding season can have a major impact on greater sage-grouse demography. Thus, conservation and management efforts should focus on enhancing female greater sage-grouse survival during the breeding and brood-rearing season.

**KEYWORDS:** *Centrocercus urophasianus*, demography, greater sage-grouse, reproductive ecology, survival

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are sagebrush (*Artemisia* spp.) obligates and the importance of a balance of sagebrush, native perennial bunchgrasses, and forbs for fulfilling their life history requirements has been well documented (Connelly et al. 2000). Despite their dependence on sagebrush, virtually no undisturbed tracts of sagebrush-steppe habitat exist within the current distribution of sage-grouse (Schneegas 1967, Braun 1998). The primary factors that affect sagebrush-steppe ecosystems are habitat deterioration, loss, and fragmentation through sagebrush control programs for agricultural production (Yocum 1956, Swensen et al. 1987), increased livestock forage (Schneegas 1967), urban development (Call 1979, Braun 1998), and resource extraction (Call and Maser 1985, Braun 1986). Additionally, improper livestock grazing practices and altered fire regimes have resulted in shrub dominance at the expense of the

herbaceous understory (Blaisdell et al. 1982, West and Hassan 1985, Laycock 1991, Winward 1991, Miller and Rose 1995). Moreover, recent research has shown that sage-grouse are sensitive to habitat fragmentation caused by anthropogenic features (Braun 1986, Lyon and Anderson 2003, Connelly et al. 2004, Aldridge 2005, Johnson et al. 2011, Knick and Hanser 2011, Wisdom et al. 2011) and human activity can affect sage-grouse habitat selection (Aldridge and Boyce 2007, Doherty et al. 2010). Global climate change also poses a significant threat to sage-grouse through a variety of mechanisms. In particular, global climate change models predict more variable and extreme weather events, higher temperatures, drier summer soil conditions, and wetter winters (Miller et al. 2011). Although research demonstrating how sage-grouse will respond to these regional anthropogenic-driven climatic shifts is lacking, models predict climate change and associated consequences will likely interact, and potentially magnify, limiting factors such as disease (Walker and Naugle 2011) and habitat loss and degradation, which are already impacting sage-grouse across the species geographic distribution (e.g., see USDI 2010, 75FR:13910-14014).

Long-term population declines and habitat loss and fragmentation have increased concern over the status of sage-grouse, a candidate species currently designated as “warranted but precluded” from protection under the United States Endangered Species Act (USDI 2010, 75FR:13910-14014). Nesting and brood survival have been identified as the most critical factors associated with sage-grouse demography and population size (Aldridge and Brigham 2001, Gregg 2006, Beck et al. 2006) and adult survival has important consequences for the population dynamics of tetraonids, including sage-grouse (Wisdom and Mills 1997, Aldridge and Brigham 2001, Sandercock et al. 2005). Although data on annual

survival rates of sage-grouse are available, information on seasonal timing of mortality is lacking. Sage-grouse demography, and ultimately population viability, is sensitive to changes in adult survival rates (e.g., Johnson and Braun 1999). Consequently, it is important to understand what factors affect survival rates across the geographic range of the species. However, few studies assessing sage-grouse demography and reproductive ecology provide seasonal survival rates. Moreover, survival estimates and patterns of variation in survival rates, identifying when sage-grouse are most susceptible to predation or other mortality factors, have not previously been published for sage-grouse populations in California.

Although demographic parameters have been well documented for sage-grouse, little is known about the reproductive ecology and survival of the species in northeastern California. Thus, understanding age-specific variation in demography, reproductive ecology, and survival rates is essential for understanding population declines and planning effective conservation and management. Given the conservation concerns raised and the need to understand the potential constraints on population growth and long-term persistence of sage-grouse in northeastern California, the objectives of this study were to: 1) evaluate nest survival rates and identify the potential factors influencing nest success in northeastern California; 2) estimate survival rates for sage-grouse broods up to 10 weeks; 3) estimate survival rates of female sage-grouse over an 8-month period (Mar-Oct); and 4) provide managers with information regarding sage-grouse demography and reproductive ecology.

## **STUDY AREA**

This study was conducted in a 597,116 ha region of sagebrush-steppe habitat in Lassen County, in northeastern California adjacent to the Nevada border (Figure 1). Elevation

ranged from 1,400 to 2,400 m. The predominant sagebrush types included Wyoming big sagebrush (*A. tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), and little sagebrush (*A. arbuscula*). Other common vegetation communities included annual grasslands and juniper (*Juniperus occidentalis*) dominated woodlands. The study area was primarily composed of 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 as irrigated alfalfa (*Medicago* spp.).

Sage-grouse populations in northeastern California have 4 distinct breeding ranges where leks are concentrated and around which females nest, which I refer to as lek complexes (Connelly et al. 2004). For the purposes of my study, I defined a lek complex as a group of sage-grouse associated with  $\geq 1$  active lek site in the same geographic proximity which, in my study area, were composed of 1 to 5 occupied leks (Figure 1). One of the largest lek complexes in Lassen County is the Upper Smoke Creek lek complex located close to the Nevada border. This area contains a significant percentage of the breeding population of sage-grouse in Lassen County. The area around Dodge Springs, to the north of the Upper Smoke Creek lek complex, contains a lek complex on the periphery of the Lassen County sage-grouse population, where western juniper has encroached in recent years. The Madeline Plains lek complex is on the western edge of the Lassen County population and has declined significantly in the past 30 years. The Shaffer Mountain lek complex contains one of the larger breeding concentrations of sage-grouse in Lassen County and populations have remained relatively stable for the past 20 years.



## **MATERIALS AND METHODS**

### **Trapping and Radio-Marking**

I trapped sage-grouse opportunistically using spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) on or near lek sites from March through April 2007-2009 from 4 lek complexes (Shaffer Mountain, Upper Smoke Creek, Dodge Springs, Madeline Plains). I classified gender and age of captured birds by plumage characteristics and wing molt (Crunden 1963, Dalke et al. 1963). Sage-grouse were fitted with a serially-numbered aluminum leg band and a  $\leq 20$ -g necklace-mounted ATS radio transmitter (Advanced Telonics Systems, Inc., Insanti, MN, USA). Mass (g) and unflattened wing chord (mm) were recorded for all birds upon capture. Condition was estimated using the residuals derived from the linear regression of wing chord on body mass (Vehrencamp et al. 1989). To evaluate whether survival of an individual female was influenced by condition, I assumed that the condition of the female at the time of capture was fixed over the lifetime of the female.

### **Demographic Variables**

I assessed demographic variables (e.g., nest initiation rate, apparent nest success, clutch size, renesting rate, and brood success) from locations of radio-collared females. Females were monitored 1-3 times per week with a hand-held Yagi antenna and portable receiver throughout the breeding season to determine nesting chronology and ascertain habitats used for nesting. Positions of radio-collared females were determined by circling the estimated location of the female, indicated by the loudest signal strength (Springer 1979). When

monitoring revealed a female had initiated a nest (i.e., 2-3 locations near the same spot), I approached the female until I observed the female on the nest and I recorded the nest location in Universal Transverse Mercator (UTM) coordinates using a Global Positioning System (GPS) unit. Nesting females were monitored remotely (>60 m) to avoid disturbance (Holloran and Anderson 2005). Once monitoring revealed that a female had moved away from the nest and incubation had likely ceased, I examined the nest to ascertain fate. I classified nests as successful if  $\geq 1$  egg hatched. Depredated nests were distinguished from successful nests by the presence of a firmly attached shell membrane in broken eggs (Wallestad and Pyrah 1974).

Date of first day of nest incubation was estimated as the midpoint between consecutive observations (e.g., see Schroeder 1997). Nest initiation rate was defined as the number of radio-collared females that initiated nests divided by the total number of radio-collared females alive at the onset of the nesting season. Apparent nest success was calculated by dividing the number of successful nests (including renests) by the total number of nests. Clutch size was assessed after hatching by examination of eggshell fragments. Egg viability was calculated as the percentage of all eggs laid in successful nests that hatched.

I monitored broods every 1-3 days with a hand-held Yagi antenna and portable receiver until the brood was lost or there was a breakdown in brood integrity. Brood locations were determined by locating the radiomarked female and circling within 25 m to avoid disturbance. Females were considered successful if  $\geq 1$  chick was recruited into the autumn population ( $\geq 60$  days). I calculated brood success by dividing the number of females

that recruited  $\geq 1$  chick to independence ( $\geq 60$  days) divided by the total number of successful nests.

I used one-way analysis of variance (ANOVA) to examine year- and age-related differences in nest initiation date and clutch size. Due to limited sample size of renesting females ( $n = 5$ ), analyses of factors affecting the likelihood of renesting occurrence (e.g., age class, nest initiation date, clutch size, timing of nest lost, and female condition) were limited. I report parameter estimates as the mean  $\pm$  SE.

### **Habitat Structure**

In order to provide a broad assessment of existing and potential sage-grouse habitat within my study area, vegetation communities were rated based on their ability to respond positively to management (i.e., R-value; Table 1). Of the 597,116 ha of potential sagebrush habitat within my study area, slightly more than 46% (R3 and R4) currently has a high percentage of cheatgrass (*Bromus tectorum*) or juniper invasion (Armentrout and Hall 2005). Moreover, approximately 19% (18.6% X3 and X4) of the sagebrush ecosystem within the study area has crossed a threshold to being dominated by cheatgrass or juniper (Armentrout and Hall 2005).

Habitat sampling at nest sites was performed after hatching for successful nests and after the predicted hatch date for depredated or abandoned nests. I measured vegetative attributes at nest sites along two, 10-m perpendicular transects intersecting at the nest bowl. Species composition and percent cover of grasses, forbs, bare ground, and litter were estimated at five, 50- x 50-cm quadrat frames spaced equidistantly along each transect (Daubenmire 1959). Within each quadrat frame, cover was ranked into 6 classes (e.g., 1: 0-1%; 2: 1.1-5%; 3: 5.1-25%; 4: 25.1-50%; 5 = 50.1-75%; 6: 75.1-100%) following Connelly

et al. (2003). Visual obstruction readings (VORs) were recorded along each 10-m transect. VORs were measured at a height of 1 m from a distance of 5 m (Robel et al. 1970). VORs provided an index of visual obstruction of all vegetation (not just grass and/or herbaceous cover). Live shrub canopy cover was quantified using the line intercept method (Canfield 1941). Vegetative attributes at paired random points within an arbitrary distance of 500 m of each nest site were sampled using the techniques described. Random points within 100 m of nests were excluded to reduce the potential of dependence among samples. To ensure continuity over the course of the 3 year study, I used the same observer to measure and record stand characteristics.

I performed an ANOVA to test for differences between vegetative characteristics at successful and unsuccessful nests. Vegetation variables with non-normal distributions were transformed (arcsine square root transformation for proportional data and logarithmic transformation for height data). Means  $\pm$  SE were computed from non-transformed data.

## **Survival Analysis**

### **Nest Survival**

I estimated daily survival rates (*DSR*) of sage-grouse nests using the nest survival model option (Rotella et al. 2004) in program MARK (White and Burnham 1999), which permits analyses of nest survival data that include a variety of ecological factors that might affect nest survival rates and allows competing models to be assessed using an information-theoretic approach (e.g., Burnham and Anderson 2002). I used data from 58 nests that were monitored during the 77-d nesting season. I standardized 4 April as day 1 of the nesting season and numbered all nest-check dates sequentially thereafter ending 19 June. To explain

potential variation in survival rates, I developed a set of *a priori* candidate models for each analysis based on results from sage-grouse literature reviews (Schroeder et al. 1999), management guidelines (Connelly et al. 2000), and previous studies which related vegetative structure at or surrounding nest sites to nest success (e.g., Gregg et al. 1994, Aldridge and Brigham 2002, Holloran et al. 2005, Moynahan et al. 2007, Kolada et al. 2009a, b). For each nest site, the following covariates were considered: (1) the date the nest was found; (2) the nest initiation date (in Julian days); (3) age of female (yearling or adult); (4) whether the nest was an initial nest attempt or reneest; (5) the R-value category, which provided a broad assessment of existing and potential sage-grouse habitat where the nest site was located (coded as 0 or 1 to distinguish among nests found in areas characterized by a high percentage of cheatgrass or juniper invasion versus areas with desired species composition); (6) the plant used as nesting cover (coded as 0 or 1 to distinguish between nests under sagebrush versus nests under non-sagebrush); and (7) vegetative attributes most likely to influence nest survival including measures of shrub and grass height at the nest bowl, shrub and grass cover within 10-m of the area that contained the nest, and vegetation visual obstruction at the nest site. Additionally, I tested for the potential effects of time-specific covariates on nest survival rate including year (2007-2009) and linear time trend (T).

### **Brood Survival**

I estimated brood survival rates ( $S$ ) to 10 weeks post-hatch as a function of time-specific and individual covariates using the known-fate model option in program MARK (White and Burnham 1999). This option estimates Kaplan-Meier survival rates (Kaplan and Meier 1958) with modifications to allow for staggered entry (Pollock et al. 1989). To explain potential

variation in survival rates, I developed a set of *a priori* candidate models for each analysis based on results from previous studies (e.g., Gregg and Crawford 2009, Dahlgren et al. 2010). Specifically, I tested for the potential effects of year (2007-2009), hatch date (in Julian days), age of female (yearling or adult), clutch size, and R-value (where the dominant R-value for each female with a brood was identified as the R-value with the greatest number of locations) on brood survival. Additionally, I assessed whether there was any temporal variation in annual survival rates (time (week) and linear (T) or quadratic ( $T^2$ ) time trends) among broods.

### **Female Survival Analysis**

I estimated survival rates ( $S$ ) of female sage-grouse over an 8-month period (Mar-Oct, 2007-2009) as a function of time-specific and individual covariates using the known-fate model option in program MARK (White and Burnham 1999). To explain potential variation in survival rates, I developed a set of *a priori* candidate models for each analysis based on results from previous studies (e.g., Moynahan et al. 2007). Specifically I tested for the potential effects of: (1) year (2007, 2008, 2009), (2) the lek complex where females were captured (Shaffer Mountain, Upper Smoke Creek, Madeline Plains, or Dodge Springs), (3) temporal variation including time (bi-weekly) and linear (T), or quadratic time ( $T^2$ ) effects, (4) female age (yearling or adult), (5) condition at time of capture, and (6) nest fate (successful or unsuccessful).

### **Model Selection**

All candidate models were run in program MARK (White and Burnham 1999) using the logit link function. I ranked each set of competing candidate models based on Akaike's

Information Criterion adjusted for small sample size ( $AIC_c$ ; Akaike 1973, Burnham and Anderson 2002). For each analysis, I considered the candidate model with the lowest  $AIC_c$  to be the best-approximating model supported by the data (Burnham and Anderson 2002). In cases in which the differences in  $AIC_c$  values ( $\Delta AIC$ ) between the most parsimonious model and alternative candidate models was  $\leq 2$ , I used model averaging to address model selection uncertainty (Burnham and Anderson 2002).

## RESULTS

### Capture and Demographic Parameters

I captured 69 female sage-grouse on or near 13 known, occupied lek sites from March through April 2007-2009 within the Lassen County study area. The age composition of females was 36 adults, 32 yearlings, and 1 unknown. Due to small sample size, observations of the same bird ( $n = 36$  females) in consecutive years were considered to be independent, thus, the effective sample size was 105 females.

Nest initiation rate was 97% (74/76; Table 2). This sample does not include 8 females killed before the onset of the breeding season, missing females ( $n = 9$ ), and females that were located  $>20$  days after capture ( $n = 12$ ), which precluded my ability to detect whether females initiated a nest (Gibson and Bachman 1992). Gibson and Bachman (1992) found that females localize to within 500 m of their nest site approximately 4 days after mating and began incubation as early as 20 days later. Thus, some nesting attempts in my study might not have been detected because monitoring of radiomarked sage-grouse was initiated  $>20$  days after capture. I assumed that females captured with brood patches ( $n = 1$ ) had initiated incubation prior to capture. Additionally, the locations of 4 nest sites were unknown,

however, I observed the females with broods in May and June, respectively, and assumed females had nested successfully.

Demographic data among years did not differ, therefore, I pooled data among years to compare nesting effort between yearling and adult females. Average date of initiation for first-nest incubation was 15 April (range = 20 March – 30 May;  $n = 68$ ). Clutch size for successful ( $n = 34$ ; mean =  $7.6 \pm 0.24$ ) and unsuccessful ( $n = 20$ ; mean =  $6.6 \pm 0.42$ ) initial nesting attempts were not significantly different ( $F_{2,56} = 2.75$ ,  $P = 0.07$ ). Collectively, clutch size varied from 3 to 11 eggs for first nests. Although a significant difference was not detected ( $F_{1,57} = 0.80$ ,  $P = 0.38$ ), initial nests had numerically larger clutch sizes ( $n = 54$ , mean =  $7.3 \pm 0.22$ ) than renests ( $n = 5$ , mean =  $6.6 \pm 0.60$ ). My ability to detect differences in clutch size might have been influenced by small sample sizes. Egg viability was 93.8% (241 of 257 eggs;  $n = 34$  nests).

Renesting rate was 18% (5/28) and renest success was 20% (1/5); 2 females killed on their initial nests were not included in calculations of renest initiation. Overall, apparent nest success (initial and renests) was 56% (44/79). This calculation does not include 1 female that nested outside the study area, which precluded my ability to ascertain the nest fate.

Diagnostic sign at depredated nests was unreliable for identifying nest predators of sage-grouse. However, potential nest predators (Schroeder and Baydack 2001) observed on the study area included ground squirrels (*Spermophilus* spp.), badgers (*Taxidea taxus*), coyotes (*Canis latrans*), bobcats (*Felis rufus*), common ravens (*Corvus corax*), and black-billed magpies (*Pica hudsonia*). Abandonment accounted for 14% (5/36) of nest failures.



I collected data on brood success for 25 females. Eleven females (44%) were known to recruit  $\geq 1$  chick to independence (i.e., chick(s) surviving  $\geq 60$  days post-hatch). These data do not include females where hatch date could not be determined ( $n = 4$ ) or missing females ( $n = 13$ ), which prohibited me from ascertaining brood success. I assumed total brood loss when females no longer displayed brooding behavior or were located with other broodless females on  $\geq 2$  occasions (Gregg and Crawford 2009). Of the 25 broods I monitored to 60 days post-hatch, I identified total loss for 14 broods. Over the course of 3 breeding seasons, 12 females with broods were killed by predators or other mortality factors, indicating death during the brood-rearing period has a significant impact on sage-grouse reproductive effort in northeastern California.

### **Habitat Structure**

Over 3 breeding seasons, I measured stand characteristics at 63 nest sites and at 63 paired random points during the nesting period. Due to small sample size, observations of females nesting across consecutive years ( $n = 17$ ) and re-nests ( $n = 5$ ) were considered to be independent. Females used a variety of plants as nesting cover (Table 3) including: silver sagebrush (*A. cana*), big sagebrush, little sagebrush, antelope bitterbrush (*Purshia tridentata*), greasewood (*Sarcobatus vermiculatus*), Douglas rabbitbrush (*Chrysothamnus viscidiflorus*), horsebrush (*Tetradymia* spp.), crested wheatgrass (*Agropyron cristatum*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and basin wildrye (*Leymus cinereous*). No attempt was made to compare habitat characteristics between years because of small sample sizes within years.

Habitat characteristics at nest sites differed from random sites (Table 4). Grass height, percent litter, canopy cover of live shrubs, and visual obstruction was greater at nest sites, suggesting females selected sites with structurally more closed habitat for nesting. However, successful nests sites could not be discriminated from unsuccessful nest locations (Table 5). I incorporated vegetation height measurements recorded at the nest bowl (nearest shrub, grass, and forb) in my analysis to test for possible microsite differences between successful and unsuccessful nests only. Nest bowl grass height was taller at successful nest sites (mean = 26.3 cm  $\pm$  2.02) than unsuccessful nests (mean = 21.1 cm  $\pm$  2.13), although not significantly ( $F_{1,56} = 2.91$ ,  $P = 0.09$ ). Differences in nest bowl shrub ( $F_{1,56} = 1.48$ ,  $P = 0.23$ ) and nest bowl forb height ( $F_{1,56} = 0.02$ ,  $P = 0.89$ ) could not be distinguished between successful and unsuccessful nests.

## **Survival Analysis**

### **Nest Survival**

I estimated nest survival for 58 nests from 2007 to 2009. I attributed abandoned nests ( $n = 5$ ) to investigator disturbance and did not include these nests in my analysis. Assuming a 28-d exposure period (i.e., the number of days from nest initiation to hatch; Moynahan et al. 2007), I estimated the true probability of nest survival was 50% (i.e.,  $0.976^{28}$ ). If my estimate of true nest survival is extrapolated to include both the egg-laying (10 days) and incubation periods (28 days) to estimate nest success (e.g., Kolada et al. 2009a) my overall estimate of actual nest survival was 39%. The best-approximating model of  $D$   $R$  included the covariates Plant and Age (Table 6). Of the 16 models considered, candidate models that included the covariate GrassHt also received support, suggesting there is evidence that  $DSR$

is higher at nest sites that contain taller residual grass than nest sites characterized with shorter grass height ( $\beta = 0.35$ ,  $SE = 0.22$  SE, 95% CI = -0.077-0.777). Models that held daily survival probability constant or which considered the remaining individual covariates of interest received little to no support ( $\Delta AIC_c > 3.87$ ), suggesting RValue, ShrubHt, ShrubCov, GrassCov, and VOR were less useful predictors of nest success for my study area. Nest attempt (first or second nesting attempts, respectively) did not improve the best-approximating model. Females that nested under vegetation other than sagebrush had increased nest survival probabilities (Figure 2). Nest success during a 77-d nesting season was dependent upon age and adult female sage-grouse ( $S = 0.59$ , 95% CI = 0.441-0.744) appeared more likely to nest successfully than yearling females ( $S = 0.31$ , 95% CI = 0.134-0.642) in northeastern California (Figure 3).

### **Brood Survival**

I monitored 42 broods 1-3 times per week from hatch to 10 weeks post-hatch. Those broods that disappeared due to a damaged radio transmitter and/or undetected movement outside the study area were right-censored on the date the brood was last observed ( $n = 13$ ).

Additionally, I excluded females when hatch date could not be determined ( $n = 4$ ) from my survival analysis.

I evaluated 26 candidate models to assess the factors affecting brood survival rates (Table 7), however, I could not rule out the null model as the best-approximating model of my data. Based on the null model, the overall survival rate of broods to 10 weeks post-hatch was 50% ( $SE = 0.09$ ) across all 3 years, with the greatest mortality occurring during the late brood-rearing period (i.e.,  $\geq 7$  weeks post-hatch; Figure 4). I identified 8 additional

competing candidate models (i.e.,  $\Delta AIC \leq 2$ ) to explain brood survival (Table 7), however, based on the cumulative  $AIC_c$  weight for each of the individual covariates I observed considerable model selection uncertainty ( $AIC_c$  weight  $< 0.90$ ). Thus, it is possible that the covariates I examined were insufficient to describe brood survival or if there was a difference in brood survival rates in northeastern California, they are not explained by the covariates included in my analysis.

### **Female Survival Analysis**

Over the 3 years of my study, I recorded 43 known mortalities. Females that died within a 2-week period after initial marking ( $n = 4$ ) were not included in my survival analysis. In addition, those females where fate of the individual was unknown due to a damaged radio transmitter and/or undetected movement outside the study area were right-censored on the date the individual was last known alive ( $n = 34$ ).

I attempted to assess the probable cause of mortality of radiomarked females by examining diagnostic sign at the recovery site and classified each as predation, legal harvest, other anthropogenic-related factors, or unknown. I recovered 1 carcass unscathed and cause of death was not determined. Additionally, 1 female was dismembered by farm machinery and 1 death was attributed to investigator error. Hunting removed 1 bird and the majority of mortalities were attributed to predation ( $n = 34$ ). Because it is possible that carcasses might have been subsequently scavenged after mortality, making it difficult to differentiate kills from scavenging events (e.g., Bumann and Stauffer 2002), I considered the diagnostic sign at kill sites as unreliable for identifying predators of female sage-grouse. Therefore, I did not distinguish between avian or mammalian predation. However, potential mammalian and

avian predators (Schroeder and Baydack 2001) observed on my study area included coyotes, bobcats, red-tailed hawks (*Buteo jamaicensis*), rough-legged hawks (*B. lagopus*), northern harriers (*Circus cyaneus*), golden eagles (*Aquila chrysaetos*), Swainson's hawks (*B. swainsoni*), and ferruginous hawks (*B. regalis*).

I evaluated 26 candidate models to assess the factors affecting survival rates of female sage-grouse over an 8-month period (i.e., breeding season through autumn migration; Table 8). I identified 2 competing candidate models (i.e.,  $\Delta AIC \leq 2$ ) to explain the probability of survival, which both included the Fate covariate as part of the competing model structure (Table 8). The best-approximating model (based on the candidate model with the lowest AIC) had an AIC weight of 0.66 suggesting model uncertainty. However, the cumulative AIC weights for the covariate Fate across all candidate models containing that individual covariate of interest was 0.97, indicating there was considerable evidence that female survival was a function of nest fate (Table 9). Linear (T) or quadratic (T<sup>2</sup>) time trends were not evident in my model selection results. Additionally, there was no support for the inclusion of additional individual covariates to the best-approximating model, indicating that the remaining covariates (Age or Condition) did not improve the fit to this model.

Based on model-averaged estimates, the survival of female sage-grouse during the 8-month period was 0.58 (SE = 0.07) across my 3-year study period, with the lowest survival occurring during early April and mid- to late May and again during the autumn (Figure 5A). Mortalities during the spring coincided with nest initiation, losses during incubation, and following hatch when successfully nesting females were tending chicks. Mortalities in September coincided with dispersal and autumn migration.

To further examine the effect of nest fate on female survival, I used a subset of seasonal encounter histories from females that nested successfully ( $n = 39$ ) and known failed nesters ( $n = 28$ ) and excluded non-nesting females or females where nest fate was unknown or could not be ascertained ( $n = 34$ ) from my analysis. Estimates of breeding season survival from the subset of data were higher among known failed nesters ( $S = 0.69$ ,  $SE = 0.10$ ) than those females that nested successfully ( $S = 0.53$ ,  $SE = 0.09$ ), suggesting female sage-grouse are exposed to greater mortality risk during incubation and brood-rearing periods (Figure 5B).

## DISCUSSION

Annual variation in reproductive success has a significant impact on sage-grouse abundance (Connelly et al. 2011). Nest initiation rates (97%) in my study were similar to nest initiation rates reported from 11 studies in Alberta, Canada; and Colorado, Idaho, Montana, Oregon, Utah, Washington, and Wyoming, USA (mean = 80%, range = 63–100%; Connelly et al. 2004). Similarly, apparent nest success of radiomarked females in my study (56%) was similar to findings in other states, which ranged from 15% to 86% (Schroeder et al. 1999). However, those studies likely overestimated nest success relative to actual nest survival because apparent nest success does not account for the lower detection probability of failed nesters (Mayfield 1961, 1975). Unlike traditional estimates of nest success, maximum likelihood-based estimators (MLE) allow visitation intervals to vary among observations and make no assumptions about when nest failure occurs within an interval (Rotella et al. 2004). Thus, the use of a MLE of daily survival probability is recommended over the use of apparent nest success estimates. The apparent nest success I observed in northeastern

California (56%) was higher than my estimates of the true probability of a nest surviving from initiation to hatch (50%). My overall estimate of actual nest survival (50%) was also higher than estimates reported for studies in northern Montana (e.g., ranging from 24% to 42%; Moynahan et al. 2007) and overall estimates of nest survival (43.4%) in Mono County, California (Kolada et al. 2009a) that also used MLE to estimate nest success. However, Kolada et al. (2009a) used an exposure period of 38 days, representing both the egg-laying period (10 days) and incubation period (28 days) to estimate nest success. Thus, nest success in Mono County would have been even greater relative to previous studies using MLE (e.g., Moynahan et al. 2007) had a comparable exposure period been used. When my estimate of true nest survival was extrapolated to include egg-laying, my overall estimate of actual nest survival (39%) is consistent with previous studies in California (Kolada et al. 2009a).

Although the nest success I observed was similar to those reported across the geographic range of sage-grouse, nest success has been observed to vary substantially both spatially and temporally (Chi 2004, Taylor et al. 2012). Thus, low nest survival during some years might be contributing to population declines within my study area and appears to be regulated by vegetative structure (e.g., taller residual grass) important to sage-grouse nest survival.

The renesting rate from my study (18%) was lower than those reported from 9 studies in Alberta, Colorado, Idaho, Oregon, and Washington (mean = 29%, range = 9–87%; Connelly et al. 2004). However, probability of renesting in northeastern California was likely influenced by the timing of nest depredations (on average, the majority of unsuccessful first nests were incubating approximately 20 days prior to nest depredation). Similarly, other studies found that sage-grouse for which initial nests failed late in incubation were less likely

to renest than those that lost nests early in incubation (Schroeder 1997, Gregg et al. 2007). In addition, it is likely that some undetected first nests failed during laying and prior to incubation, which would result in misclassification of some renests as initial nest attempts. Clutch size of first nests in my study was extremely variable (range = 3–11 eggs), but was similar to mean clutch size previously reported for the species (Wallestad and Pyrah 1974, Sveum 1995, Schroeder 1997, Aldridge and Brigham 2001). Differences in clutch size was attributed to the difficulty in estimating clutch size precisely (because eggs were counted following hatch some counts were likely low as egg shells might have been removed by scavengers of sage-grouse nests; Schroeder 1997). Other demographic parameters were comparable to those reported across the geographic range of sage-grouse.

Females used a variety of plants as nesting cover. Although sage-grouse typically nest under sagebrush (Patterson 1952, Klebenow 1969, Connelly et al. 1991, Gregg et al. 1994, Sveum et al. 1998, Moynahan et al. 2007), these studies have also documented that sage-grouse used plants other than sagebrush for nest sites, suggesting sage-grouse selection of nest sites is based on vegetation structure more than plant species. I found similar results in northeastern California, with 51% (40/78) of nests located under sagebrush plants. Connelly et al. (1991) found that nests under non-sagebrush plants were less successful. In contrast, Popham and Gutierrez (2003) reported moderately higher nest success in northeastern California when females nested under non-sagebrush plants (42%) compared to those that nested under big sagebrush (31%). In Mono County, California, Kolada et al. (2009b) also found increased cover of shrubs other than sagebrush increased nest survival of sage-grouse. Similarly, in my study, nest success appeared to be influenced by nest cover.



Sage-grouse use of non-sagebrush plants suggests sagebrush nesting habitat is limited on my study area. Sagebrush canopy cover was considerably lower in my study area (approximately 10% on random plots) compared with sagebrush cover described across the geographic range of sage-grouse (>15%; e.g., Connelly et al. 2000). Limited sage-grouse nesting information is available for northeastern California, however, Popham and Gutierrez (2003) also found that sage-grouse in Lassen County used more diverse vegetation than previously reported and concluded that the observed response was due to a landscape altered by anthropogenic factors.

Several studies have described sage-grouse nesting habitat, selection of habitat components by females, and the relationship of nest site characteristics with habitat availability (see Schroeder et al. 1999). In Montana, successful nests had greater shrub cover surrounding the nest site and were associated with cover types with higher density of shrub cover than unsuccessful nests (Wallestad and Pyrah 1974). Other authors noted residual grass cover (Klebenow 1969, Moynahan et al. 2007) and grass height (Wakkinen 1990) were related to nest-site selection and nest success. Gregg et al. (1994) and DeLong et al. (1995) identified relationships between vegetational cover and successful nesting by sage-grouse. In contrast, Kolada et al. (2009b) and Holloran et al. (2005) found no association between residual grass height or cover and daily nest survival. Results from my study indicated tall, residual grass cover influenced nest success of sage-grouse in northeastern California and is consistent with results from previous studies that indicate residual grass cover is positively correlated with nest success.

Nest and brood survival have been identified as the most critical factors associated with sage-grouse demography and population size (Aldridge and Brigham 2001, Gregg 2006, Beck et al. 2006). Overall brood success in my study (44%) was similar to that recorded in north-central Washington (49.5%; Schroeder 1997) where sage-grouse populations are declining (Connelly et al. 2004, Garton et al. 2011). Population trends in Lassen County (i.e., the peak number of males per active lek) decreased 20-30% from 2006 to 2008 and increased by 27% in 2009 (CDFG, unpublished data). Of the 25 broods I monitored to 10 weeks post-hatch, 14 (56%) suffered total brood losses and few chicks survived the 2007 and 2009 breeding seasons, ultimately recruiting few yearlings in the next spring's breeding population. Previous studies report that approximately 45% of all birds captured during the breeding season are yearlings (Dalke et al. 1963, Wallestad 1975). I observed similar results in my study. Over 3 breeding seasons, the proportion of yearlings captured varied annually (approximately 40% in 2007, 36% in 2008, and 45% in 2009), suggesting recruitment was low for sage-grouse in northeastern California during some years. If brood success and chick survival account for annual changes in population size observed on my study area then understanding the mechanisms accounting for the relatively poor recruitment of sage-grouse chicks would be of critical importance for maintaining the long-term viability of sage-grouse populations in northeastern California.

Sage-grouse chick survival is highly variable and estimates of brood survival range from 16% to 68% across their geographic range (Bean 1941, Rothenmaier 1979, Schroeder 1997, Aldridge and Brigham 2001). In Idaho, Beck et al. (2006) found that once juvenile sage-grouse reached 10 weeks of age they experienced low to moderate mortality (14-36%).

Thompson (2012) also found chick survival increased with age, however, mortalities still accounted for a significant loss of chicks through 16 weeks of age. Although chick survival was not directly measured in my study, brood survival varied from 44% to 59% on an annual basis. My findings are consistent with those found in other gallinaceous species (Riley et al. 1998, Fields et al. 2006) and sage-grouse (Gregg et al. 2007, Aldridge and Boyce 2007, Thompson 2012). Recent studies have identified the importance of chick survival in maintaining population growth and persistence among galliforms (Wisdom and Mills 1997, Clark et al. 2008, Sandercock et al. 2008, Hagen et al. 2009). Thus, high mortality of sage-grouse chicks (0-10 weeks of age) is likely an important factor related to sage-grouse declines in northeastern California. Although sage-grouse chick survival directly affects recruitment into the autumn population and, ultimately, our understanding of the long-term declines in sage-grouse populations, factors influencing chick survival remain largely unknown and represent the largest gap of knowledge in sage-grouse reproductive ecology (Crawford et al. 2004). In my study, the null model with constant apparent survival was the best-approximating model of brood survival, suggesting my sample size was not sufficient to distinguish clearly among all competing candidate models. Thus, future efforts should attempt to obtain data that are sufficient to assess annual variation in brood survival, reduce model selection uncertainty, and assess cause-specific mortality of chicks.

Female survival, evaluated over an 8-month period (Mar-Oct), was 58% with the lowest survival occurring during the breeding season (i.e., nesting and brood-rearing) and again during autumn. Over 3 breeding seasons, predators killed 3 incubating females and 12 females with broods. Further, 75% of mortalities of females with broods occurred  $\geq 7$  weeks

post-hatch. Variation in female survival was dependent upon nest success during the breeding season. Successfully nesting females appeared to be more susceptible to predation or other mortality factors during incubation and brood-rearing, suggesting an added cost to survival for females during the nesting and brood-rearing period in my study. Although I did not evaluate the possible effects of observer visits on survival rates, I monitored successful and unsuccessful females in the same way and do not believe observer effects contributed to the lower survival rates of females that nested successfully. Successful nesters might be more visible during the brood-rearing period, which could have predisposed successful female sage-grouse to greater vulnerability to predation or other mortality factors.

Decreased survival rates of nesting and brood-rearing females have been reported in other prairie grouse species. In eastern Washington, McDonald (1998) found the probability of survival of Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) was significantly lower for females with broods compared to broodless females. Survival was also considerably lower for female plains sharp-tailed grouse (*T. p. jamesi*) during the breeding season in Alberta, Canada and accounted for approximately 82% of the annual mortality (Manzer and Hannon 2008). Similarly, Hagen et al. (2007) found the annual variation in seasonal survival of lesser prairie-chickens (*T. pallidicinctus*) in Kansas was closely related to mortality rates of incubating females on nests. In Kansas, female greater prairie-chickens (*T. cupido*) were susceptible during incubation and brood-rearing suggesting predation of nests and females was the main demographic factor limiting population viability (Augustine and Sandercock 2011, McNew et al. 2012). These results suggest increased mortality risk during the breeding season can have a major impact on grouse demography.

My research suggested that female mortality during the breeding season could potentially be influencing population declines of sage-grouse in my study area. Land management practices that reduce key habitat components for survival and reproductive success in sagebrush-steppe communities will be detrimental to the recovery of sage-grouse populations. Loss and degradation of existing sagebrush habitats and conversion of large tracts of sagebrush to other vegetation (e.g., annual grasslands, juniper woodlands) will likely result in declining sage-grouse populations in northeastern California because of reduced nest and brood success. Connelly et al. (2000) recommended that 15-25% sagebrush canopy cover, >10% forbs, >15% grass and an herbaceous height of 18 cm is required for sage-grouse breeding habitats. In my study, sage-grouse used areas with only 8-11% sagebrush cover for nesting. My estimates suggest that sagebrush canopy is lower than those recommended in the published guidelines for the management of sage-grouse and suggests sagebrush availability was low across my study area. Aldridge and Brigham (2002) also reported a lack of sagebrush cover at the northern fringe of the sage-grouse range in Canada and speculated unsuitable nesting and brood-rearing habitat contributed to decreases in productivity. Thus, management of sage-grouse in northeastern California should focus on habitat manipulations that reduce mortality during the nesting and brood-rearing periods.

## **MANAGEMENT IMPLICATIONS**

My results demonstrate the loss and degradation of existing sagebrush communities and conversion of large tracts of sagebrush to other vegetation (e.g., annual grasslands, juniper woodlands) will result in declining sage-grouse populations in northeastern California because of reduced nest and brood success. If management goals are to mitigate both

historical and recent habitat loss, management efforts for sage-grouse in northeastern California must focus on habitat manipulations that decrease mortality during the nesting season and brood-rearing period. Land management practices should minimize the impact of exotic annual grasses and invasion of western juniper on sagebrush-steppe communities and create suitable habitat structure for nesting, brood-rearing, and winter habitats.

Implementation of land management practices, which result in increased forb production and arthropod abundance, will influence reproductive success of pre-laying sage-grouse by improving their physiological condition and potentially influencing nesting and reneesting (Barnett and Crawford 1994), as well as enhancing brood survival and recruitment of chicks (Drut et al. 1994, Gregg and Crawford 2009). Thus, managers must ensure sage-grouse breeding habitats meet published guidelines for sagebrush canopy cover (15-25%), forb (>10%) and native, perennial grass (>15%) cover, and an herbaceous height of 18 cm (Connelly et al. 2000).

Although this study, examined demographic parameters and factors influencing nest and brood survival of sage-grouse in northeastern California, careful attention still needs to be given to managing sagebrush-steppe habitats during other life history stages. Extreme, prolonged weather during the winter (e.g., extremely low temperatures and snow depth) can affect survival rates of sage-grouse (Moynahan et al. 2006, Anthony and Willis 2008), particularly if sagebrush-steppe habitat that provides food and cover on sage-grouse winter ranges is limited. Consequently, ensuring winter habitat with adequate sagebrush canopy cover (12-43%) and height (25-56 cm; Connelly et al. 2000) will be necessary to support wintering populations. In the long-term, management practices that achieve a mosaic of food

and cover suitable for sage-grouse and that recast the balance of native herbaceous species in degraded sagebrush communities will be necessary for restoration of sagebrush ecosystems in northeastern California, and ultimately, the recovery of sage-grouse populations occupying the western periphery of the species' range.

## LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. *Ecological Applications* 17:508–526.
- Aldridge, C. L., and R. M. Brigham. 2001. Nesting and reproductive activities of greater sage-grouse in a declining northern fringe population. *Condor* 103:537–543.
- Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. *Journal of Wildlife Management* 66:433–444.
- Anthony, R. G., and M. J. Willis. 2008. Survival rates of female greater sage-grouse in autumn and winter in southeastern Oregon. *Journal of Wildlife Management* 73:538–545.
- Armentrout, D. J., and F. Hall. 2005. Conservation strategy for sage-grouse (*Centrocercus urophasianus*) and sagebrush ecosystems within the Buffalo-Skedaddle population management unit. Bureau of Land Management, Eagle Lake Field Office, Susanville, California, USA.
- Augustine, J. K., and B. K. Sandercock. 2011. Demography of female greater prairie-chickens in unfragmented grasslands in Kansas. *Avian Conservation and Ecology* 6:2. <<http://www.ace-eco.org/vol6/iss1/art2/>>. Accessed 12 October 2012.
- Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. *Journal of Range Management* 47:114–118.

- Bean, R. W. 1941. Life history studies of the sage grouse (*Centrocercus urophasianus*) in Clark County, Idaho. Thesis. Utah State College, Logan, Utah, USA.
- Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. *Wildlife Society Bulletin* 34:107-1078.
- Blaisdell, J. P., R. B. Murray, and E. D. McArthur. 1982. Managing inter-mountain rangelands – sagebrush-grass ranges. U.S. Department of Agriculture, Forest Service General Technical Report INT-134.
- Braun, C. E. 1986. Changes in sage grouse lek counts with advent of surface coal mining. *Proceedings of Issues and Techniques in the Management of Impacted Western Wildlife* 2:227-231.
- Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? *Proceedings of the Western Association State Fish and Game Wildlife Agencies* 78:139-156.
- Bumann, G. B., and D. F. Stauffer. 2002. Scavenging of ruffed grouse in the Appalachians: influence and implications. *Wildlife Society Bulletin* 30:853-860.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Call, M. W. 1979. Habitat requirements and management recommendations for sage grouse. Technical Note 330. U.S. Department of Interior, Bureau of Land Management, Denver, Colorado, USA.
- Call, M., and C. Maser. 1985. Wildlife habitats in managed rangelands – the Great Basin of southeastern Oregon: sage grouse. U.S. Department of Agriculture, Forest Service General Technical Report PNW-187.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. *Journal of Forestry* 39:388-394.
- Chi, R. Y. 2004. Greater sage-grouse on Parker Mountain, Utah. Thesis. Utah State University, Logan, Utah, USA.
- Clark, W. R., T. R. Bogenschutz, and D. H. Tessin. 2008. Sensitivity analyses of a population projection model of ring-necked pheasants. *Journal of Wildlife Management* 72:1605-1613.



- Connelly, J. W., C. A. Hagen, and M. A. Schroeder. 2011. Characteristics and dynamics of greater sage-grouse populations. Pages 53-67 in S. T. Knick and J. W. Connelly, editors. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, Idaho, USA.
- Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 28:967-985.
- Connelly, J. W., M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Unpublished report. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.
- Connelly, J. W., W. L. Wakkinen, A. P. Apa, and K. P. Reese. 1991. Sage grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55:521-524.
- Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosely, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. Journal of Range Management 57:2-19.
- Crunden, C. W. 1963. Age and sex of sage grouse from wings. Journal of Wildlife Management 27:846-850.
- Dahlgren, D. K., T. A. Messmer, and D. N. Koons. 2010. Achieving better estimates of greater sage-grouse chick survival in Utah. Journal of Wildlife Management 74:1286-1294.
- Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. Journal of Wildlife Management 27:811-841.
- Daubenmire, R. F. 1959. A canopy coverage method of vegetation analysis. Northwest Science 33:224-227.
- DeLong, A. K., J. A. Crawford, and D. C. DeLong. 1995. Relationships between vegetational structure and predation of artificial sage grouse nests. Journal of Wildlife Management 59:88-92.

- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. *Journal of Wildlife Management* 74:1544-1553.
- Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994. Technical note: diets and food selection by sage grouse chicks in Oregon. *Journal of Range Management* 47:90-93.
- Fields, T. L., G. C. White, W. C. Gilgert, and R. D. Rodgers. 2006. Nest and brood survival of lesser prairie-chickens in west central Kansas. *Journal of Wildlife Management* 70:931-938.
- Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and S. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pages 293-381 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Gibson, R. M., and G. C. Bachman. 1992. The cost of female choice in a lekking bird. *Behavioral Ecology* 3:299-309.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224-231.
- Gregg, M. A. 2006. Greater sage-grouse reproductive ecology: linkages among habitat resources, maternal condition, and chick survival. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Gregg, M. A., and J. A. Crawford. 2009. Survival of greater sage-grouse chicks and broods in the northern Great Basin. *Journal of Wildlife Management* 73:904-913.
- Gregg, M. A., J. A. Crawford, M. S. Drut, and A. K. DeLong. 1994. Vegetational cover and predation of sage grouse nests in Oregon. *Journal of Wildlife Management* 58:162-166.
- Gregg, M. A., M. R. Dunbar, and J. A. Crawford. 2007. Use of implanted transmitters to estimate survival of greater sage-grouse chicks. *Journal of Wildlife Management* 71:646-651.
- Hagen, C. A., J. C. Pitman, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2007. Age-specific survival and probable causes of mortality in female lesser prairie-chickens. *Journal of Wildlife Management* 71:518-525.
- Hagen, C. A., B. K. Sandercock, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2009. Spatial variation in lesser prairie-chicken demography: a sensitivity analysis of

- population dynamics and management alternatives. *Journal of Wildlife Management* 73:1325-1332.
- Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous habitats. *Condor* 107:742-752.
- Holloran, M. J., B. J. Heath, A. G. Lyon, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2005. Greater sage-grouse nesting habitat selection and success in Wyoming. *Journal Wildlife Management* 69:638–649.
- Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997-2007. Pages 407-450 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Johnson, K. H., and C. E. Braun. 1999. Viability of an exploited sage grouse population. *Conservation Biology* 13:77-94.
- Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation for incomplete observations. *Journal of American Statistical Association* 53:457-481.
- Klebenow, D. A. 1969. Sage grouse nesting and brood habitat in Idaho. *Journal of Wildlife Management* 33:649-661.
- Knick, S. T., and S. E. Hanser . 2011. Connecting pattern and process in greater sage-grouse populations and sagebrush landscapes. Pages 383-405 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Kolada, E. J., M. L. Casazza, and J. S. Sedinger. 2009a. Ecological factors influencing nest survival of greater sage-grouse in Mono County, California. *Journal of Wildlife Management* 73:1341-1347.
- Kolada, E. J., J. S. Sedinger, and M. L. Casazza. 2009b. Nest site selection by greater sage-grouse in Mono County, California. *Journal of Wildlife Management* 73:1333-1340.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands – a viewpoint. *Journal of Range Management* 44:427-433.
- Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:486–491.

- Manzer, D. M., and S. J. Hannon. 2008. Survival of sharp-tailed grouse *Tympanuchus phasianellus* chicks and hens in a fragmented prairie landscape. *Wildlife Biology* 14:16- 25.
- Mayfield, H. R. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456–466
- McDonald, M. W. 1998. Ecology of Columbian sharp-tailed grouse in eastern Washington. Thesis. University of Idaho, Moscow, Idaho, USA.
- McNew, L. B., A. J. Gregory, S. M. Wisely, B. K. Sandercock. 2012. Demography of greater prairie-chickens: regional variation in vital rates, sensitivity values, and population dynamics. *Journal of Wildlife Management* 76:987-1000.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145-184 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. *Studies in Avian Biology* (vol. 38), University of California Press, Berkeley, California, USA.
- Miller, R. F., and J. A. Rose. 1995. Western juniper expansion in eastern Oregon. *Great Basin Naturalist* 55:37-45.
- Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. *Journal of Wildlife Management* 71:1773-1783.
- Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2006. Factors contributing to process variation in annual survival of female greater sage-grouse in Montana. *Ecological Application* 16:1529-1538.
- Patterson, R. L. 1952. The sage grouse in Wyoming. Sage Books Inc., Denver, Colorado, USA.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- Popham, G. P., and R. J. Gutierrez. 2003. Greater sage-grouse (*Centrocercus urophasianus*) nesting success and habitat use in northeastern California. *Wildlife Biology* 9:327-334.

- Riley, T. Z., W. R. Clark, D. E. Ewing, and P. A. Vohs. 1998. Survival of ring-necked pheasant chicks during brood-rearing. *Journal of Wildlife Management* 62:36-44.
- Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295-297.
- Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27.1:187-205.
- Rothenmaier, D. 1979. Sage grouse reproductive ecology: breeding season movements, strutting ground attendance and site characteristics and nesting. Thesis. University of Wyoming, Laramie, Wyoming, USA.
- Sandercock, B. K., W. E. Jensen, C. K. Williams, and R. D. Applegate. 2008. Demographic sensitivity of population change in northern bobwhite. *Journal of Wildlife Management* 72:970-982.
- Sandercock, B. K., K. Martin, and S. J. Hannon. 2005. Demographic consequences of age-structure in extreme environments: population models for arctic and alpine ptarmigan. *Oecologia* 146:13-24.
- Schneegas, E.R. 1967. Sage grouse and sagebrush control. *Transactions of the North American Wildlife and Natural Resource Conference* 32:270-274.
- Schroeder, M. A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. *Condor* 99:933-941.
- Schroeder, M. A., and R. K. Baydack. 2001. Predation and the management of prairie grouse. *Wildlife Society Bulletin* 29:24-32.
- Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). In *The Birds of North America*, No. 425. (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Springer, J. T. 1979. Some source of bias and sampling error in radio triangulation. *Journal of Wildlife Management* 43:926-935.
- Sveum, C. M. 1995. Habitat selection by sage grouse hens during the breeding season in south-central Washington. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Sveum, C. M., W. D. Edge, and J. A. Crawford. 1998. Nesting habitat selection by sage grouse in southcentral Washington. *Journal of Range Management* 51:265-269.

- Swensen, J. E., C. A. Simmons, and C. D. Eustace. 1987. Decrease of sage grouse *Centrocercus urophasianus* after ploughing of sagebrush steppe. *Biological Conservation* 41:125-132.
- Taylor, R. L., B. L. Walker, D. E. Naugle, and L. S. Mills. 2012. Managing multiple vital rates to minimize greater sage-grouse population growth. *Journal of Wildlife Management* 76:336-347.
- Thompson, T. R. 2012. Dispersal ecology of greater sage-grouse in northwestern Colorado: evidence from demographic and genetic methods. Dissertation. University of Idaho, Moscow, Idaho, USA.
- United States Department of Interior (USDI). 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. *Federal Register* 75:13910-14014 (23 March 2010).
- Vehrencamp, S. L., J. W. Bradbury, and R. M. Gibson. 1989. The energetic cost of display of male sage grouse. *Animal Behaviour* 38:885-896.
- Wakkinen, W. L. 1990. Nest site characteristics and spring-summer movements of migratory sage-grouse in southeastern Idaho. Thesis. University of Idaho, Moscow, Idaho, USA.
- Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. *Wildlife Society Bulletin* 20:425-426.
- Walker, B. L., and D. E. Naugle. 2011. West Nile virus ecology in sagebrush habitat and impacts on greater sage-grouse populations. Pages 127-142 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology Series (vol. 38)*, University of California Press, Berkeley, California, USA.
- Wallestad, R. O. 1975. Life history and habitat requirements of sage grouse in central Montana. Game Management Division, Montana Department of Fish and Game, Helena, Montana, USA.
- Wallestad, R. O., and D. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. *Journal of Wildlife Management* 38:630-633.
- West, N. E., and M. A. Hassan. 1985. Recovery of sagebrush grass vegetation following wildfire. *Journal of Range Management* 38:131-134.

- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Winward, A. H. 1991. A renewed commitment to management of sagebrush grasslands *in* Management in the sagebrush steppe. Agricultural Experiment Station. Oregon State University, Corvallis, Oregon, USA.
- Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. *Journal of Wildlife Management* 61:302-312.
- Wisdom, M. J., C. W. Meinke, S. T. Knick, and M. A. Schroeder. 2011. Factors associated with extirpation of sage-grouse. Pages 451-472 *in* Knick, S. T., and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Yocom, C. N. 1956. The sage hen in Washington State. *Auk* 73:540-550.

Table 1. R-value categories developed to provide a broad assessment of existing and potential greater sage-grouse habitat within the Lassen County, California study area (Armentrout and Hall 2005).

R-Value	Area (ha)	Percentage of habitat	Description
R0	50,229	8.4%	Areas with desired species composition which have sufficient, but not excessive, sagebrush canopy and sufficient grasses and forbs in the understory to provide adequate cover and forage to meet seasonal needs of sage-grouse (nesting, early brood, summer, and fall/winter).
R1	131,104	22%	Areas with potential to produce sagebrush plant communities that have good understory composition of desired grasses and forbs, but lacks sufficient sagebrush canopy.
R2	26,820	4.5%	Areas with potential to produce sagebrush plant communities that have a sagebrush overstory, but lack sufficient herbaceous understory.
R3	1,720	0.3%	Areas with potential to produce sagebrush communities that have not crossed the threshold to becoming juniper woodlands but are in various stages of becoming dominated by juniper (mature sagebrush and seedlings present).
X3	39,345	6.6%	Areas which have crossed the threshold from sagebrush plant communities (sagebrush seedlings absent) into juniper woodlands.
R4	277,058	46%	Areas with potential to produce sagebrush communities (mature sagebrush and seedlings present) but whose understories are currently dominated by annual grass, forbs, or bareground.
X4	70,836	12%	Areas that have crossed the threshold from sagebrush communities (seedlings absent) into annual grasslands, forbs, or bareground.



Table 2. Demographic parameters of radiomarked female greater sage-grouse, Lassen County, California, 2007-2009.

Parameter	Year			Totals
	2007	2008	2009	
Nest initiation, % ( <i>n</i> )	94 (15/16)	100 (34/34)	96 (25/26)	97 (74/76)
Renesting rate, % ( <i>n</i> )	20 (1/5)	7 (1/14)	33 (3/9)	18 (5/28)
Renest success, % ( <i>n</i> )	0 (0/1)	0 (0/1)	33 (1/3)	20 (1/5)
Nest success, % ( <i>n</i> )	50 (8/16)	49 (17/35)	61 (17/28)	56 (44/79)
Clutch size, (mean $\pm$ SE)	6.9 $\pm$ 0.45	7.5 $\pm$ 0.36	7.2 $\pm$ 0.37	7.3 $\pm$ 0.22
Brood Success, % ( <i>n</i> )	33 (2/6)	71 (5/7)	33 (4/12)	44 (11/25)

Table 3. Nest success and nest cover used by radiomarked female greater sage-grouse, Lassen County, California, 2007-2009.

Nest cover	Fate				Totals
	Successful	Depredated	Abandoned	Unknown	
Big sagebrush	12	12	0	0	24
Silver sagebrush	5	2	3	0	10
Little sagebrush	2	4	0	0	6
Douglas rabbitbrush	3	4	0	0	7
Greasewood	9	4	1	0	14
Antelope bitterbrush	1	0	0	0	1
Horsebrush	2	0	1	0	3
Crested wheatgrass	1	0	0	0	1
Bluebunch wheatgrass	1	0	0	0	1
Basin wildrye	1	0	0	0	1
Unknown <sup>1</sup>	7	3	0	1	11
Totals	44	29	5	1	79

<sup>1</sup>Nest cover was not measured.

Table 4. Habitat structure (mean  $\pm$  SE) at nest sites of radiomarked greater sage-grouse and paired random locations, Lassen County, California, 2007-2009.

Habitat Structure	Nest site ( <i>n</i> = 63)			
	Use	Random	<i>F</i>	<i>P</i> -value
Cover (%)				
Sagebrush	11.3 $\pm$ 1.14	9.8 $\pm$ 1.06	1.14	0.29
Shrub	17.1 $\pm$ 1.12	12.3 $\pm$ 1.00	7.78	<0.01
Grass	18.5 $\pm$ 1.43	16.2 $\pm$ 1.12	0.97	0.33
Forb	9.9 $\pm$ 0.85	11.4 $\pm$ 1.19	0.46	0.50
Litter	46.0 $\pm$ 1.87	39.7 $\pm$ 1.88	5.72	0.02
Bare ground	44.7 $\pm$ 1.96	50.3 $\pm$ 1.91	4.20	0.04
Height (cm)				
Shrub	49.8 $\pm$ 2.13	45.7 $\pm$ 2.45	1.63	0.20
Grass	17.6 $\pm$ 0.74	13.9 $\pm$ 0.69	13.74	<0.001
Forb	10.3 $\pm$ 0.62	8.9 $\pm$ 0.46	1.03	0.31
VOR (dm)	4.6 $\pm$ 0.24	2.9 $\pm$ 0.21	22.23	0.00

Table 5. Habitat structure (mean  $\pm$  SE) at successful and depredated greater sage-grouse nest sites, Lassen County, California, 2007-2009.

	Fate <sup>†</sup>			
Habitat structure	Successful ( <i>n</i> = 35)	Depredated ( <i>n</i> = 23)	<i>F</i>	<i>P</i> -value
Cover (%)				
Sagebrush	11.0 ± 1.65	11.3 ± 1.65	0.50	0.48
Shrub	17.4 ± 1.58	16.6 ± 1.78	0.14	0.71
Grass	18.2 ± 1.99	19.5 ± 2.42	0.25	0.61
Forb	10.0 ± 1.06	10.5 ± 1.68	0.00	0.95
Litter	47.2 ± 2.48	44.0 ± 3.32	0.49	0.48
Bare ground	46.7 ± 2.43	46.1 ± 3.76	0.33	0.57
Height (cm)				
Shrub	47.5 ± 2.87	51.9 ± 3.67	0.92	0.34
Grass	17.9 ± 1.01	17.1 ± 1.29	0.24	0.62
Forb	10.5 ± 0.89	10.7 ± 0.95	0.02	0.88
VOR (dm)	4.6 ± 0.31	4.6 ± 1.74	0.00	0.95

<sup>†</sup>Abandoned nests were excluded from our analysis.

Table 6. Candidate models and model selection results for estimation of daily survival rates of greater sage-grouse nests in Lassen County, California, USA, 2007-2009.

Model <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>	$\Delta$ AIC <sub>c</sub>	$w_i^c$	$K^d$	Deviance
S(Plant + Age)	129.3	0.00	0.23	3	123.296
S(Plant)	129.8	0.50	0.18	2	125.809
S(Plant + Age + GrassHt)	129.9	0.53	0.18	4	121.811
S(Plant + GrassHt)	130.3	0.97	0.14	3	124.263
S(Age)	132.1	2.74	0.06	2	128.047
S(GrassHt)	132.5	3.17	0.05	2	128.477
S(.)	133.2	3.87	0.03	1	131.187
S(InitiationDate)	134.1	4.81	0.02	2	130.121
S(Year)	134.5	5.22	0.02	3	130.537
S(NestAttempt)	134.6	5.28	0.02	2	130.591
S(T)	134.9	5.58	0.01	2	130.885
S(GrassCov)	135.1	5.75	0.01	2	131.063
S(ShrubHt)	135.1	5.81	0.01	2	131.121
S(RValue)	135.1	5.81	0.01	2	131.123
S(ShrubCov)	135.2	5.83	0.01	2	131.144
S(VOR)	135.2	5.84	0.01	2	131.152

<sup>a</sup>Candidate models include the effects of time (Year (2007-2009) and linear time trend (T)) and covariates including Age = age of female (yearling or adult), NestAttempt = whether the nest was an initial nest attempt or reneat, RValue = assessment of existing and potential sage-grouse habitat where the nest site was located (coded as 0 or 1 to distinguish among nests found in areas characterized by a high percentage of cheatgrass or juniper invasion versus areas with desired species composition), Plant = plant used as nesting cover (coded as 0 or 1 to distinguish between nests under sagebrush versus nests under non-sagebrush), and vegetative attributes most likely to influence nest survival including measures of shrub (ShrubHt) and grass height (GrassHt) at the nest bowl, shrub (ShrubCov) and grass (GrassCov) cover within 10 m of the area that contained the nest, and vegetation visual obstruction at the nest site (VOR).

<sup>b</sup>Akaike's Information Criterion corrected for small sample size

<sup>c</sup>AIC<sub>c</sub> weight

<sup>d</sup>Number of parameters

Table 7. Candidate models and model selection results for estimation of weekly survival rates of greater sage-grouse broods in Lassen County, California, USA, 2007-2009.

Model <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>	$\Delta$ AIC <sub>c</sub>	$w_i^c$	$K^d$	Deviance
S(.)	104.9	0.00	0.15	1	102.871
S(T)	105.3	0.38	0.12	2	101.212
S(Hatch)	106.4	1.47	0.07	2	102.307
S(Age)	106.4	1.50	0.07	2	102.334
S(Year)	106.5	1.64	0.07	3	102.476
S(T + Age)	106.7	1.80	0.06	3	100.578
S(T + Hatch)	106.8	1.87	0.06	3	100.647
S(RValue)	106.9	1.98	0.06	2	102.809
S(T + Year)	106.9	2.00	0.06	4	100.769
S(Clutch)	106.9	2.02	0.05	2	102.852
S(T + RValue)	107.2	2.30	0.05	3	101.073
S(T <sup>2</sup> )	107.2	2.34	0.05	3	101.118
S(T + Clutch)	107.3	2.39	0.05	3	101.160
S(T + Hatch + Age)	108.3	3.42	0.03	4	100.113
S(T + Hatch + Year)	108.5	3.61	0.02	4	100.313
S(Hatch + Week)	111.8	6.88	0.00	11	92.865
S(Age + Week)	111.8	6.95	0.00	11	92.940
S(T * RValue)	111.9	7.04	0.00	12	90.826
S(T * Hatch)	112.0	7.14	0.00	12	90.921
S(T * Age)	112.0	7.14	0.00	12	93.131
S(Year + Week)	112.0	7.15	0.00	12	93.143
S(RValue + Week)	112.1	7.24	0.00	11	93.234
S(Clutch + Week)	112.3	7.36	0.00	11	93.352
S(Week)	114.5	9.65	0.00	10	93.431
S(T * Clutch)	116.8	11.92	0.00	11	95.702
S(Year * Week)	118.9	14.03	0.00	21	84.099

<sup>a</sup>Candidate models included the effects of time, including Week, Year (2007-2009), and linear (T) or quadratic (T<sup>2</sup>) time trends and covariates such as Age = age of female (yearling or adult), Hatch = hatch date, Clutch = clutch size, and RValue = a broad assessment of existing and potential sage-grouse habitat. The dominant R-value for each female with a brood was identified as the R-value with the greatest number of locations.

<sup>b</sup>Akaike's Information Criterion corrected for small sample size

<sup>c</sup>AIC<sub>c</sub> weight

<sup>d</sup>Number of parameters

Table 8. Known-fate candidate models and model selection results of female greater sage-grouse bi-weekly survival (Mar-Oct) rates in Lassen County, California, USA, 2007-2009.

Model <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>	$\Delta$ AIC <sub>c</sub>	$w_i$ <sup>c</sup>	$K$ <sup>d</sup>	Deviance
S(Fate + Year * bi-weekly)	290.9	0.00	0.66	34	245.631
S(Fate * bi-weekly)	292.6	1.75	0.27	32	249.491
S(Fate + bi-weekly)	297.2	6.34	0.03	17	268.710
S(Fate)	299.3	8.42	0.01	2	295.277
S(Year * bi-weekly)	299.7	8.85	0.01	33	254.485
S(T <sup>2</sup> )	300.2	9.36	0.01	3	294.200
S(Age + Year * bi-weekly)	301.6	10.73	0.00	34	254.245
S(Condition + Year * bi-weekly)	301.7	10.88	0.00	34	254.398
S(Year + T <sup>2</sup> )	301.8	10.91	0.00	5	293.735
S(Complex + Year * bi-weekly)	301.8	10.93	0.00	34	254.450
S(Year * T <sup>2</sup> )	301.9	11.04	0.00	20	269.257
S(Complex * Year * bi-weekly)	303.4	12.64	0.00	48	241.119
S(T)	304.6	13.68	0.00	2	300.583
S(.)	305.5	14.64	0.00	1	303.500
S(Year + bi-weekly)	306.1	15.22	0.00	18	277.578
S(Condition + bi-weekly)	306.5	15.60	0.00	17	277.958
S(Age + bi-weekly)	306.5	15.61	0.00	17	277.970
S(Complex + bi-weekly)	306.6	15.69	0.00	17	278.050
S(Year)	307.1	16.27	0.00	2	303.119
S(Age)	307.4	16.56	0.00	2	303.418
S(Condition)	307.5	16.62	0.00	2	303.476
S(Complex)	307.5	16.64	0.00	2	303.491
S(bi-weekly)	310.7	19.86	0.00	16	278.072
S(Complex * bi-weekly)	312.6	21.69	0.00	32	265.207
S(Condition * bi-weekly)	313.0	22.16	0.00	32	259.299
S(Age * bi-weekly)	315.9	25.01	0.00	32	264.281

<sup>a</sup>Candidate models include the effects of time (bi-weekly), linear time trend (T), quadratic time trend (T<sup>2</sup>), year (2007, 2008, 2009), lek complex (Shaffer Mtn., Upper Smoke Creek, Madeline Plains, or Dodge Springs), Fate = successful nest vs. unsuccessful nest, Age = yearling vs. adult, and Condition (estimated using the residuals derived from the linear regression of wing chord on body mass recorded at time of capture; Vehrencamp et al. 1989).

<sup>b</sup>Akaike's Information Criterion corrected for small sample size

<sup>c</sup>AIC<sub>c</sub> weight

<sup>d</sup>Number of parameters

Table 9. Cumulative AIC<sub>c</sub> weight of individual covariates,  $\beta$ -estimates, and associated standard errors and 95% confidence intervals for Fate, Age, Condition, and Complex for female greater sage-grouse, Lassen County, California, 2007-2009.

Covariate	Cumulative AIC <sub>c</sub> weight		SE	95% Confidence interval
Fate	0.968	-0.687	0.238	-1.13 < < -0.20
Age	0.004	-0.101	0.355	-0.80 < < 0.59
Condition	0.006	0.002	0.017	-0.03 < < 0.04
Complex	0.004	-0.021	0.223	-0.46 < < 0.42

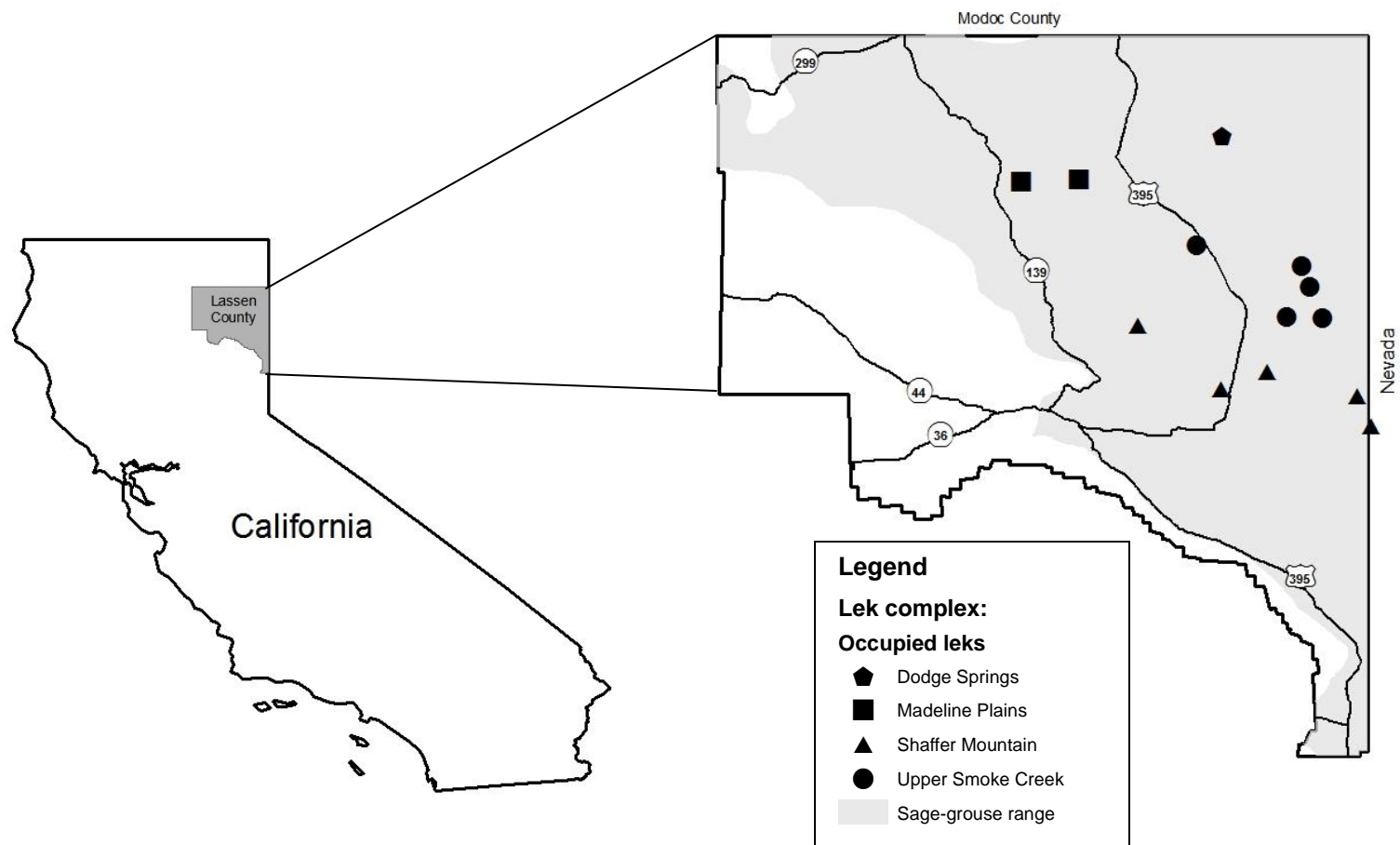


Figure 1. Map of the Lassen County, California study area. Symbols represent geographical locations of occupied greater sage-grouse lek sites and the distribution of respective lek complexes.

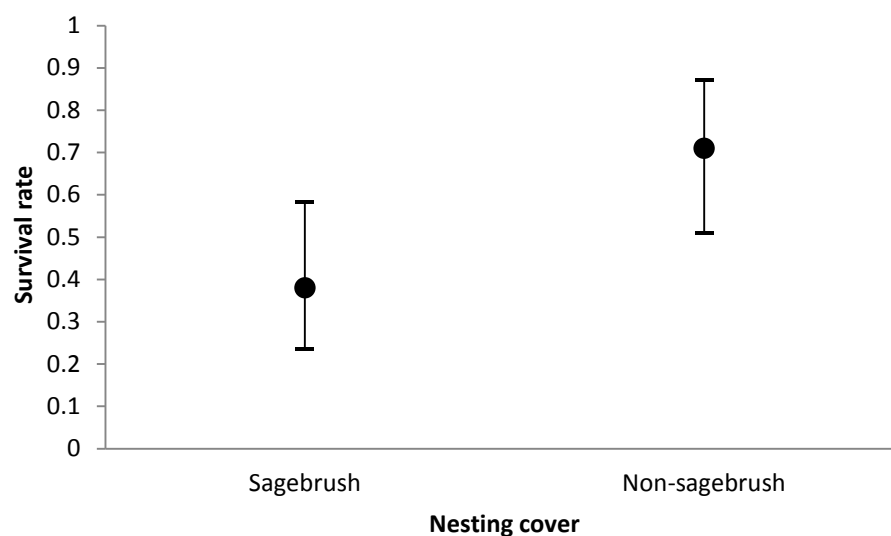


Figure 2. The role of plant species used as nesting cover on extrapolated nest survival rates during a 77-d nesting season and the associated 95% confidence intervals for greater sage-grouse nests under sagebrush versus nests under non-sagebrush plant species, Lassen County, California, 2007–2009.

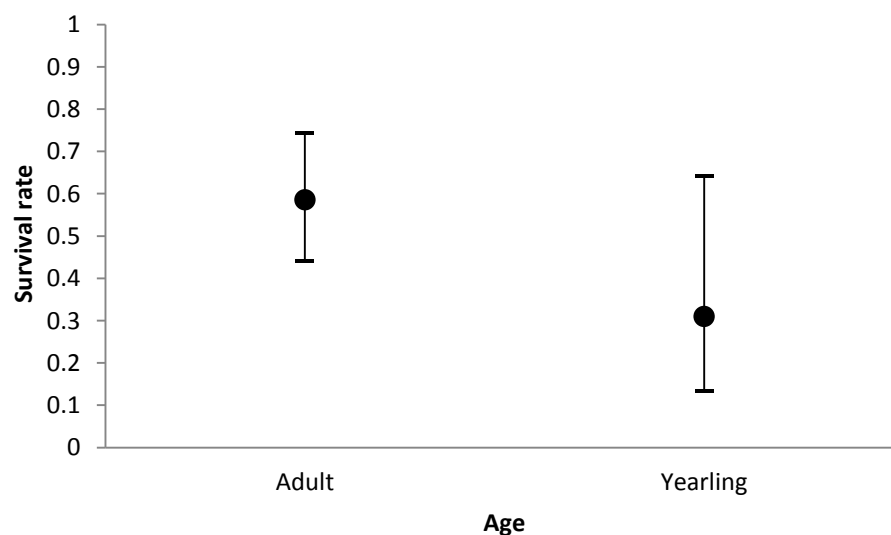


Figure 3. The role of female age on extrapolated nest survival rates during a 77-d nesting season and the associated 95% confidence intervals for greater sage-grouse nests, Lassen County, California, 2007–2009.



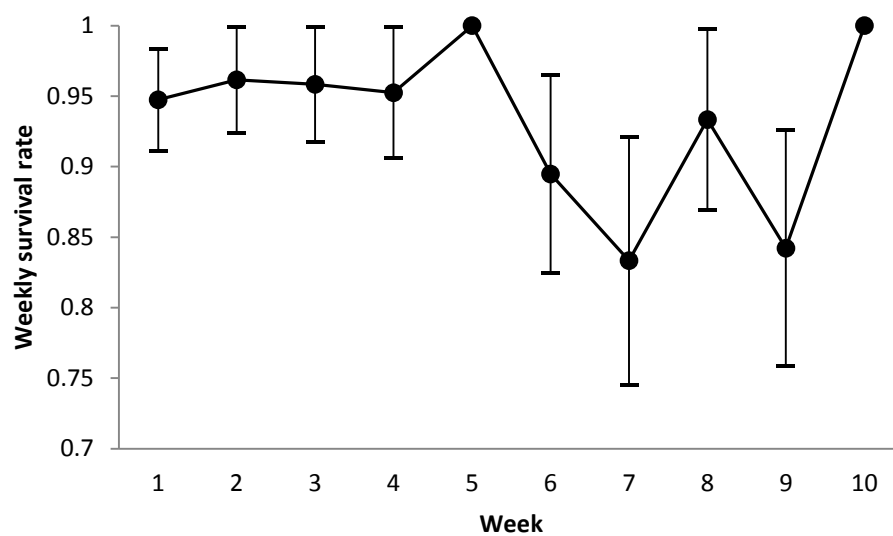


Figure 4. Weekly survival estimates ( $\pm$  SE) for greater sage-grouse broods, Lassen County, California, 2007-2009.

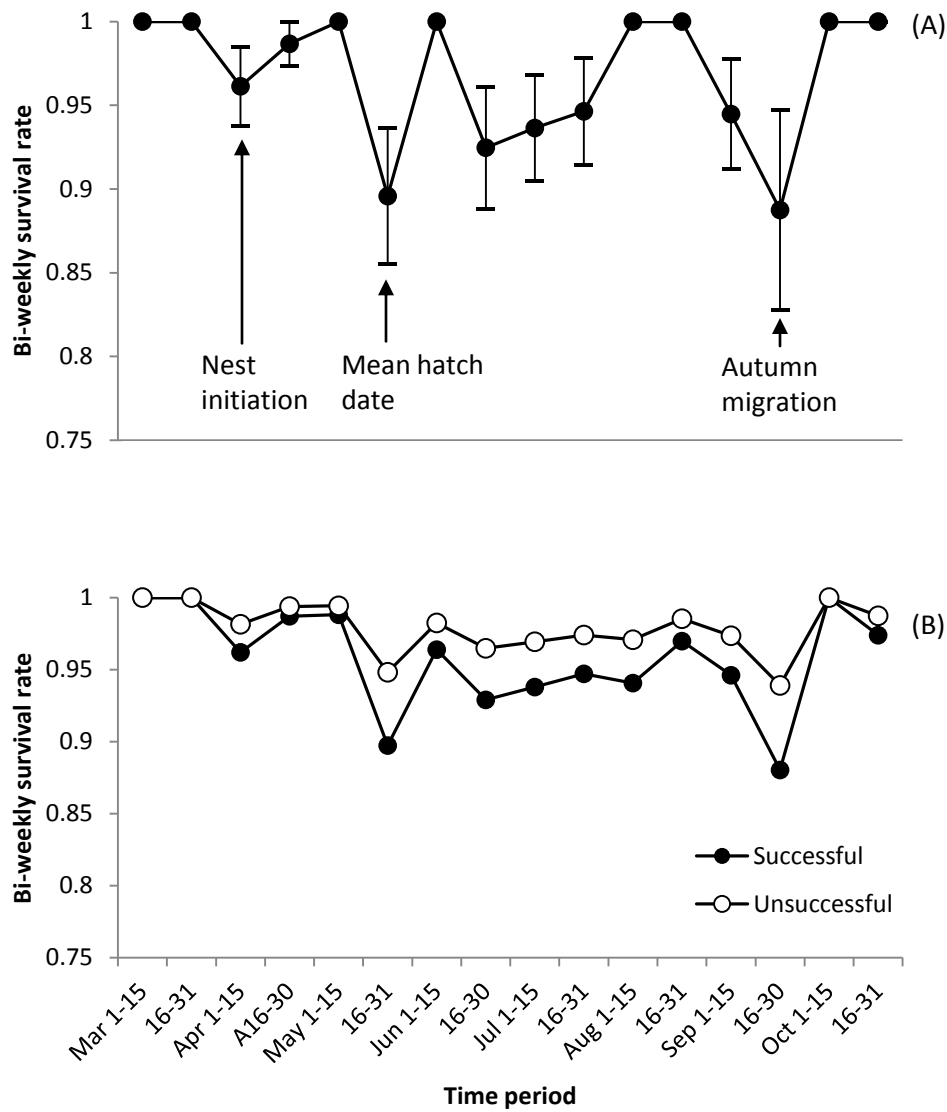


Figure 5. (A) Bi-weekly survival estimates ( $\pm$  SE) from Mar through Oct for female greater sage-grouse, Lassen County, California, 2007-2009. (B) Breeding season survival estimates for failed nesters (white circles) and those females that nested successfully (black circles) in northeastern California. Standard errors were omitted for clarity.

### **CHAPTER 3. DIURNAL SPACE USE AND SEASONAL MOVEMENT PATTERNS OF GREATER SAGE-GROUSE AT THE WESTERN PERIPHERY OF THEIR GEOGRAPHIC RANGE**

**ABSTRACT** – Greater sage-grouse (*Centrocercus urophasianus*) populations have declined throughout their geographic range and are considered both a candidate species under the United States Endangered Species Act and are currently regarded as a bird species of special concern in California. Although demographic parameters have been well documented for this species, populations occupying the western periphery of their range have largely remained unstudied. To gain insight into greater sage-grouse spatial ecology and to elucidate home range dynamics of this species, I examined diurnal space use and seasonal movement patterns of greater sage-grouse in a declining, peripheral population in northeastern California. I collected 3,072 diurnal locations from 132 greater sage-grouse radiomarked between 2007 and 2009. My results indicate that greater sage-grouse in my study used large areas and exhibited wide-ranging seasonal movements. Although female greater sage-grouse sought suitable nesting habitat within 5 km of a lek site, of the 29% of females nesting >5 km from an occupied lek site, 62% nested successfully. This result suggests that the proportion of nesting females located >5 km from an occupied lek site is important for population viability in northeastern California. Moreover, the annual range of birds in the population indicates that conserving greater sage-grouse habitat within 5 km of active lek sites is insufficient to maintain long-term population persistence. Therefore, larger areas of habitat are needed to conserve greater sage-grouse in northeastern California to accommodate

seasonal movements, annual variation in habitat requirements, and to maintain connectivity between lek complexes.

**KEYWORDS:** *Centrocercus urophasianus*, diurnal space use, greater sage-grouse, spatial ecology

Traditionally, home range analysis has been applied in wildlife research and management to elucidate the movement and space use of animals, determine species distributions, and gain insight into population dynamics, habitat use, and movement and/or dispersal of individuals. Burt (1943:351) was among the first to formally define an animal's home range as the "area traversed by the individual in its normal activities of food gathering, mating, and caring for young." Since then, numerous authors have reviewed and compared methods of home range estimators (e.g., van Winkle 1975, Worton 1987, Harris et al. 1990, Kernohan et al. 2001, Horne and Garton 2006b) resulting in extensive developments and advances in home range estimation and application. An accurate analysis and depiction of animal space use provides insights into an animal's behavior and their needs in terms of habitat size, shape, and juxtaposition. This is especially true for greater sage-grouse (*Centrocercus urophasianus*, hereafter sage-grouse), a candidate species under the United States Endangered Species Act (USDI 2010, 75FR:13910-14014) and a bird species of special concern in California (Remsen 1978, CDFG 1992).

Sage-grouse populations have declined throughout much of their geographic range (Connelly and Braun 1997, Braun 1998, Schroeder et al. 2004). As populations decline, peripheral populations have a higher risk of extinction and, ultimately, the geographic range of the species is expected to contract (Tracy and George 1992, Vucetich et al. 2000). This

outcome is of concern for declining sage-grouse populations along the western periphery of their range, such as sage-grouse populations in northeastern California, which have a higher risk of extirpation compared with larger, core populations (Wisdom et al. 2011). Studying peripheral populations would prove critical to our understanding of the dynamics associated with declining sage-grouse populations, particularly before such phenomena begin to affect populations within the core of sage-grouse range.

Information on the timing and distance of seasonal movements is necessary for: defining sage-grouse populations; identifying breeding, nesting, brood-rearing, and wintering habitats; and evaluating impacts of landuse practices on sage-grouse (Connelly et al. 1988). Previous studies describing space use and seasonal movement patterns of radiomarked sage-grouse (e.g., see Schroeder et al. 1999) indicated that sage-grouse are a highly vagile species, which are generally characterized by extensive seasonal movements (18-160 km; Connelly et al. 1988, Leonard et al. 2000) and large annual home ranges ( $>2700 \text{ km}^2$ ; Leonard et al. 2000). Although some data on seasonal movements and home range size are available across the geographic range of sage-grouse, information on diurnal space use in northeastern California is lacking and the spatial distribution of locations, annual and seasonal use areas, and fidelity between seasonal ranges have not been examined. Understanding seasonal movement patterns and space use is necessary for identifying annual variation in habitat requirements, evaluating sage-grouse response to landscape change, identifying critical habitats for protection and restoration, and is an essential step in effective long-term conservation planning and management of the species. Thus, the goal of my study was to examine the diurnal space use and seasonal movement patterns of sage-grouse in a declining,

peripheral population in northeastern California. Specifically, my objectives were to: 1) delineate annual and seasonal home ranges; 2) characterize the degree of overlap between seasonal home ranges; 3) describe seasonal movements of individuals to gain insight into the underlying distribution of space use; and 4) evaluate female fidelity to nest areas.

## **STUDY AREA**

This study was conducted in a 597,116 ha region of sagebrush-steppe habitat that included portions of the Buffalo-Skedaddle Population Management Unit (PMU) in Lassen County, California (Figure 1), where sage-grouse populations occupy the western periphery of the species' geographic range. Elevation ranged from 1,400 to 2,400 m. The predominant sagebrush types included Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), and little sagebrush (*A. arbuscula*). Other common vegetation communities included annual grasslands and juniper (*Juniperus occidentalis*) dominated woodlands. The study area was primarily composed of public lands (>60%) administered by the Bureau of Land Management. The primary landuse was domestic livestock grazing including both sheep and cattle. Other land uses included agricultural crops, primarily as irrigated alfalfa (*Medicago* spp.).

Sage-grouse populations in northeastern California have 4 distinct breeding ranges where leks are concentrated and around which females nest, which I refer to as a lek complex (Connelly et al. 2004). For the purposes of my study, I defined a lek complex as a group of sage-grouse associated with  $\geq 1$  active lek site in the same geographic proximity which, in my study area, were composed of 1 to 5 occupied leks (Figure 1). One of the largest lek complexes in Lassen County is the Upper Smoke Creek lek complex located close to the

Nevada border. This area contains a significant percentage of the breeding population of sage-grouse in Lassen County. The area around Dodge Springs, to the north of the Upper Smoke Creek lek complex, contains a lek complex on the periphery of the Lassen County sage-grouse population, where western juniper has encroached in recent years. The Madeline Plains lek complex is on the western edge of the Lassen County population and has declined significantly in the past 30 years. The Shaffer Mountain lek complex contains one of the larger breeding concentrations of sage-grouse in Lassen County and populations have remained relatively stable for the past 20 years.

## **MATERIALS AND METHODS**

### **Trapping and Radio-Marking**

I trapped sage-grouse opportunistically using spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992b) on or near lek sites from March through April 2007-2009 from 4 lek complexes (Shaffer Mountain, Upper Smoke Creek, Dodge Springs, Madeline Plains). I classified gender and age of captured birds by plumage characteristics and wing molt (Crunden 1963, Dalke et al. 1963). Sage-grouse were fitted with a serially-numbered aluminum leg band and a  $\leq 20$ -g necklace-mounted ATS radio transmitter (Advanced Telonics Systems, Inc., Insanti, MN, USA).

### **Diurnal Space Use and Seasonal Movement Patterns**

To assess diurnal space use and seasonal movement patterns, I located radiomarked sage-grouse weekly through direct observation using a hand-held Yagi antenna and portable receiver from March to October, 2007-2009. Due to limited personnel resources and restricted access to my study area due to weather, I was unable to monitor radiomarked sage-

grouse from the ground between November and February in any year of my study. Instead, aerial surveys from fixed-wing aircraft were conducted at approximately monthly intervals to assess seasonal movement patterns of sage-grouse.

### **Annual and Seasonal Ranges**

Composite home ranges of all marked birds within my study area were used to delineate annual and seasonal home ranges using a 95% fixed kernel home ranges and 50% fixed kernel core areas (Worton 1989) with the least squares cross-validation smoothing parameter (LSCV; Silverman 1986, Worton 1995). In addition, I calculated a 100% minimum convex polygon (MCP; Mohr 1947) to compare my annual and seasonal home range estimates with data from other studies. Home range estimates were mapped using the Home Range Tool (HRT; Rodgers et al. 2005) in ArcGIS 9.3 (Environmental Systems Research Institute, Inc., Redlands, CA, USA). Seasons were defined as spring (Mar-May), summer (June-Aug), autumn (Sept-Nov), and winter (Dec-Feb) following Leonard et al. (2000). I also examined annual home ranges delineated by lek complex using a 95% fixed kernel home range estimator with LSCV smoothing parameter. The Dodge Springs lek complex was excluded from my analysis due to inadequate sample size ( $n = 1$  radiomarked sage-grouse over the course of 3 breeding seasons), and the only known occupied lek site within the Dodge Springs lek complex was inactive during the last 2 years of my study. Because I was not concerned with identifying differences between years and gender, I pooled data across all 3 years from all radiomarked sage-grouse.



I estimated the degree of overlap between seasonal ranges 2 ways. First, I quantified the degree of home range overlap by overlaying MCP home range estimates and compared area-based measures calculated as:

$$\text{overlap} = A_{1,2}/[(A_1 + A_2) - A_{1,2}]$$

where  $A_1$  and  $A_2$  represent the area used in the first and second seasons, respectively, and  $A_{1,2}$  is the area shared by both seasons (Millspaugh et al. 2004). Second, I calculated the volume of intersection index (VI), which directly compares space-use sharing among seasons (Seidel 1992). The VI statistic was calculated as:

$$\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} [\hat{f}_1(x,y), \hat{f}_2(x,y)] dx dy$$

where  $f_1$  and  $f_2$  are the adjacent seasonal home ranges. The resulting value ranges from 0 for no overlap (i.e., implying no overlap in space use) to 1 for complete overlap between the 2 distributions.

### **Individual Home Range Analysis**

I attempted to collect >30-50 location estimates per radiomarked individual (Seaman et al. 1999), however, my ability to collect adequate sample sizes for individual home range analysis was limited as a result of incomplete data due to predation or other mortality factors, damaged radio transmitter(s) and/or undetected movement(s) outside the study area, which precluded my ability to detect and monitor individuals, restricted access to my study area due to weather, and limited personnel resources. Thus, I assumed an individual was adequately sampled to sufficiently quantify diurnal space use if  $\geq 20$  radio telemetry locations were

obtained. Although fixed kernel density estimates with LSCV have traditionally been recommended for home range analysis (Worton 1995, Seaman and Powell 1996, Seaman et al. 1999, Kernohan et al. 2001), Seaman et al. (1999) reported poor performance of LSCV when sample sizes are  $<30$ . As an alternative, Horne and Garton (2006a) recommended using likelihood cross-validation (CV; Silverman 1986), particularly at sample sizes  $< \sim 50$ . Accordingly, I calculated individual home ranges for all sage-grouse with sample sizes  $\geq 20$  locations using the 95% fixed kernel method using the HRT (Rodgers et al. 2005) for ArcGIS 9.3. Because my study was confounded by limited sample sizes, I used Animal Space Use 1.3 (Horne and Garton 2009) to estimate the smoothing parameter ( $h$ ) using the likelihood CV smoothing parameter.

To examine the spatial distribution of seasonal locations, I computed the central tendency in locations (e.g., mean center calculated for  $\geq 3$  locations per season) for each individual using CrimeStat III (2004). The linear distance (km) sage-grouse moved was assessed by calculating the straight-line Euclidean distance from the lek of capture to mean center of the spring seasonal ranges. In addition, I computed linear distances that sage-grouse moved between spring and summer, summer and autumn, and autumn and winter ranges, respectively, from geographic coordinates calculated for each seasonal range mean center.

To evaluate gender-specific variation in movements and home range sizes, I compared home range overlap across gender using the VI statistic (Siedel 1992). Siedel (1992) reported large sampling errors were associated with VI statistics when the numbers of individual observations are low ( $<50$  locations). Based on Siedel's (1992) observations, my

location data were not sufficient to calculate VI for individual sage-grouse. Rather, seasonal locations of each radiomarked sage-grouse were combined for females ( $n = 1,902$  telemetry locations) and males ( $n = 563$  telemetry locations), respectively. Additionally, I calculated cumulative home range estimates by gender (95% fixed kernel method with the LSCV smoothing parameter) for location point data using the HRT (Rodgers et al. 2005) for ArcGIS 9.3.

### **Nest Site Fidelity**

I calculated the median and mean lek-to-nest distance (nearest lek and lek of capture) for all nesting females. To evaluate fidelity to nest areas I calculated the straight-line Euclidean distance between first nests and renests and nesting attempts across consecutive years. I calculated a two-sample  $t$ -test to assess whether age class influenced the distance between first nests and renests. In addition, I tested for effects of age and nest fate on the distance between nest sites in subsequent years.

The current management guidelines for sage-grouse (Connelly et al. 2000) recommend using leks as focal points for managing nesting habitat and suggest protecting areas within 3 km of occupied leks in areas characterized by uniformly distributed habitat and within 5 km of active lek sites in more heterogeneous landscapes. Accordingly, I mapped all known active lek sites within the Lassen County study area and placed 3- and 5-km radius buffers around all active lek sites to identify whether nest distribution was related to lek location (Figure 2). Due to a potential lack of independence, renests ( $n = 5$ ) and nests from the same bird in consecutive years ( $n = 17$ ) were omitted from analysis.

## RESULTS

### Annual and Seasonal Ranges

I collected a total of 3,072 diurnal locations from 132 radiomarked sage-grouse (89 female and 43 male) pooled over 3 years (2007-2009). Based on the 100% MCP home range estimator, the annual range of sage-grouse in Lassen County comprised 3,382 km<sup>2</sup> (Figure 3). Comparatively, the annual 95% fixed kernel home range size was 750 km<sup>2</sup> and the combined 50% core area size was 81 km<sup>2</sup> for all radiomarked sage-grouse observed across the 3 years of my study (Figure 3).

Seasonal home ranges of the sage-grouse population in northeastern California largely overlapped (Table 1), likely due to the wide-ranging seasonal movements that sage-grouse made between lek complexes. The areas of overlap I observed between seasonal ranges using area-based measures were high, ranging from 0.67-0.90, suggesting space use sharing was similar across seasons. Comparatively, I observed similar seasonal variation in the spatial extent of home range overlap between seasons based on my results from the VI statistic (range = 0.59-0.72). However, differences between seasonal ranges might have been influenced by sample size and the statistical properties of the home range estimator. This is particularly true of the winter seasonal home range estimate, which was based on smaller sample sizes than other seasonal range estimates (Table 2).

The cumulative annual home range size was smaller for sage-grouse monitored in the Madeline Plains lek complex (37 km<sup>2</sup>,  $n = 650$ ) forming distinct ranges separate from the Upper Smoke Creek and Shaffer Mountain lek complexes (Figure 4). Sage-grouse from the Madeline Plains lek complex appeared to be non-migratory and seasonal ranges had no

overlap with neighboring lek complexes. In comparison, the annual home ranges of the Upper Smoke Creek ( $249 \text{ km}^2$ ,  $n = 1,198$ ) and Shaffer Mountain lek complexes ( $499 \text{ km}^2$ ,  $n = 1,171$ ) largely overlapped, likely due to the wide-ranging seasonal movements sage-grouse made between lek complexes (Figure 5). Sage-grouse captured in the Upper Smoke Creek lek complex exhibited similar directional movements, generally moving north between spring and summer ranges (Figure 5). Sage-grouse captured from the Shaffer Mountain lek complex showed greater directional variability. Although several sage-grouse moved north and some exchanges between the Upper Smoke Creek and Shaffer Mountain lek complexes were observed, most birds remained east of Highway 395 and west of the Nevada border (Figure 5). My information about winter use was limited, however, wintering areas were contiguous with breeding areas and largely overlapped breeding season and summer ranges.

### **Individual Home Range Analysis**

I examined the annual home range size from 41 individual sage-grouse, including 32 females and 9 males. Additionally, I assessed the general seasonal movement patterns for 65 sage-grouse ( $n = 45$  females, 20 males). Mean number of observations per female was  $32.7 \pm 1.82$  SE (range = 20–56). In comparison, number of telemetry locations per male ranged from 21–35 observations (mean =  $27.4 \pm 1.30$  SE). Mean home range size was  $116.4 \text{ km}^2 \pm 28.67$  SE (range =  $5.1\text{--}713.3 \text{ km}^2$ ) and  $59.2 \pm 24.17$  SE (range =  $4.7\text{--}180.5$ ) for females and males, respectively. In general, yearling males appeared to have larger home ranges (mean =  $105.9 \text{ km}^2 \pm 46.29$  SE;  $n = 4$ ) than adult males (mean =  $21.8 \pm 5.7$ ;  $n = 5$ ). While the home range size of individual sage-grouse was highly variable, the cumulative annual range of sage-grouse by gender was  $696 \text{ km}^2$  and  $464 \text{ km}^2$  for females ( $n = 2,400$  individual telemetry

locations) and males ( $n = 590$  individual telemetry locations), respectively. However, differences in home range size between female and male sage-grouse might have been influenced by limited sample size and the statistical properties of the home range estimator.

The straight-line distance of movements from lek of capture to spring ranges ranged from 0.1-22.1 km ( $n = 40$ ), and 0.04-9.6 km ( $n = 15$ ) for females and males, respectively (Table 3). The cumulative spring range encompassed 474 km<sup>2</sup> for both genders combined. In the spring, female sage-grouse on average moved 7.1 km  $\pm$  8.48 (SD;  $n = 40$ ) and males moved 12.1 km  $\pm$  15.04 (SD;  $n = 11$ ) to individual summer ranges that averaged 430 km<sup>2</sup> for both sexes combined (Table 3). Distances of female and male movements from summer to autumn ranges were 0.22 -30.0 km ( $n = 45$ ) and 0.68-28.5 km ( $n = 20$ ), respectively (Table 3). Female sage-grouse moved from 1.2-32.9 km between autumn and winter ranges and male movements ranged from 2.9-24.4 km. The cumulative autumn and winter range for both genders encompassed 521 km<sup>2</sup> and 54 km<sup>2</sup>, respectively. The most extensive straight-line unidirectional movement I observed was 44.3 km for females and 53.3 km for males; both were related to movements between spring and summer ranges. Although I did not evaluate the extent of home range overlap among individual sage-grouse, the overall pattern of space-use sharing between female and male sage-grouse was high (VI = 0.80).

### **Nest site fidelity**

The average distance females moved from lek sites of capture to initial nest locations was 4.67 km  $\pm$  4.30 (SD);  $n = 59$ . Seventeen females nested an average of 0.99 km  $\pm$  1.48 (SD) from the preceding year's nest (range = 0.04 km – 5.80 km), suggesting strong fidelity to nesting areas (Table 4). There was no difference in straight-line distances moved between

nests from individual females in consecutive years ( $t_{0.05, 15} = -1.16$ ,  $P = 0.27$ ) by adult (mean =  $1.22 \text{ km} \pm 1.63$ ,  $n = 13$ , range =  $0.04 \text{ km} - 5.80 \text{ km}$ ) and yearling females (mean =  $0.25 \text{ km} \pm 0.06$ ,  $n = 4$ , range =  $-0.18 \text{ km} - 0.31 \text{ km}$ ). I observed 4 of 11 successful and 2 of 6 unsuccessful nesting sage-grouse shift nest sites  $>1 \text{ km}$  in successive years. Therefore, nest fate did not influence the distance moved between consecutive nests ( $t_{0.05, 15} = 1.3$ ,  $P = 0.21$ ). Renesting females ( $n = 5$ ) moved an average of  $0.58 \text{ km} \pm 0.36$  (SD) to renest. Sample size was insufficient to test whether movements to renests following unsuccessful nesting attempts were related to age.

## DISCUSSION

Previous investigations describing space use by sage-grouse have been constrained by highly variable seasonal movement patterns within and among populations, limited sample size, variation in the duration of the study, and variation in methods of home range estimation. Moreover, the extensive movements between seasonal ranges and highly clustered distributions of sage-grouse (Hagen 1999) have made estimating home range size and comparisons between studies difficult. On an annual basis, previous studies reported individual home range sizes have ranged from  $>4 - 615 \text{ km}^2$  (MCP; Hagen 1999, Leonard et al. 2000). In Colorado, Hausleitner (2003) reported sage-grouse occupied areas ranging from  $66-86 \text{ km}^2$  annually (95% fixed kernel). Within a season, results from 5 studies compiled by Schroeder et al. (1999) indicated that individuals occupy areas, which can vary from  $0.1-28.6 \text{ km}^2$  during the breeding season,  $0.1-25.9 \text{ km}^2$  during summer,  $22.5-44.2 \text{ km}^2$  during autumn, and  $0.6-18.2 \text{ km}^2$  during winter. Leonard et al. (2000) reported migratory sage-grouse populations in Idaho occupy areas up to  $673 \text{ km}^2$  during the breeding season,  $1,825 \text{ km}^2$

during the summer, 1,564 km<sup>2</sup> during autumn, and 439 km<sup>2</sup> during the winter. During winter, migratory sage-grouse in southeastern Idaho occupied an area of 140 km<sup>2</sup> (Robertson 1991). In contrast, a nonmigratory population in central Montana occupied winter home ranges of 11-31 km<sup>2</sup> (Wallestad 1975).

Diurnal space use and seasonal movement patterns observed in my study exceeded estimates of individual home range size reported in previous investigations. While the home range size of individual sage-grouse observed in my study was highly variable, collectively sage-grouse occupied a core range of 81 km<sup>2</sup> across seasons. The cumulative annual range for all radiomarked sage-grouse across my 3 year study period (based on fixed kernel estimators) were within a 750 km<sup>2</sup> home range area (MCP: 3,072 km<sup>2</sup>).

Over the course of 3 years, I observed wide-ranging seasonal movements between the Upper Smoke Creek and Shaffer Mountain lek complexes and movement of sage-grouse between these lek complexes was a regular occurrence. Only the Madeline Plains lek complex appeared to be non-migratory, exhibiting relatively short seasonal movements (<10 km), however, it is possible some birds used additional areas that were not detected. In general, I observed extensive unidirectional movements (e.g., up to 53.3 km) between seasonal ranges. My findings are consistent with observations in eastern Idaho where sage-grouse reportedly moved an average of 32 km and 18 km between seasonal ranges for males ( $n = 42$ ) and females ( $n = 27$ ), respectively (Connelly et al. 1988). Similarly, a study in southwestern Idaho indicated that male ( $n = 27$ ) and female ( $n = 22$ ) sage-grouse moved an average of 24 km and 17 km, respectively, between breeding and summer ranges (Wik 2002). Other studies of sage-grouse in the Upper Snake River Plains of Idaho reported more



extensive movements of 80-160 km between seasonal ranges (Dalke et al. 1963, Leonard et al. 2000). Similarly in Wyoming, sage-grouse moved >50 km between seasonal ranges (Fedy et al. 2012).

Differences in annual and seasonal ranges reported in my study might have been influenced by sample size and the statistical properties of the home range estimator. One disadvantage of the MCP estimator is that the size of the home range estimate increases as sample size increases (Boulanger and White 1990), which resulted in the inclusion of areas not used by sage-grouse, producing an overestimate of true home range area for sage-grouse in northeastern California. Thus, MCP home range estimates were of limited use for drawing meaningful population-level comparisons within my study area. Additionally, comparisons with previous studies documenting home range size could be erroneous unless the number of observations used to calculate home range size is approximately equal (Halloran and Bekoff 2000).

Kernel estimators have been regarded as a more accurate means of estimating home range size compared to traditional methodologies such as MCP (Worton 1987, 1989, 1995; Seaman and Powell 1996, Swihart and Slade 1997, Seamen et al. 1999), however, comparisons across studies could lead to spurious conclusions if similar methods are not employed (Laver and Kelly 2008). Although I assumed an individual was adequately sampled to sufficiently quantify diurnal space use if  $\geq 20$  radio telemetry locations were obtained, I acknowledge the potential bias in my individual home range estimates. While my estimates possibly underestimated home range size (e.g., Seaman et al. 1999), my data represent the most current information available on home range size of sage-grouse in my

study area and to my knowledge this is the first published estimate of diurnal space use of sage-grouse in California. I know of only 1 other study (Hausleitner 2003) which calculated sage-grouse home range size using comparable methods (95% fixed kernel estimate with LSCV-smoothing and calculated using the Animal Movement Analysis extension (Hooge and Eichenlaub 2000)). However, several authors have cautioned against inconsistencies among software programs (Larkin and Halkin 1994, Lawson and Rodgers 1997, Larson 2001, Horne and Garton 2006a). Moreover, others have stressed the importance of selecting an appropriate home range model (Anderson 1982, Boulanger and White 1990, Harris et al. 1990, White and Garrott 1990, Worton 1995, Seaman et al. 1999, Kernohan et al. 2001, Horne and Garton 2006b) and choosing a suitable smoothing parameter (Silverman 1986, Worton 1995, Jones et al. 1996, Seaman et al. 1999, Horne and Garton 2006b) when describing animal space use. Thus, understanding the potential biases of different home range estimators has significant implications for implementing effective management strategies across the range of sage-grouse.

Consecutive year nesting data demonstrated nest-site fidelity by female sage-grouse in northeastern California. The degree of nest site fidelity observed in my study is similar to that reported for sage-grouse in other studies (Berry and Eng 1985, Fischer et al. 1993, Schroeder and Robb 2003, Holloran and Anderson 2005, Herman-Brunson 2007, Moynahan et al. 2007, Kaczor 2008). The average distance females moved from lek sites of capture to initial nest locations was  $4.67 \text{ km} \pm 4.30 \text{ (SD; } n = 59)$ . Although this distance is within the range reported for other sage-grouse studies (0.40 to 29.75 km; Schroeder et al. 1999, Aldridge and Brigham 2001, Moynahan et al. 2007) only 39% of all nests occurred within 3

km of a known lek site, while a 5-km buffer included 73% of nests. Other studies have reported the average lek-to-nest distance was larger for the lek of capture compared to the distance to the nearest lek (Peterson 1980, Wakkinen et al. 1992a, Fischer 1994, Schroeder et al. 1999, Herman-Brunson 2007). In my study, the average distance between a female's nest and the nearest lek was  $3.69 \text{ km} \pm 2.94$  (SD;  $n = 74$ ) and ranged from 0.14 km – 14.10 km. My results are consistent with other studies which reported similar variation in lek-to-nest distances. The average nearest lek-to-nest distance was 1.3 – 1.5 km in Idaho (Wakkinen et al. 1992a, Fischer 1994), 2.7 km in North Dakota (Herman-Brunson 2007), 2.8 in Colorado (Peterson 1980), 4.9 km in Alberta (Aldridge 2005), and 5.1 km in Washington (Schroeder et al. 1999).

Distances moved from lek sites to nest locations is an important consideration in sage-grouse management, and nest-site fidelity might be of even greater importance, particularly to evaluate impacts of landuse changes on sage-grouse habitats (Berry and Eng 1985). For example, the distance recorded between consecutive nests in highly fragmented habitats of eastern Washington (mean = 2.8 km between nests in consecutive years,  $n = 122$ ; Schroeder and Robb 2003) exceeded distances reported for females nesting in relatively intact habitats of southeastern Idaho (mean = 0.7 km,  $n = 22$ ; Fischer et al. 1993). Further, females from leks disturbed by natural gas development in southwestern Wyoming on average moved twice as far to nest sites (4.1 km) as females from undisturbed leks (2.1 km; Lyon and Anderson 2003), suggesting size and juxtaposition of habitats, anthropogenic disturbance, and extent of fragmentation influences the location of nests with respect to lek sites (Lyon and Anderson 2003, Connelly et al. 2004, Schroeder and Robb 2003)

My results indicate that sage-grouse used relatively large areas and my annual and seasonal ranges likely represent minimum estimates. It is possible sage-grouse used additional areas that were not detected over the course of my study. The current management guidelines for sage-grouse recommend managing sagebrush habitat within 5 km of active lek sites to benefit the majority of nesting and brood-rearing locations for non-migratory populations and within 18 km for migratory populations (Connelly et al. 2000, Knick and Hanser 2011). Given the conservation concern over the status of sage-grouse throughout its geographic range, long-term management and conservation strategies should prevent future habitat loss and fragmentation, improve existing habitat quality, and consider the protection of broader areas to encompass potential changes in the habitat needs of this species. The annual range of sage-grouse in northeastern California indicates that conserving sage-grouse habitat within 5 km of active lek sites is insufficient to maintain long-term population viability. Therefore, larger areas of habitat are needed to conserve sage-grouse in northeastern California to accommodate seasonal movements, annual variation in resource availability, and to maintain connectivity between lek complexes.

## **MANAGEMENT IMPLICATIONS**

Sage-grouse require vast expanses of suitable habitat (Eng and Schladweiler 1972, Berry and Eng 1985), which necessitates management on a landscape scale to ensure that life history needs of sage-grouse are met. To make certain that critical sage-grouse habitat is not lost, seasonal use areas for nesting, brood-rearing, and migration routes must be identified and managed appropriately to ensure that these habitats are available. Although trends of traditional habitat use by sage-grouse have been observed (Eng and Schladweiler 1972, Berry

and Eng 1985, Connelly et al. 1988), site fidelity in sage-grouse remains poorly understood, necessitating the need for long-term telemetry studies, which follow individually marked birds over consecutive years. My results provided significant insights into the general space use requirements (e.g., size, shape, and overlap of home ranges) to fulfill the basic life history requirements of sage-grouse in Lassen County. Although location data were of value in describing sage-grouse movements and the general patterns of annual and seasonal space use by sage-grouse in northeastern California, the paucity of individual sage-grouse locations and home range data for certain periods of the year limited my ability to identify the ecological processes affecting sage-grouse movements within their respective home range. A better understanding of spatial ecology and precise estimates of the home range of sage-grouse has significant implications for developing effective management strategies and an accurate assessment of the factors affecting space use by sage-grouse in northeastern California is needed. Moreover, identifying seasonal migration routes and movement corridors will be important for maintaining viable sage-grouse populations occupying the western periphery of the species range. Therefore, I suggest future research should establish a more comprehensive assessment of sage-grouse space use to effectively manage sage-grouse populations in northeastern California.

## LITERATURE CITED

- Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Aldridge, C. L., and R. M. Brigham. 2001. Nesting and reproductive activities of greater sage-grouse in a declining northern fringe population. *Condor* 103:537–543.

- Anderson, D. J. 1982. The home range: a new nonparametric estimation technique. *Ecology* 63:103-112.
- Berry, J. D., and R. L. Eng. 1985. Interseasonal movements and fidelity to seasonal use areas by female sage grouse. *Journal of Wildlife Management* 49:237-240.
- Boulanger, J. G., and G. C. White. 1990. A comparison of home-range estimators using Monte Carlo simulation. *Journal of Wildlife Management* 54:310-315.
- Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? *Proceedings of the Western Association State Fish and Game Wildlife Agencies* 78:139-156.
- Burt, W. H. 1943. Territoriality and home range as applied to mammals. *Journal of Mammalogy* 24:346-315.
- California Department of Fish and Game (CDFG). 1992. Bird species of special concern. Unpublished list, July 1992. California Department of Fish and Game, Sacramento, California, USA.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- Connelly, J. W., H. W. Browsers, and R. J. Gates. 1988. Seasonal movements of sage grouse in southeastern Idaho. *Journal of Wildlife Management* 52:116-122.
- Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished Report. Cheyenne, Wyoming, USA.
- Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin* 28:967:985.
- CrimeStat III. 2004. A spatial statistics program for the analysis of crime incident locations. National Institute of Justice, Washington, D.C., USA.
- Crunden, C.W. 1963. Age and sex of sage grouse from wings. *Journal of Wildlife Management* 27:846-850.
- Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. *Journal of Wildlife Management* 27:810-841.

- Eng, R. L., and P. Schladweiler. 1972. Sage grouse winter movements and habitat use in central Montana. *Journal of Wildlife Management* 36:141-146.
- Fedy, B. C., C. L. Aldridge, K. E. Doherty, M. O'Donnell, J. L. Beck, B. Bedrosian, M. J. Holloran, G. D. Johnson, N. W. Kaczor, C. P. Kirol, C. A. Mandich, D. Marshall, G. McKee, C. Olson, C. C. Swanson, and B. L. Walker. 2012. Interseasonal Movements of greater sage-grouse, migratory behavior, and an assessment of the core regions concept in Wyoming. *Journal of Wildlife Management* 76:1062-1071.
- Fischer, R. A. 1994. The effects of prescribed fire on the ecology of migratory Sage Grouse in southeastern Idaho. Dissertation. University of Idaho, Moscow, Idaho, USA.
- Fischer, R. A., A. D. Apa, W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1993. Nesting area fidelity of sage grouse in southeastern Idaho. *Condor* 95:1038-1041.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224-231.
- Hagen, C. A. 1999. Sage Grouse habitat use and seasonal movements in a naturally fragmented landscape, northwestern Colorado. Thesis. University of Manitoba, Winnipeg, Manitoba, Canada.
- Halloran, M. E., and M. Bekoff. 2000. Home range use by Abert squirrels: a comparative analysis. *The Southwestern Naturalist* 45:253-257.
- Harris, S. W., W. J. Cresswell, P. G. Fordge, W. J. Trehwella, T. Woolard, and S. Wray. 1990. Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* 20:97-123.
- Hausleitner, D. 2003. Population dynamics, habitat use and movements of greater sage-grouse in Moffat County, Colorado. Thesis. University of Idaho, Moscow, Idaho, USA.
- Herman-Brunson, K. M. 2007. Nesting and brood-rearing success and habitat selection of greater sage-grouse and associated survival of hens and broods at the edge of their historic distribution. Thesis. South Dakota State University, Brookings, South Dakota, USA.
- Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous habitats. *Condor* 107:742-752.
- Hooge, P. N., and B. Eichenlaub. 2000. Animal movement extension to ArcView. Ver. 2.0. Alaska Science Center – Biological Science Office, USGS, Anchorage, Alaska, USA.

- Horne, J. S., and E. O. Garton. 2006a. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. *Journal of Wildlife Management* 70:641-648.
- Horne, J. S., and E. O. Garton. 2006b. Selecting the best home range model: an information-theoretic approach. *Ecology* 87:1146-1152.
- Horne, J. S., and E. O. Garton. 2009. Animal Space Use 1.3. [Online.] Available from [http://www.cnr.uidhaho.edu/population\\_ecology/animal\\_space\\_use](http://www.cnr.uidhaho.edu/population_ecology/animal_space_use).
- Jones, M. C., J. S. Marron, and S. J. Sheather. 1996. A brief survey of bandwidth selection for density estimation. *Journal of the American Statistical Association* 91:401-407.
- Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. Thesis. South Dakota State University, Brookings, South Dakota, USA.
- Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125-166 in J. J. Millspaugh and J. M. Marzluff, editors. *Radio tracking and animal populations*. Academic, New York, New York, USA.
- Knick, S. T., and S. E. Hanser. 2011. Connecting pattern and process in greater sage-grouse populations and sagebrush landscapes. Pages 383-405 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Larkin, R. P., and D. Halklin. 1994. A review of software packages for estimating animal home ranges. *Wildlife Society Bulletin* 22:274-287.
- Larson, M. A. 2001. A catalog of software to analyze radio telemetry data. Pages 397-406 in J. J. Millspaugh and J. M. Marzluff, editors. *Radiotracking and animal populations*. Academic Press, San Diego, California, USA.
- Laver, P. N., and M. J. Kelly. 2008. A critical review of home range studies. *Journal of Wildlife Management* 73:290-298.
- Lawson, E. J. G., and A. R. Rodgers. 1997. Differences in home-range size computed in commonly used software programs. *Wildlife Society Bulletin* 25:721-729.
- Leonard, K. M., K. P. Reese, and J. W. Connelly. 2000. Distribution, movements and habitats of sage grouse *Centrocercus urophasianus* on the Upper Snake River Plan of Idaho: changes from the 1950s to the 1990s. *Wildlife Biology* 6:265-270.



- Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:486–491.
- Millsbaugh, J. J., R. A. Gitzen, B. J. Kernohan, M. A. Larson, and C. L. Clay. 2004. Comparability of three analytical techniques to assess joint space use. *Wildlife Society Bulletin* 32:148-157.
- Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37:223-249.
- Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in northcentral Montana. *Journal of Wildlife Management* 71:1773–1783
- Petersen, B. E. 1980. Breeding and nesting ecology of female sage grouse in North Park, Colorado. Thesis. Colorado State University, Fort Collins, Colorado, USA.
- Remsen, J. V., Jr. 1978. Bird species of special concern in California: an annotated list of declining or vulnerable bird species. Nongame Wildlife Investigations, Wildlife Management Branch Administration Report 78-1, California Department of Fish and Game, Sacramento, California, USA.
- Robertson, M. D. 1991. Winter ecology of migratory sage grouse and associated effects of Prescribed fire in southeastern Idaho. Thesis. University of Idaho, Moscow, Idaho, USA.
- Rodgers, A. R., A. P. Carr, L. Smith, and J. G. Kie. 2005. HRT: home range tools for ArcGIS. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada, <http://blue.lakeheadu.ca/hre/>.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. *Condor* 106:363-376.
- Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. *Wildlife Biology* 9:291–299.
- Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage Grouse (*Centrocercus urophasianus*). In A. Poole, and F. Gill (editors.) *The Birds of North America*, No. 425. The Academy of Natural Sciences, Philadelphia, PA and The American Ornithologists' Union, Washington, DC.

- Seaman, D. E., J. J. Millsaugh, B. J. Kernohan, G. C. Brundige, K. J. Raideke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739-747.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075-2085.
- Seidel, K. D. 1992. Statistical properties and applications of a new measure of joint space use for wildlife. Thesis. University of Washington, Seattle, Washington, USA.
- Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, UK.
- Swihart, R. K., and N. A. Slade. 1997. The importance of statistical power for testing independence in animal movements. *Ecology* 67:255-258.
- Tracy, C. R., and T. L. George. 1992. On the determinants of extinction. *American Naturalist* 150:73-82.
- United States Department of Interior (USDI). 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. *Federal Register* 75:13910-14014 (23 March 2010).
- van Winkle, W. 1975. Comparison of several probabilistic home-range models. *Journal of Wildlife Management* 39:118-123.
- Vucetich, J. A., T. A. Waite, L. Qvarnemark, and S. Ibarguen. 2000. Population variability and extinction risk. *Conservation Biology* 14:1704-1714.
- Wakkinen, W. L., K. P. Reese, and J. W. Connelly. 1992a. Sage grouse nest locations in relation to leks. *Journal of Wildlife Management* 56:381-383.
- Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992b. An improved spotlighting technique for capturing sage-grouse. *Wildlife Society Bulletin* 20:425-426.
- Wallestad, R. O. 1975. Life history and habitat requirements of sage grouse in central Montana. Montana Department of Fish, Game, and Parks, Helena, Montana, USA.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, New York, USA.

- Wik, P. A. 2002. Ecology of greater sage-grouse in south-central Owyhee County, Idaho. Thesis. University of Idaho, Moscow, Idaho, USA.
- Wisdom, M. J., C. W. Meinke, S. T. Knick, and M. A. Schroeder. 2011. Factors associated with extirpation of sage-grouse. Pages 451-472 *in* Knick, S. T., and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Worton, B. J. 1987. A review off models of home range for animal movement. *Ecological Modelling* 38:277-298.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.
- Worton, B. J. 1995. Using Monte Carlo simulations to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794-800.

Table 1. Pairwise comparison matrix of VI statistic (0-1; below diagonal) and proportion of 100% MCP home range boundary overlap (0-100; above diagonal) between greater sage-grouse seasonal ranges, Lassen County, California, 2007-2009.

	Spring	Summer	Autumn	Winter
Spring		0.90	0.85	0.73
Summer	0.64		0.84	0.67
Autumn	0.59	0.72		0.79
Winter	0.65	0.61	0.65	

Table 2. Annual and seasonal home range estimates (km<sup>2</sup>) for the population of radiomarked greater sage-grouse in Lassen County, California, 2007-2009.

Season	Number of locations	100% MCP	95% fixed kernel
Spring	950	2,914	474
Summer	1,210	3,226	430
Autumn	819	2,851	521
Winter	90	2163	54
Annual	3,072	3,382	750

Table 3. Mean distances (km) greater sage-grouse moved between seasonal ranges, Lassen County, California, 2007-2009.

Season	Female			Male			Totals		
	Mean	Range	<i>n</i>	Mean	Range	<i>n</i>	Mean	Range	<i>n</i>
Spring	4.8	0.1-22.1	40	1.7	0.04-9.6	15	3.9	0.04-22.1	55
Summer	7.1	0.1-44.3	40	12.1	0.9-53.3	11	8.2	0.1-53.3	51
Autumn	5.9	0.2-30.0	45	6.2	0.7-28.5	20	6.0	0.2-30.0	65
Winter	11.6	1.2-32.9	17	11.2	2.9-24.4	4	11.5	1.2-32.9	21

Table 4. Nest-site fidelity as demonstrated by mean distances (km) between first nests and renests and between nests in consecutive years for female greater sage-grouse in Lassen County, California, 2007-2009.

Category	<i>n</i>	Within-year <sup>a</sup>		<i>n</i>	Consecutive years <sup>b</sup>	
		Median	Mean ±SD		Median	Mean ± SD
Age class						
Yearling	1	0.59	0.59	4	0.26	0.25 ± 0.06
Adult	4	0.41	0.57 ± 0.41	13	0.41	1.22 ± 1.63
Nest fate						
Successful	1	0.49	0.49	11	0.29	0.82 ± 1.67
Unsuccessful	3	0.59	0.70 ± 0.44	6	1.22	1.30 ± 1.10
Abandoned	1	0.30	0.30			
Totals	5	0.49	0.58 ± 0.36	17	0.31	0.99 ± 1.48

<sup>a</sup>Distance between first nest and the renest.

<sup>b</sup>Nests located in consecutive years.

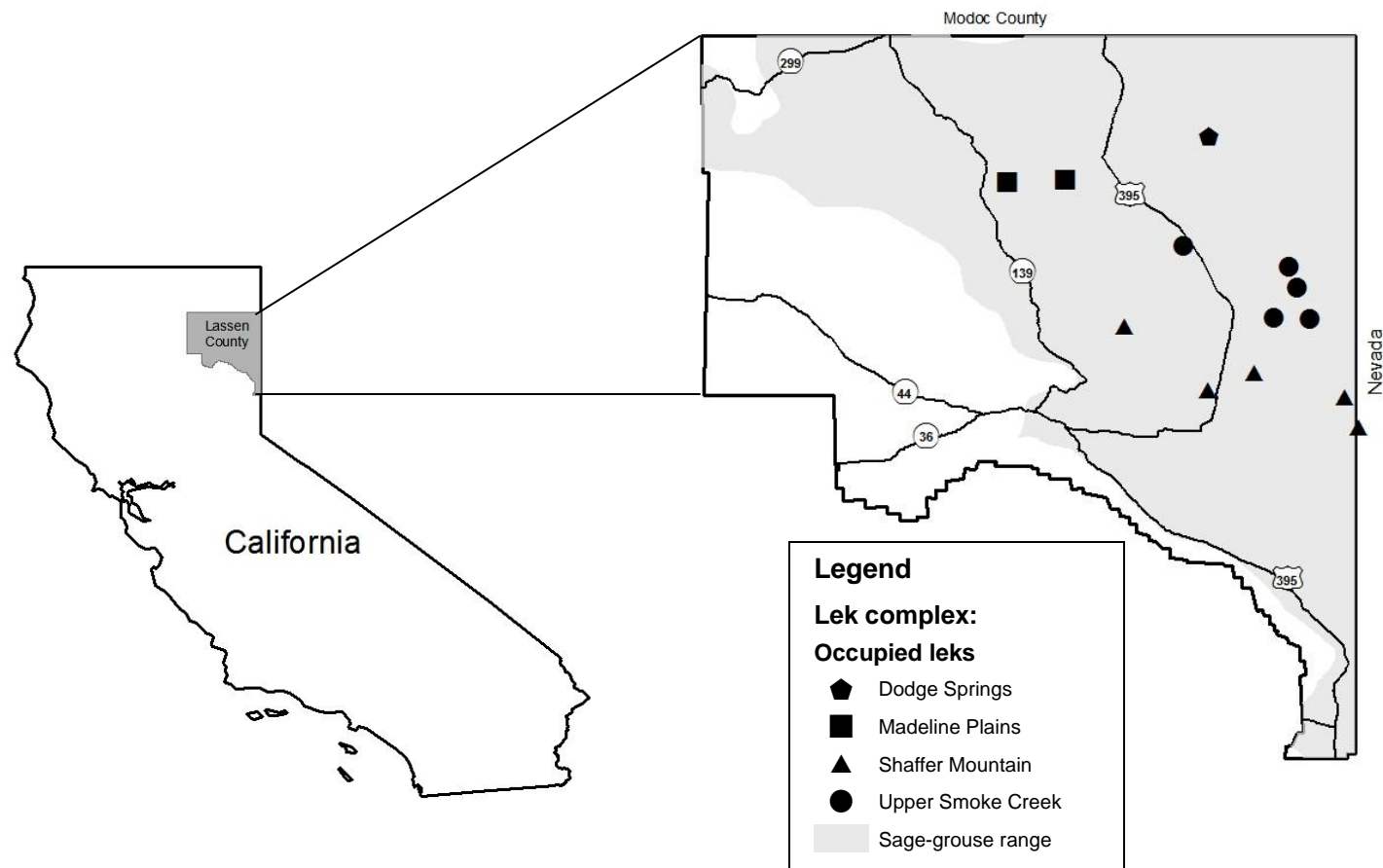


Figure 1. Map of the Lassen County, California study area. Symbols represent geographical locations of occupied greater sage-grouse lek sites and the distribution of respective lek complexes.

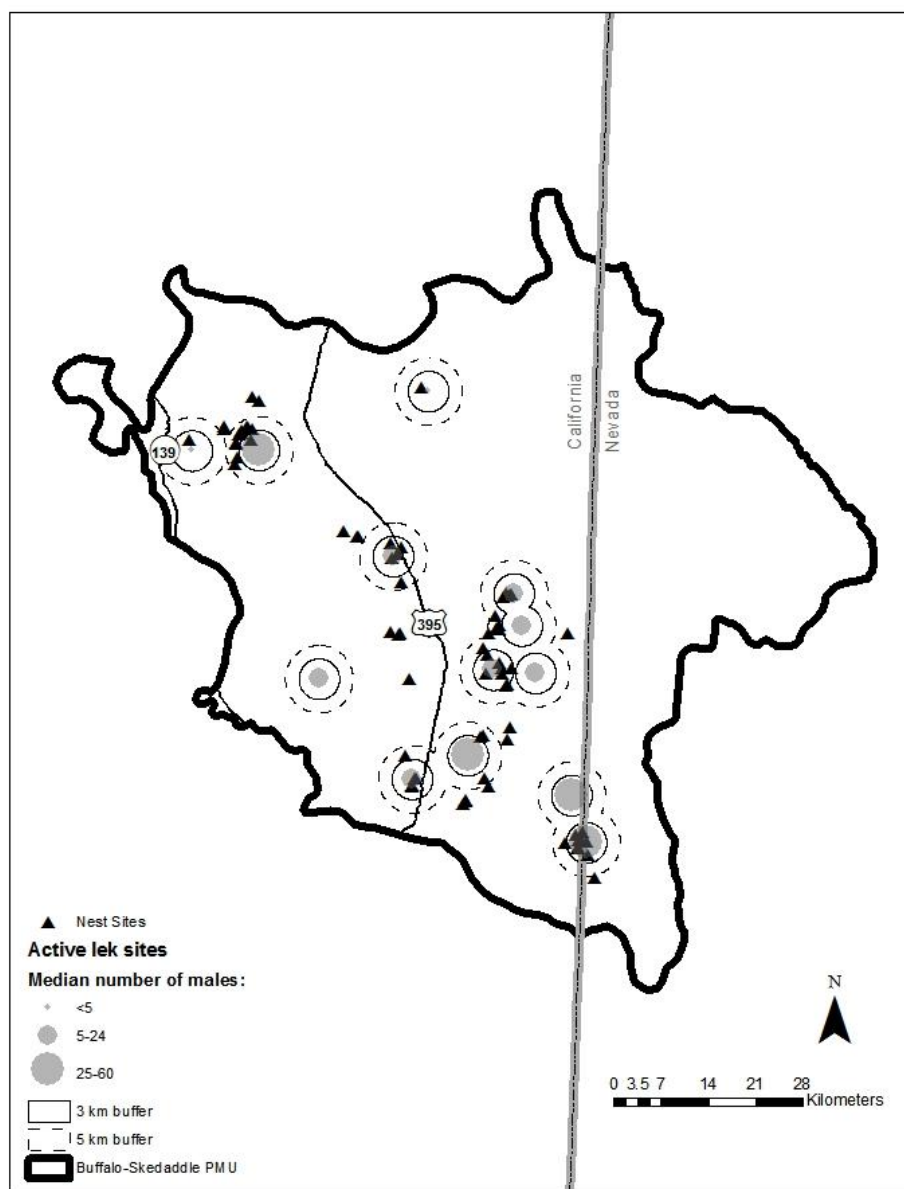


Figure 2. Distribution of greater sage-grouse nest sites relative to lek sites in Lassen County, California, 2007-2009.

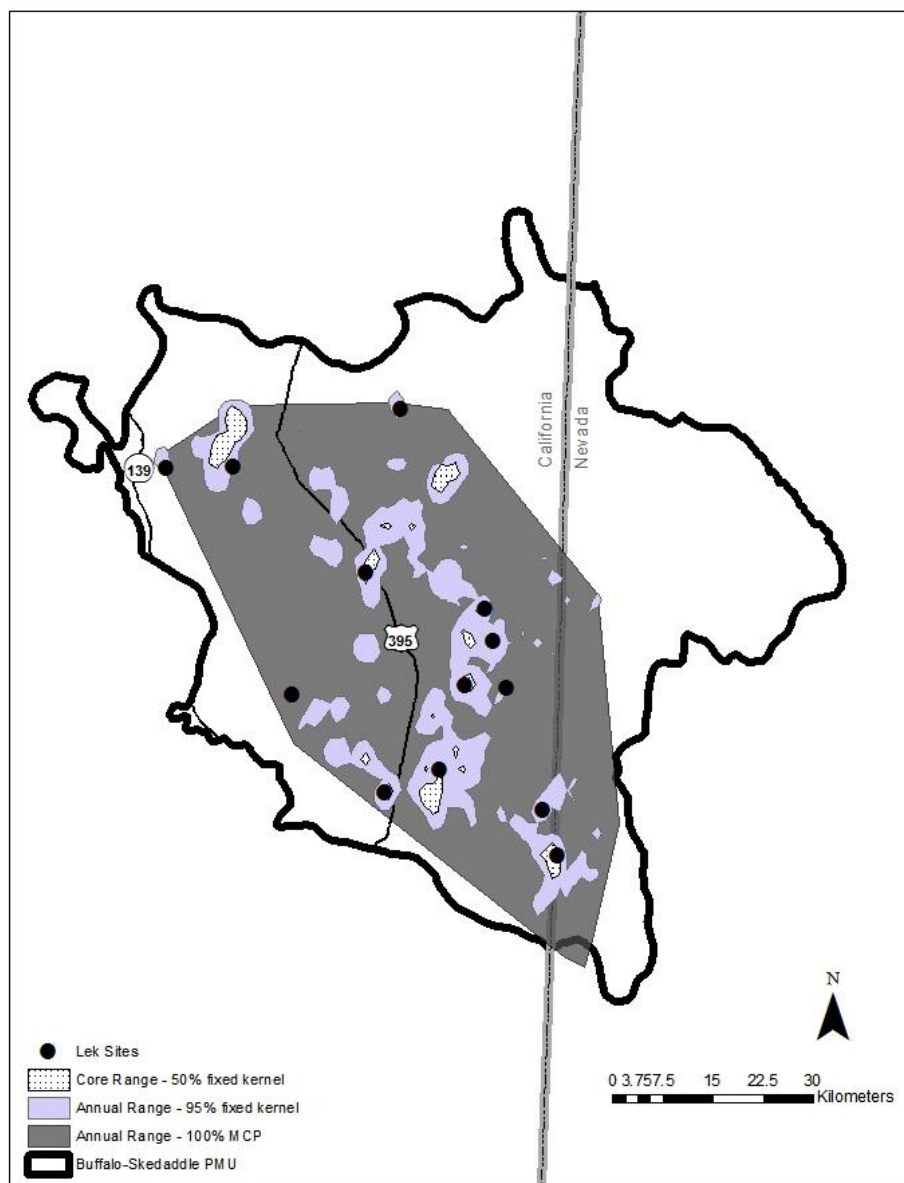


Figure 3. Annual and core occupied ranges of greater sage-grouse in Lassen County, California, 2007-2009.



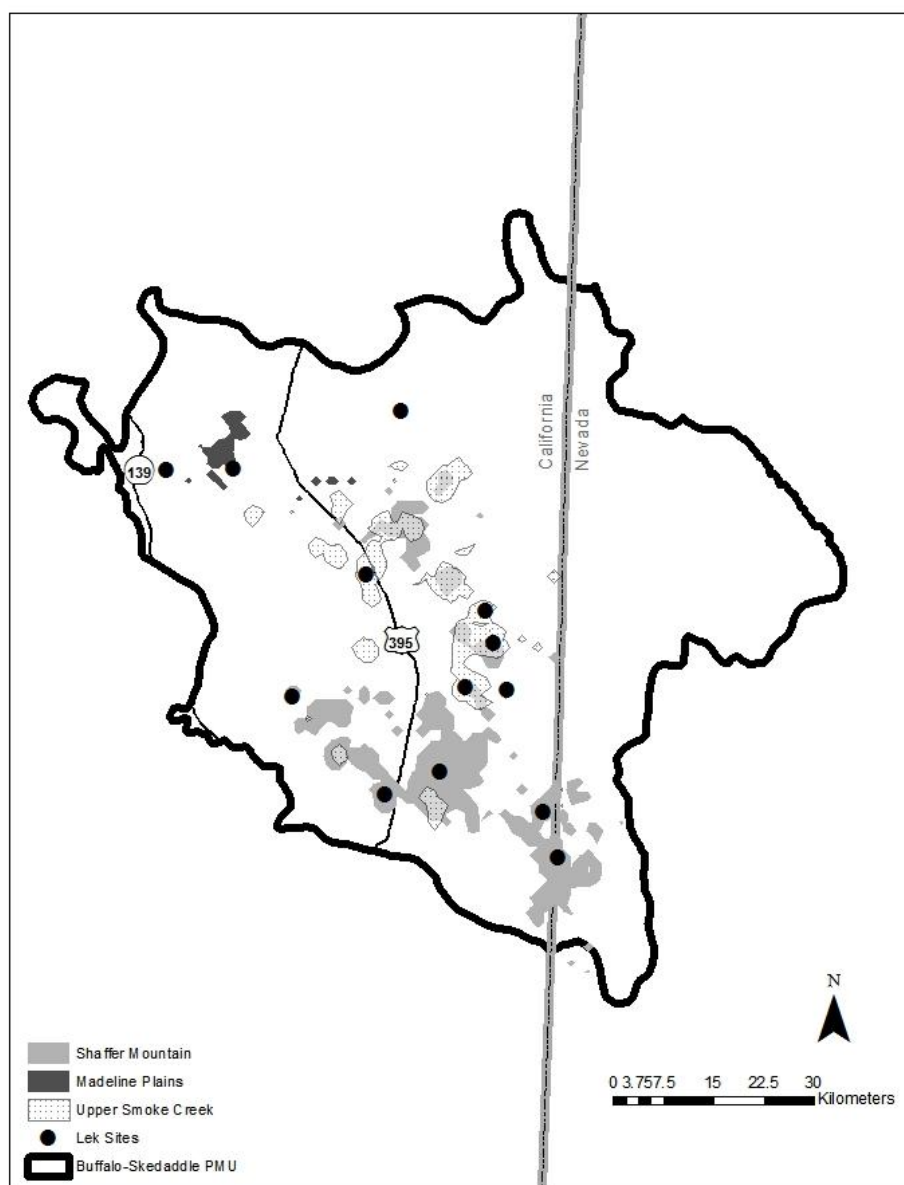


Figure 4. Extent of overlap between annual home ranges by lek complex for radiomarked greater sage-grouse in Lassen County, California, 2007-2009.

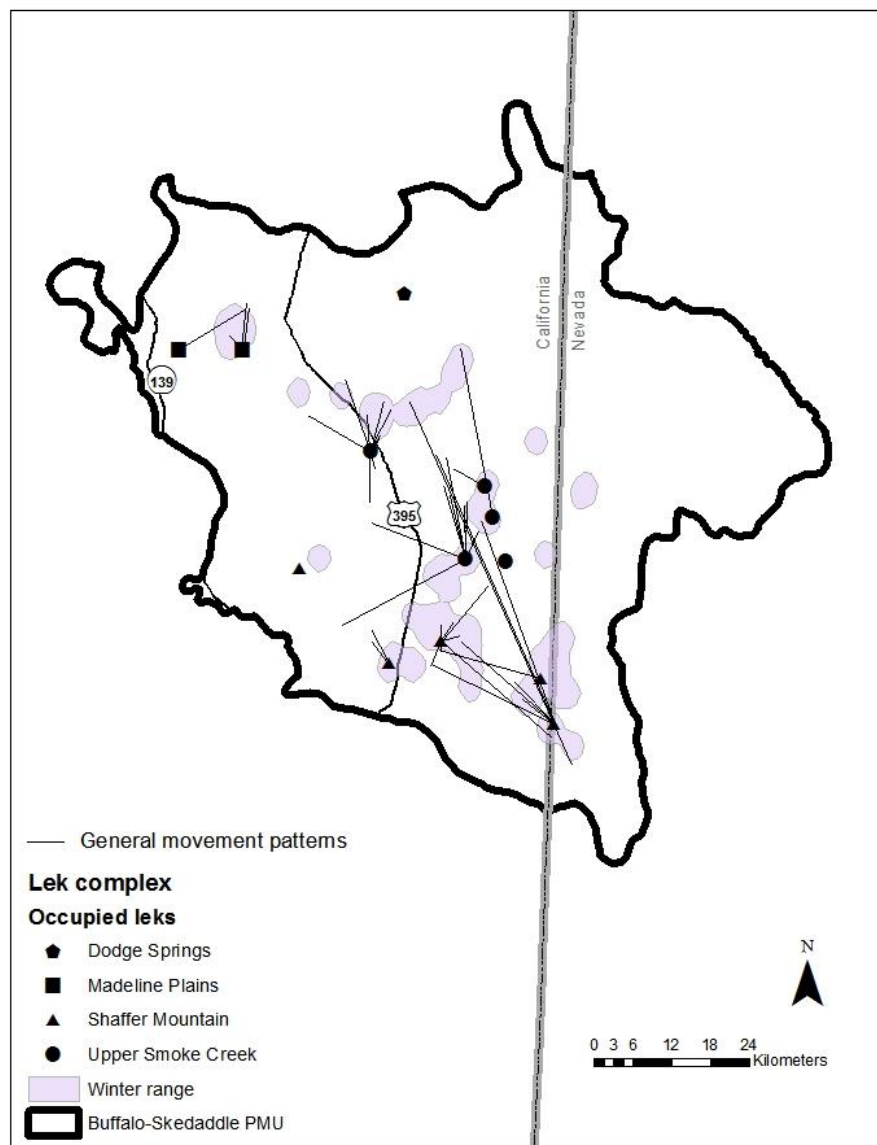


Figure 5. Winter range and general movement patterns between seasonal ranges for radiomarked greater sage-grouse in Lassen County, California, 2007-2009. General movement patterns represent distance and unidirectional movements of individual sage-grouse from leks of capture to summer ranges.

**CHAPTER 4. GENETIC STRUCTURE OF GREATER SAGE-GROUSE  
(*CENTROCERCUS UROPHASIANUS*) IN A DECLINING, PERIPHERAL  
POPULATION**

**ABSTRACT** – I assessed the genetic structure of greater sage-grouse (*Centrocercus urophasianus*) in a declining, peripheral population in northeastern California. A total of 167 blood samples from greater sage-grouse captured on 13 active leks and 20 blood samples collected from greater sage-grouse off-lek during the autumn were genotyped at 19 microsatellite loci. Although greater sage-grouse are declining and have lost a significant portion of their range in northeastern California, greater sage-grouse in my study exhibited high genetic diversity. I observed no population structure and despite population declines and habitat loss, leks were not differentiated. My results showed significant isolation-by-distance among males, suggesting male greater sage-grouse are the more philopatric sex and females have a greater predisposition to disperse. Greater sage-grouse in northeastern California appear to maintain gene flow across the sampled region and have tolerated some degree of habitat fragmentation and deterioration without losing genetic diversity, however, continued habitat loss could result in small, isolated sage-grouse populations at risk of losing genetic variation. Thus, improving habitat quality and connectivity of greater sage-grouse habitats in northeastern California is critical for maintaining gene flow and is important for the long-term persistence of greater sage-grouse occurring on the geographic periphery of the species' distribution.

**KEYWORDS:** *Centrocercus urophasianus*, genetic structure, fragmentation, isolation by distance, sage-grouse

## INTRODUCTION

Loss of suitable habitat and the subsequent fragmentation of populations are recognized as important factors in the decline and extinction of many species, as 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 due to random genetic drift and inbreeding depression, 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 peripheral populations, on the fringe of a species' geographic distribution. Geographically peripheral populations exhibit lower genetic variation than populations occurring in the core of the species' distribution because they are subject to colonization and founder effects, which increases 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, Autenrieth 1981, Schroeder et al. 2004). However, populations have declined throughout much of their range (Connelly and Braun 1997, Braun 1998, Schroeder et al. 2004). Alteration of sage-grouse habitats by expanding agriculture and urban development, sagebrush control programs, over-utilization of rangelands by domestic livestock, altered fire regimes, and prolonged drought throughout the sagebrush-steppe in the 1930s and again in the late 1980s and early 1990s have been attributed to the decline in sage-grouse numbers (Crawford et al. 2004). Additionally, recent research has shown that sage-

grouse are sensitive to habitat fragmentation caused by anthropogenic features (Braun 1986, Lyon and Anderson 2003, Connelly et al. 2004, Aldridge 2005, Johnson et al. 2011, Knick and Hanser 2011, Wisdom et al. 2011), and human activity can affect sage-grouse habitat selection (Aldridge and Boyce 2007, Doherty et al. 2010). Global climate change also poses a significant threat to sage-grouse through a variety of mechanisms. In particular, global climate change models predict more variable and extreme weather events, higher temperatures, drier summer soil conditions, and wetter winters (Miller et al. 2011). Although research demonstrating how sage-grouse will respond to these regional anthropogenic-driven climatic shifts is lacking, models predict climate change and associated consequences will likely interact with, and potentially magnify, limiting factors such as disease (Walker and Naugle 2011) and habitat loss and degradation, which are already impacting sage-grouse across the species geographic distribution (e.g., see USDI 2010, 75FR:13910-14014). In response to declining sage-grouse abundance and distribution, the sage-grouse was listed as “warranted but precluded,” under the United States Endangered Species Act, and sage-grouse remain a candidate species for federal listing (USDI 2010, 75FR:13910-14014).

In California, sage-grouse populations occupy the western periphery of the species’ geographic distribution. Although little published information is available on sage-grouse population trends in California (Garton et al. 2011), sage-grouse have lost a significant portion of their range in northern California over the past 35 years (Connelly et al. 2004, Schroeder et al. 2004, Shuford and Gardali 2008). Invasion 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 (S. C. Gardner, personal communication). Further, results from an analysis of factors associated with extirpation of sage-grouse suggest that populations in northeastern California have a higher risk of extinction compared with larger, core populations (Wisdom et al. 2011).

Populations that have undergone large decreases in population size, such as sage-grouse in northeastern California, are more likely to lose genetic variation (Nei et al. 1975, Maruyama and Fuerst 1985). Although no deleterious effects to demographic rates have been documented in sage-grouse populations in California (Chapter 2), a loss in genetic diversity might be associated with inbreeding and a reduction in reproductive fitness (Bouzat et al. 1998a, b; Johnson et al. 2003, Johnson et al. 2004). 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 impact the long-term viability of sage-grouse populations in northeastern California.

Genetic analysis of 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 would allow us to evaluate the degree (if any) to which sparse and scattered populations in northeastern California have experienced a loss of genetic diversity through processes such as genetic drift or inbreeding depression.

Reports of local and range-wide declines in sage-grouse populations have traditionally focused attention on demographic factors influencing the distribution and

abundance of sage-grouse (Braun 1998, Connelly et al. 2004). These declines are generally attributed to habitat loss and fragmentation, yet, little is known about the genetic structure of sage-grouse populations. In northeastern California, it appears loss and fragmentation of sagebrush habitat has split sage-grouse populations into smaller, loosely connected lek complexes where connectivity is unknown. At the current population level and spatial distribution, movement between leks is necessary to facilitate population persistence and genetic variability. However, information on whether leks in northeastern California are interconnected by gene flow is lacking. Therefore, the objectives of this study were to: 1) investigate the genetic structure in a declining, peripheral population of sage-grouse in northeastern California; 2) assess genetic variation and diversity within and among sage-grouse leks; 3) ascertain whether there is evidence for any sex-specific differences in dispersal; and 4) evaluate within-lek relatedness.

## **METHODS**

### Study Area and Tissue Collection

I 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 include Wyoming big sagebrush (*A. tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), and little sagebrush (*A. arbuscula*).

I trapped sage-grouse opportunistically on or near lek sites using spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) from March through April 2007-2009. I classified gender and age of captured birds by plumage characteristics and wing molt

(Crunden 1963, Dalke et al. 1963). I collected blood samples from sage-grouse at 13 known, active lek sites within the Buffalo-Skedaddle PMU in northeastern California (Figure 1).

Two of 13 leks (LAS0105, LAS0150) were inactive by 2008 and remained abandoned through 2009. I acquired a genetic sample by collecting approximately 3 drops of blood from a slightly over-clipped hallux nail and stored samples in Queen's lysis buffer (Seutin et al. 1991) or a microfuge tube previously coated with EDTA (Oyler-McCance et al. 1999).

Where possible, I sampled approximately equal numbers of males and females. Additional sage-grouse were captured off lek during the late summer and autumn of 2007 and 2008. All birds sampled off-lek were assigned an "unknown" lek status and were not used in any lek-specific analyses. I included leks with low samples sizes ( $n < 5$  individuals sampled) in global (i.e., population-level) estimates of genetic diversity, but only data from leks with  $>5$  individuals sampled ( $n = 8$  leks) were retained for lek-specific analysis. In addition, only yearling and adult birds were included in my 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-year sampling period (Chapter 2), which could potentially alter allele frequency, so samples were combined across all years.

#### DNA Extraction and Microsatellite Genotyping

DNA was extracted using DNeasy Tissue Kits (Qiagen, Inc.), following manufacturer's protocols and incorporating modifications from Bush et al. (2005). Individual DNA samples were genotyped for every bird captured at 19 polymorphic microsatellite loci originally developed for the domestic chicken (*Gallus gallus*; ADL230, Cheng et al. 1995), turkey



(*Meleagris gallopavo*; RHT0094, Burt et al. 2003), sage-grouse (SGCA9, SGCA5; Taylor et al. 2003), and other grouse species, including capercaillie (*Tetrao urogallus*; TUT3, TUT4, TUD1, TUD3 and TUD4; Segelbacher et al. 2000), black grouse (*T. tetrix*; BG6, BG14, BG15 and BG16, Piertney and Höglund 2001; TTD1, TTD2, TTD6 and TTT1, Caizergues et al. 2001; TTT3 Caizergues et al. 2003b), and red grouse (*Lagopus lagopus scoticus*; LLSD8, Piertney and Dallas 1997).

I performed all polymerase chain reactions (PCR) divided into 3 multiplex panels using the Qiagen Multiplex PCR kit, which were performed in a 7- $\mu$ l reaction volumes containing 1  $\mu$ l of DNA. Multiplex 1 consisted of primers ADL230, BG14, BG15, BG16, LLSD8, SGCA5, and SGCA9. Multiplex 2 consisted of primers TUD1, TUD3, TUD4, TUT3, and TUT4. Multiplex 3 consisted of primers BG6, RHT0094, TTD1, TTD2, TTD6, TTT1, and TTT3. Cycling was performed using a PTC-240 DNA Engine Tetrad 2 Peltier Thermal Cycler as described by 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° to 47° C for 90 s, elongation at 72° C for 1 min; followed by 27 cycles of denaturing (20 and 31 cycles for Multiplex 2 and 3, respectively) at 94° C for 30 s, 45° C (annealing at 47° C and 55° C for Multiplex 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 a LIZ 500 size standard on an ABI 3130xl automated sequencer (Applied Biosystems, Foster City, California). I used GENEMAPPER version 3.7 (Applied Biosystems) software, followed by visual inspection and verification, to genotype all samples.

### Genetic Diversity, Differentiation, and Gene Flow

To investigate genetic diversity within and between lek sites, I calculated expected ( $H_E$ ) and observed ( $H_O$ ) heterozygosity for each locus and tested for deviations from Hardy-Weinberg equilibrium for each locus separately and over all loci and linkage disequilibrium between all pairs of loci using GENEPOP on the web (Raymond and Rousset 1995; <http://wbiomed.curtin.edu.au/genepop/>). Genetic variability at each lek site was assessed using allele frequency data from which the number of alleles per locus ( $A$ ), allelic richness ( $AR$ ) and the inbreeding coefficient ( $F_{IS}$ ) were calculated using FSTAT, version 2.9.3 (Goudet 2001) and GenAlEx 6.3 (Peakall and Smouse 2006). I calculated  $F_{IS}$  using Weir and Cockerham's (1984) estimator. To investigate population genetic structure and levels of genetic differentiation, pairwise  $F_{ST}$  estimates (Weir and Cockerham 1984) were obtained from GENEPOP. I used the program Micro-Checker 2.2.3 (van Oosterhout et al. 2004) to check for the presence of null alleles, scoring errors due to stuttering, and allelic dropout across all loci. To investigate spatial genetic structure within northeastern California, I used the Bayesian program STRUCTURE 2.3.3 (Pritchard et al. 2000), which infers the optimal number of genetic clusters ( $K$ ) from the multilocus genotypes without prior population information. I 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.

I calculated the straight-line Euclidean distance from the geographic coordinates between known, active lek sites within my study area. To test for isolation-by-distance (IBD) across the sampled region, I applied a Mantel test (Mantel 1967) using the program 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). I assessed IBD of males and females separately to identify sex-specific differences in dispersal.

### Relatedness

I computed mean coefficients of relatedness ( $R$ ) for the overall population and 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 ( $K = 1$ ; see Results below); therefore, I used allelic frequencies from the overall population for all analyses. The standard error of 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, I compared sample means to a null expectation of zero using a one-sample  $t$ -test (e.g., see Gibson et al. 2005). In addition, to evaluate whether genetic relatedness was related to geographic distance, I tested for correlations between the pairwise genetic relatedness among lek sites and Euclidean distance using a Mantel test (Mantel 1967).

## **RESULTS**

### Genetic Diversity, Differentiation, and Gene Flow

I collected blood samples from 167 sage-grouse from 13 known, active lek sites in the spring of 2007-2009, and an additional 20 samples were collected off-lek during autumn of 2007 and 2008 (Table 1). Sixteen of 19 loci were in Hardy-Weinberg disequilibrium at the population level after the significance level was adjusted for the number of comparisons with

Bonferroni (Dunn-Šidák) techniques (Ury 1976). At the lek level, 9 of 247 pairwise comparisons deviated from Hardy-Weinberg equilibrium. Five of 171 comparisons at the population level were in linkage disequilibrium, but I did not detect linkage disequilibrium between loci at the lek level after corrections for multiple comparisons. Two loci (SGCA9 and TUD3) were out of Hardy-Weinberg equilibrium and had significant heterozygote deficiencies, but I believe the frequency of allelic dropout and null alleles was low for these loci. No loci were in disequilibrium at the lek level, I 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 SGCA and TUD3 (see Bush et al. 2010, 2011), therefore, all loci were considered unlinked and retained for analysis.

All 19 microsatellite loci were polymorphic (Table 2), with the number of alleles ranging from 4 (TTD1) to 16 (TUD4). In general, the observed genetic diversity measures in northeastern California were high and consistent across all leks, with the lowest number of alleles in the LAS0001 lek site and the highest number of alleles 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, which represents one of the most genetically diverse leks within my study area (based on both allelic richness and expected heterozygosity) and LAS0011, which had one of the lowest levels of allelic richness. Additionally, the inbreeding coefficient for the LAS0011 lek was 0.173, possibly indicating a departure from random mating and that some level of inbreeding might be occurring at this site.

Bayesian analysis using STRUCTURE did not indicate the presence of substructure in this sample of sage-grouse ( $K = 1$ ), suggesting sage-grouse in northeastern California are a single genetic population. Overall genetic differentiation between leks observed in my study was low and ranged from 0.002 to 0.037 indicating a high rate of gene flow among leks (Table 4). Pairwise  $F_{ST}$  comparisons among lek sites did not differ significantly, suggesting gene flow occurs across the sampled region.

A significant positive relationship between genetic and geographic distance was found among leks (Figure 2), indicating high gene flow among neighboring lek sites with decreasing gene flow as lek-to-lek distance increases. In addition, I assessed IBD of males and females separately to identify sex-specific differences in dispersal. Isolation-by-distance was detected in males ( $r = 0.656$ ,  $P = 0.003$ ) but not females ( $r = 0.029$ ,  $P = 0.499$ ), suggesting male sage-grouse are the more philopatric sex and that females have a greater predisposition to disperse.

### Relatedness

There was a significant negative relationship between lek-to-lek relatedness and geographic distance for all birds combined indicating leks are not currently differentiated from each other ( $r = -0.656$ ,  $P = 0.002$ ). The lack of genetically differentiated lek complexes, as determined by  $F_{ST}$  and relatedness, suggests that gene flow occurs across the study area. To further assess lek genetic structure, I computed the mean coefficients of relatedness across all leks and for males and females, separately (Figure 3). When data for both genders were analyzed collectively, the global average  $R$  taken across all leks was near but significantly different from zero (mean  $\pm$  SE =  $0.015 \pm 0.006$ ,  $t_{0.05(1),7} = 2.60$ ,  $P = 0.04$ ), indicating the

overall pattern of relatedness within leks was weak. A separate analysis by gender indicated that both males (mean  $\pm$  SE =  $0.011 \pm 0.010$ ,  $t_{0.05(1),7} = 1.16$ ,  $P = 0.28$ ) and females (mean  $\pm$  SE =  $-0.012 \pm 0.014$ ,  $t_{0.05(1),7} = -0.79$ ,  $P = 0.45$ ) exhibited low average relatedness within leks, suggesting that sage-grouse leks are largely assemblages of unrelated conspecifics.

## DISCUSSION

Although sage-grouse are declining and have lost a significant portion of their range in northeastern California, sage-grouse in my study exhibited high genetic diversity. I observed no population structure and despite population declines and habitat loss, leks in northeastern California were not highly differentiated from one another. Bush et al. (2011) also 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. The only significant difference I observed in measures of genetic diversity between lek sites was  $F_{IS}$  (i.e., the inbreeding coefficient;  $P = 0.024$ ) between LAS0004, which represents one of the most genetically diverse leks within my study area (based on both allelic richness and expected heterozygosity) and LAS0011, which had one of the lowest levels of allelic richness. In addition, the inbreeding coefficient for the LAS0011 lek ( $F_{IS} = 0.173$ ), indicated a possible departure from random mating and that some level of inbreeding might be occurring at this site. Whether my results for lek LAS0011 are an indication of consanguineous mating or the presence of null alleles is unclear. However, Höglund et al. (2007) reported similar  $F_{IS}$  values in small and isolated populations of black grouse, possibly indicating increased levels of inbreeding. Overall, my results are consistent with a range-wide genetic survey of sage-grouse previously conducted

by Oyler-McCance et al. (2005), which assigned birds from northern California to clusters that included populations from northwestern Nevada and southeastern Oregon. This suggests that sage-grouse in northeastern California form a single genetic population and that high levels of genetic diversity are likely being maintained through gene flow 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 if sage-grouse currently disperse between the 2 regions. Therefore, the high genetic diversity I observed within northeastern California could indicate either historic or contemporary gene flow with Nevada, but I had no samples from Nevada to test either hypothesis.

Within-lek relatedness was low in northeastern California, suggesting that sage-grouse lek sites are largely assemblages of unrelated males and females. The overall pattern of relatedness I observed are similar to those reported in other sage-grouse studies (Gibson et al. 2005, Bush et al. 2010, Bush et al. 2011) where no patterns of kin structure at the lek level were observed. In addition, my results showed a significant negative relationship between lek relatedness and geographic distance, indicating that leks are not differentiated from each other (i.e., higher relatedness occurs at shorter geographic distances). This pattern is consistent with other studies examining the effects of habitat fragmentation on the genetic structure of Cantabrian capercaillie (*Tetrao urogallus cantabricus*) occupying the periphery of their range in northern Spain (Alda et al. 2011, Vázquez et al. 2012) and has been previously demonstrated for capercaillie in the Alps (Storch and Segelbacher 2000). Authors attributed the pattern they observed, in part, to the limited natal dispersal of males (Regnaut

et al. 2006b) and other factors such as habitat quality and configuration, which could reduce dispersal capabilities among subpopulations (Alda et al. 2011, Vázquez et al. 2012)

I observed a significant positive relationship between genetic ( $F_{ST}$  and relatedness) and geographic distance among leks, indicating high gene flow among neighboring lek sites (i.e., adjacent leks are more similar to each other than geographically distant leks). Isolation-by-distance has also been observed in other tetraonids (e.g., Piertney et al. 1998b, Caizergues et al. 2003 a, b; Segelbacher and Storch 2002, Johnson et al. 2003, Segelbacher et al. 2003, Regnaut et al. 2006a, Fedy et al. 2008, Bech et al. 2009, Bush et al. 2011) and suggests that sage-grouse populations in northern California are either connected by contemporary gene flow or that isolation from the core of the species' geographic range has occurred so recently that the effects on genetic structure are not yet detectable.

In addition, my results showed a significant pattern of IBD among males but not females. This, combined with females having lower within-lek relatedness than males, suggests male sage-grouse are the more philopatric sex and that females have a greater predisposition to disperse. Among avian species for which natal dispersal has been documented, a common finding is that females are less philopatric than males (see review in Greenwood 1980). However, few data are available for species with lek mating systems (Clarke et al. 1997) and among grouse species in which natal dispersal has been investigated using direct (i.e., demographic) methods, only 2 studies (e.g., Dunn and Braun 1985, Thompson 2012) have examined sex-specific movement patterns of juvenile sage-grouse during natal dispersal. In Colorado, Dunn and Braun (1985) found, on average, female sage-grouse (mean = 8.8 km) dispersed further than males (mean = 7.4 km). Female-biased



dispersal has been reported in other tetraonids (Hines 1986, Schroeder 1986, Martin and Hannon 1987, Small and Rusch 1989, Giesen and Braun 1993, Smith 1997, Caizergues and Ellison 2002, Warren and Baines 2002, Caizergues et al. 2003a, Segelbacher et al. 2008) and is consistent with the typical avian pattern of female-biased dispersal I observed. In contrast, Thompson (2012) found the median dispersal distance was greater for radiomarked juvenile male sage-grouse ( $3.84 \pm 1.26$  km) compared to females ( $2.68 \pm 0.30$  km), however, both females and males remained philopatric to their natal breeding population. In a study using indirect (e.g., genetic) methods, Bush et al. (2010) reported that dispersal was not sex-specific and found no genetic evidence that sage-grouse in Alberta followed the typical avian pattern of male philopatry or the female-biased dispersal that was observed in sage-grouse in Colorado (Dunn and Braun 1985). Recent genetic studies on other grouse species (Piertney et al. 1998a, Mäki-Petäys et al. 2007, Fedy et al. 2008) and individual movement data (Carleos and López-Díaz 2010) have also documented either female-biased or equal rates of dispersal between genders. Although my results serve as an important step towards understanding patterns of sex-biased dispersal in sage-grouse, more research is needed on the proximate and ultimate causes behind the patterns I observed.

Dispersal appears to be a critical demographic factor in maintaining genetically viable grouse populations (Caizergues et al. 2003a, b; 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 of time (<50 years) 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 might significantly impact the fitness and viability of remaining grouse populations (Bouzat et al. 1998a, b; Segelbacher and Storch 2002, Segelbacher et al. 2003, Caizergues et al. 2003b, Johnson et al. 2004, Höglund et al. 2007, Segelbacher et al. 2008).

Although sage-grouse in northeastern California have maintained gene flow across the sampled region and have tolerated some degree of habitat deterioration and fragmentation without losing genetic diversity, continued habitat loss will likely result in small, isolated sage-grouse populations at risk of losing genetic variation. 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 impact gene flow and genetic diversity.

Maintaining and possibly 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. Despite their dependence on sagebrush, virtually no undisturbed tracts of sagebrush-steppe habitat exist within the current distribution of sage-grouse (Schneegas 1967, Braun 1998, Knick et al. 2003). Observations by Patterson (1952:192) suggest that sage-grouse have not, and likely will not, adapt their life history to fit landuse practices that disturb large tracts of sagebrush rangelands upon which they depend. To maintain sage-grouse populations in northeastern California, conservation

measures should focus on securing connectivity between spatially discrete lek complexes by enhancing existing habitat patches and preventing future habitat loss and fragmentation. Thus, conservation actions for sage-grouse must consider the processes and patterns of gene flow operating at landscape scales to ensure persistence of this species in northeastern California.

## LITERATURE CITED

- Alda, F., P. Sastre, P. J. De La Cruz-Cardiel, and I. Doadrio. 2011. Population genetics of the endangered Cantabrian capercaillie in northern Spain. *Animal Conservation* 14:249-260.
- Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*) in Alberta, Canada. Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. *Ecological Applications* 17:508-526.
- Allendorf, F. W. 1986. Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biology* 5:181-190.
- Autenrieth, R. E. 1981. Sage grouse management in Idaho. Idaho Department of Fish and Game. Wildlife Bulletin 9.
- Bech, N., J. Boissier, S. Drovetski, and C. Novoa. 2009. Population genetic structure of rock ptarmigan in the 'sky islands' of French Pyrenees: implications for conservation. *Animal Conservation* 12:138-145.
- Beetle, A. A. 1960. A study of sagebrush. The section Tridentata of *Artemisia*. University of Wyoming Agricultural Experiment Station Bulletin 368.
- Bouzat, J. L., H. H. Cheng, H. A. Lewin, R. I. Westemeier, J. D. Brawn, and K. N. Paige. 1998a. Genetic evaluation of a demographic bottleneck in the greater prairie-chicken. *Conservation Biology* 12:836-849.
- Bouzat, J. L., H. A. Lewin, and K. N. Paige. 1998b. The ghost of genetic diversity past: historical DNA analysis of the greater prairie-chicken. *American Naturalist* 152:1-6.

- Braun, C. E. 1986. Changes in sage grouse lek counts with advent of surface coal mining. *Proceedings of Issues and Techniques in the Management of Impacted Western Wildlife* 2:227-231.
- Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? *Proceedings of the Western Association State Fish and Game Wildlife Agencies* 78:139-156.
- Burt, D. W., D. R. Morrice, A. Sewalem, J. Smith, I. R. Paton, E. J. Smith, J. Bentley, P. M. Hocking. 2003. Preliminary linkage map of the turkey (*Meleagris gallopavo*) based on microsatellite markers. *Animal Genetics* 34:399-409.
- Bush, K. L., C. L., Aldridge, J. E. Carpenter, C. A. Paszkowski, M. S. Boyce, and D. W. Coltman. 2010. Birds of a feather do not always lek together: genetic diversity and kinship structure of greater sage-grouse (*Centrocercus urophasianus*) in Alberta. *Auk* 127:343-353.
- Bush, K. L., C. K. Dyte, B. J. Moynahan, C. L. Aldridge, H. S. Sauls, A. M. Battazzo, B. L. Walker, K. E. Doherty, J. Tack, J. Carlson, D. Eslinger, J. Nicholson, M. S. Boyce, D. E. Naugle, C. A. Paskowski, D. W. Coltman. 2011. Population structure and genetic diversity of greater sage-grouse (*Centrocercus urophasianus*) in fragmented landscapes at the northern edge of their range. *Conservation Genetics*. 12:527-452..
- Bush, K. L., M. D. Vinsky, C. L. Aldridge, and C. A. Paszkowski. 2005. A comparison of sample types varying in invasiveness for use in DNA sex determination in an endangered population of greater sage-grouse (*Centrocercus urophasianus*). *Conservation Genetics* 6:867-870.
- Caizergues, A., and L. N. Ellison. 2002. Natal dispersal and its consequences in black grouse *Tetrao tetrix*. *Ibis* 144:478-487.
- Caizergues, A., A. Bernard-Laurent, J. F. Brenot, L. Ellison, and J. -Y. Rasplus. 2003a. Population genetic structure of rock ptarmigan *Lagopus mutus* in northern and western Europe. *Molecular Ecology* 12:2267-2274.
- Caizergues, A., S. Dubois, G. Mondor, and J-Y Rasplus. 2001. Isolation and characterization of microsatellite loci in black grouse (*Tetrao tetrix*). *Molecular Ecology Notes* 1:36-38.
- Caizergues, A., O. Rätti, P. Helle, L. Rotelli, L. Ellison, and J.-Y. Rasplus. 2003b. Population genetic structure of male black grouse (*Tetrao tetrix* L.) in fragmented vs. continuous landscapes. *Molecular Ecology* 12:2297-2305.

- Carleos, C., and M. López-Díaz. 2010. An indexed dispersion criterion for testing the sex-biased dispersal of lek-mating behavior of capercaillies. *Environmental and Ecological Statistics* 17:283-301.
- Casgrain P., and P. Legendre. 2001. The R Package for Multivariate and Spatial Analysis, version 4.0. User's Manual. Department des Sciences Biologiques, Université de Montréal. [Online]. Available at [www.bio.umontreal.ca/casgrain/en/labo/R/index.html](http://www.bio.umontreal.ca/casgrain/en/labo/R/index.html).
- Cheng, H. H., I. Levin, and R. L. Vellejo. 1995. Development of a genetic map of the chicken with high-utility markers. *Poultry Science* 74:1855-1874.
- Clarke, A. L., B. E. Saether, and E. Roskaft. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429-438.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished report, Cheyenne, Wyoming, USA.
- Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosely, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. Ecology and management of sage-grouse and sage-grouse habitat. *Journal of Range Management* 57:2-19.
- Crunden, C.W. 1963. Age and sex of sage grouse from wings. *Journal of Wildlife Management* 27:846-850.
- Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. *Journal of Wildlife Management* 27:811-841.
- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. *Journal of Wildlife Management* 74:1544-1553.
- Dunn, P. O., and C. E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. *Auk* 102:621-627.
- Fedy, B. C., K. Martin, C. Ritland, and J. Young. 2008. Genetic and ecological data provide incongruent interpretations of population structure and dispersal in naturally divided

- populations of white-tailed ptarmigan (*Lagopus leucura*). *Molecular Ecology* 17:1905-1917.
- Frankham, R., J. D. Ballou, and D. A. Briscoe. 2002. *Introduction to conservation genetics*. Cambridge University Press, Cambridge.
- Garton, E. O., J. W. Connelly, J. S. Horne, C. A. Hagen, A. Moser, and S. Schroeder. 2011. Greater sage-grouse population dynamics and probability of persistence. Pages 293-381 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Gibson, R. M., D. Pires, K. S. Delaney, and R. K. Wayne. 2005. Microsatellite DNA analysis shows that greater sage grouse leks are not kin groups. *Molecular Ecology* 14:4453-4459.
- Giesen, K. M., and C. E. Braun. 1993. Natal dispersal and recruitment of juvenile white-tailed ptarmigan in Colorado. *Journal of Wildlife Management* 57:72-77.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224-231.
- Goudet, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices, version 2.9.3. [Online.] Available from [www.unil.ch/popgen/softwares/fstat.htm](http://www.unil.ch/popgen/softwares/fstat.htm).
- Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behaviour* 28:1140-1162.
- Hardy, O. J., and X. Vekemans. 2002. SPAGEDI: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes* 2:618-620.
- Hines, J. E. 1986. Survival and reproduction of dispersing blue grouse. *Condor* 88:43-49.
- Höglund, J., J. K. Larsson, H. A. H. Jansman, and G. Segelbacher. 2007. Genetic variability in European black grouse (*Tetrao tetrix*). *Conservation Genetics* 8:239-243.
- Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997-2007. Pages 407-450 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.

- Johnson, J. A., J. E. Toepfer, and P. O. Dunn. 2003. Contrasting patterns of mitochondrial and microsatellite population structure in fragmented populations of greater prairie-chickens. *Molecular Ecology* 12:3335-3347.
- Johnson, J. A., M. R. Bellinger, J. E. Toepfer, and P. Dunn 2004. Temporal changes in allele frequencies and low effective population size in greater prairie-chickens. *Molecular Ecology* 13:2617-2630.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611-634.
- Knick, S. T., and S. E. Hanser . 2011. Connecting pattern and process in greater sage-grouse populations and sagebrush landscapes. Pages 383-405 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. *Studies in Avian Biology* (vol. 38), University of California Press, Berkeley, California, USA.
- Lacy, R. C. 1997. Importance of genetic variation to the viability of mammalian populations. *Journal of Mammalogy* 78:320-335
- Lesica, P., and F. W. Allendorf. 1995. When are peripheral populations valuable for conservation biology? *Conservation Biology* 9:753-760.
- Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:486-491.
- Mäki-Petäys, H. J. Corander, J. Aalto, T. Liukkonen, P. Helle, and M. Orell. 2007. No genetic evidence of sex-biased dispersal in a lekking bird, the capercaillie (*Tetrao urogallus*). *Journal of Evolutionary Biology* 20:865-873.
- Mantel, N. 1967. The detection of disease clustering and generalized regression approach. *Cancer Research* 27:209-220.
- Martin, K. and S. J. Hannon. 1987. Natal philopatry and recruitment of willow ptarmigan in north central and northwestern Canada. *Oecologia* 71:518-524.
- Maruyama, T., and P. A. Fuerst. 1985. Number of alleles in a small population that was formed by a recent bottleneck. *Genetics* 111:675-689.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145-184 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. *Studies*

- in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29:1-10.
- Oyler-McCance, S. J., N. W. Kahn, K. P. Burnam, C. E. Braun, and T. W. Quinn. 1999. A population genetic comparison of large- and small-bodied sage grouse in Colorado using microsatellite and mitochondrial DNA markers. *Molecular Ecology* 8:1457-1465.
- Oyler-McCance, S. J., S. E. Taylor, and T. W. Quinn. 2005. A multilocus population genetic survey of the greater sage-grouse across their range. *Molecular Ecology* 14:1293-1310.
- Patterson, R. L. 1952. The sage grouse in Wyoming. Sage Books Inc., Denver, Colorado, USA.
- Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6:288-295.
- Piertney, S. B., and J. F. Dallas. 1997. Isolation and characterization of hypervariable microsatellites in red grouse *Lagopus lagopus scoticus*. *Molecular Ecology* 6: 93-95.
- Piertney, S. B., and J. Höglund. 2001. Polymorphic microsatellite DNA markers in black grouse (*Tetrao tetrix*). *Molecular Ecology Notes* 1:303-304.
- Piertney, S. B., D. C. MacColl, P. J. Bacon, and J. F. Dallas. 1998a. Local genetic structure in red grouse (*Lagopus lagopus scoticus*): an analysis using microsatellite DNA. *Molecular Ecology* 7:1645-1654.
- Piertney, S. B., A. D. C. MacColl, P. J. B. Dallas, and J. F. Dallas. 1998b. Local genetic structure of red grouse (*Lagopus lagopus scoticus*): evidence from microsatellite DNA markers. *Molecular Ecology* 12:1645-1654.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945-959.
- Queller, D. C., and K. F. Goodnight. 1989. Estimating relatedness using genetic markers. *Evolution* 43:258-275.
- Raymond, M., and F. Rousset. 1995. GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86:248-249.



- Regnaut, S., P. Christe, M. Chapulsat, and L. Fumagalli. 2006a. Genotyping faeces reveals facultative kin association on capercaillie's leks. *Conservation Genetics* 7:665-674.
- Regnaut, S., F. S. Lucas, and L. Fumagalli. 2006b. DNA degradation in avian faecal samples and feasibility of non-invasive genetic studies of threatened capercaillie populations. *Conservation Genetics* 7:449-453.
- Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics* 145:1219-1228.
- Schroeder, M. A. 1986. The fall phase of dispersal in juvenile spruce grouse. *Canadian Journal of Zoology* 64:16-20.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. *Condor* 106:363-376.
- Schneegas, E. R. 1967. Sage grouse and sagebrush control. *Transactions of the North American Wildlife and Natural Resource Conference* 32:270-274.
- Segelbacher, G., J. Höglund, and I. Storch. 2003. From connectivity to isolation: genetic consequences of population fragmentation in capercaillie across Europe. *Molecular Ecology* 12:1773-1780.
- Segelbacher, G., S. Manel, and J. Tomiuk. 2008. Temporal and spatial analyses disclose consequences of habitat fragmentation on the genetic diversity in capercaillie (*Tetrao urogallus*). *Molecular Ecology* 17:2356-2367.
- Segelbacher, G., R. J. Paxton, G. Steinbrück, P. Trontelj, and I. Storch. 2000. Characterization of microsatellites in capercaillie *Tetrao urogallus* (AVES). *Molecular Ecology* 9:1934-1935.
- Segelbacher, G., and I. Storch. 2002. Capercaillie in the Alps: the genetic evidence of metapopulation structure and population decline. *Molecular Ecology* 11:1669-1677.
- Seutin, G., B. N. White, and P. T. Boag. 1991. Preservation of avian blood and tissue samples for DNA analyses. *Canadian Journal of Zoology* 69:82-90.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *Biosciences* 31:131-134.

- Shuford, W. D., and T. Gardali. 2008. California Bird Species of Special Concern: A ranked assessment of species, subspecies, and distinct populations of birds of immediate conservation concern in California. Studies of Western Birds 1. Western Field Ornithologists, Camarillo, California, and California Department of Fish and Game, Sacramento, California, USA.
- Small, R.J., and D. H. Rusch. 1989. The natal dispersal of ruffed grouse. *Auk* 106:72–79.
- Smith, A. A. 1997. Dispersal and movements in a Swedish willow grouse *Lagopus lagopus* population. *Wildlife Biology* 3:279.
- Storch, I., and G. Segelbacher. 2000. Genetic correlates of spatial population structure in central European capercaillie *Tetrao urogallus* and black grouse *T. tetrix*: a project in progress. *Wildlife Biology* 6:305-310.
- Taylor, S. E., S. J. McCance, and T. W. Quinn. 2003. Isolation and characterization of microsatellite loci in greater sage-grouse (*Centrocercus urophasianus*). *Molecular Ecology Notes* 3:262-263.
- Thompson, T. R. 2012. Dispersal ecology of greater sage-grouse in northwestern Colorado: evidence from demographic and genetic methods. Dissertation. University of Idaho, Moscow, Idaho, USA.
- Ury, H. K. 1976. A comparison of four procedures for multiple comparison among means (pairwise contrasts) for arbitrary sample sizes. *Technometrics* 18:89-97.
- United States Department of Interior (USDI). 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. *Federal Register* 75:13910-14014 (23 March 2010).
- van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills, and P. Shipley. 2004. Micro-checker: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology* 4:535–538.
- Vásquez, J. F., T. Pèrez, F. Quirós, J. R. Obeso, J. Albornoz, and A. Domínguez. 2012. Population genetic structure and diversity of the endangered Cantabrian capercaillie. *Journal of Wildlife Management* 76:957-965.
- Wakkinen, W. L., K. P. Reese, J.W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. *Wildlife Society Bulletin* 20: 425-426.

- Walker, B. L., and D. E. Naugle. 2011. West Nile virus ecology in sagebrush habitat and impacts on greater sage-grouse populations. Pages 127-142 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Warren, P. K., and D. Baines. 2002. Dispersal, survival and causes of mortality in black grouse *Tetrao tetrix* in northern England. Wildlife Biology 8:91–97.
- Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358-1370.
- Wisdom, M. J., C. W. Meinke, S. T. Knick, and M. A. Schroeder. 2011. Factors associated with extirpation of sage-grouse. In Knick, S. T., and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.

Table 1. Location of greater sage-grouse genetic samples collected in northeastern California, 2007-2009. Autumn capture refers to samples collected off-lek which could not be assigned to any lek complex. Data for these individuals were not used in any lek-specific analysis.

Lek	Mean number of males/lek (2007-2009)	No. genetic samples		
		Female	Male	Totals
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
Totals		88	99	187

Table 2. Summary of the average genetic variability ( $H_O$  = observed heterozygosity,  $H_E$  = expected heterozygosity,  $A$  = number of alleles per locus,  $AR$  = allelic richness,  $F_{IS}$  = inbreeding coefficient, and  $R$  = average relatedness) by locus for greater sage-grouse in northeastern California, 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	0.644	0.737	10.11	9.997	0.126	-0.0058

Table 3. Genetic diversity estimates of greater sage-grouse leks in northeastern California, 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, and  $R$  = average relatedness).

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

Table 4. Pairwise comparison matrix of  $F_{ST}$  values (below diagonal) and geographic distance (km; above diagonal) between greater sage-grouse lek sites in northeastern California.

Lek	LAS0071	LAS0004	LAS0011	WAS0002	LAS0057	LAS0001	LAS0080	LAS0002
LAS0071		8.92	16.4	21.7	13.2	20.8	31.5	57.7
LAS0004	0.003		26.6	27.3	20.1	27.9	33.1	53.6
LAS0011	0.004	0.019		7.32	21.9	26.1	44.1	68.8
WAS0002	0.016	0.017	0.012		29.0	33.5	51.0	75.5
LAS0057	0.002	0.017	0.010	0.021		7.76	22.4	47.4
LAS0001	0.020	0.019	0.013	0.032	0.009		21.6	46.7
LAS0080	0.012	0.015	0.008	0.019	0.004	0.005		25.3
LAS0002	0.028	0.031	0.021	0.027	0.023	0.037	0.019	

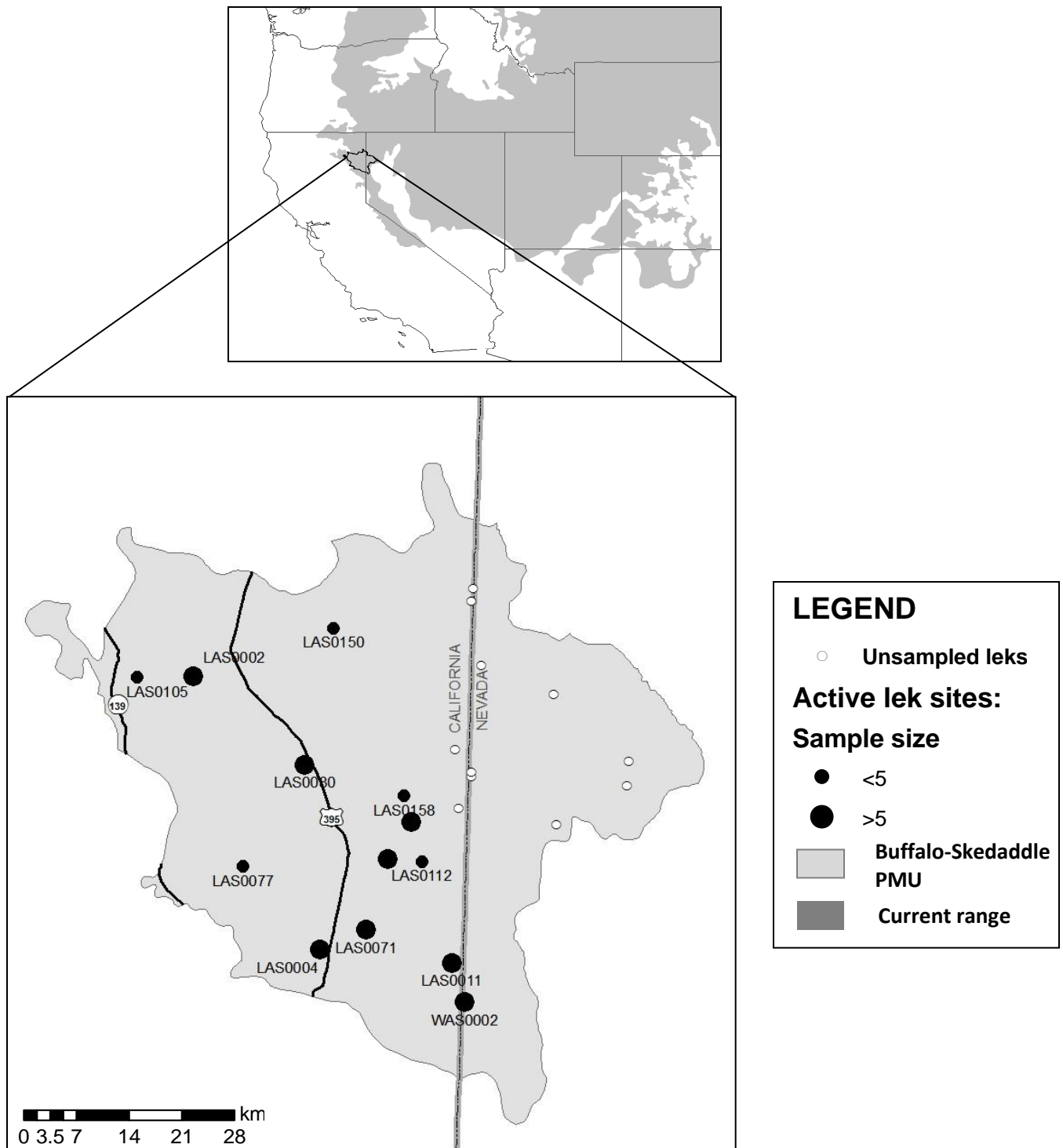


Figure 1. Geographical location of sampled greater sage-grouse leks (black circles) in northeastern California. Leks LAS0105 and LAS0150 each contained <5 males in 2007 and became inactive in 2008 and remained abandoned through 2009.

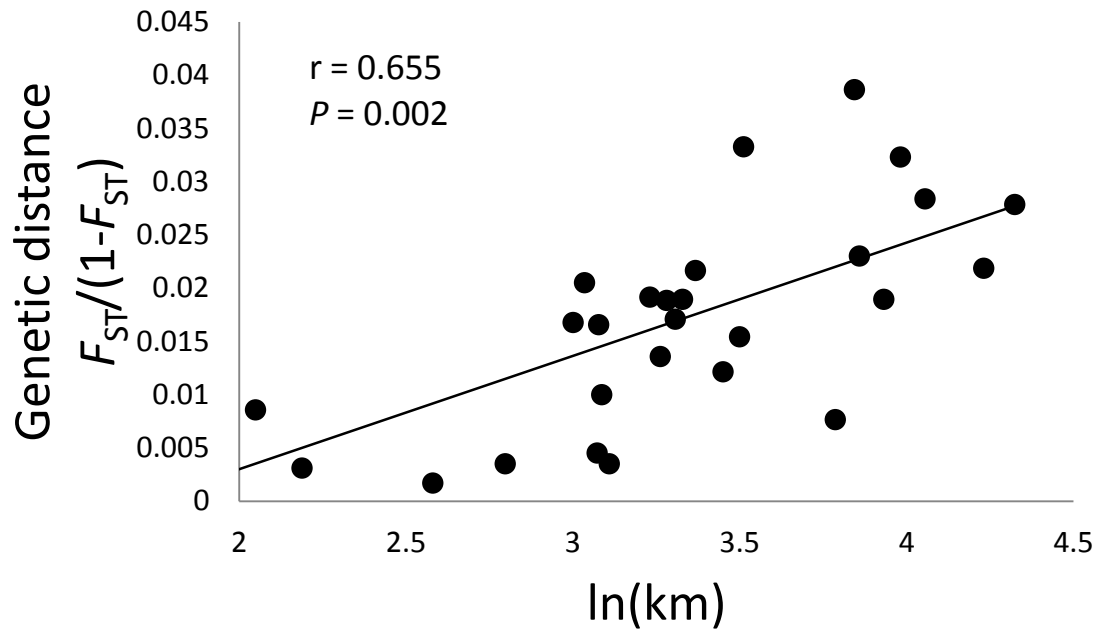


Figure 2. Analysis of isolation-by-distance. Genetic distance ( $F_{ST}/(1-F_{ST})$ ) are plotted against geographic distance for pairwise comparisons of 8 lek sites of greater sage-grouse in northeastern California, 2007-2009.



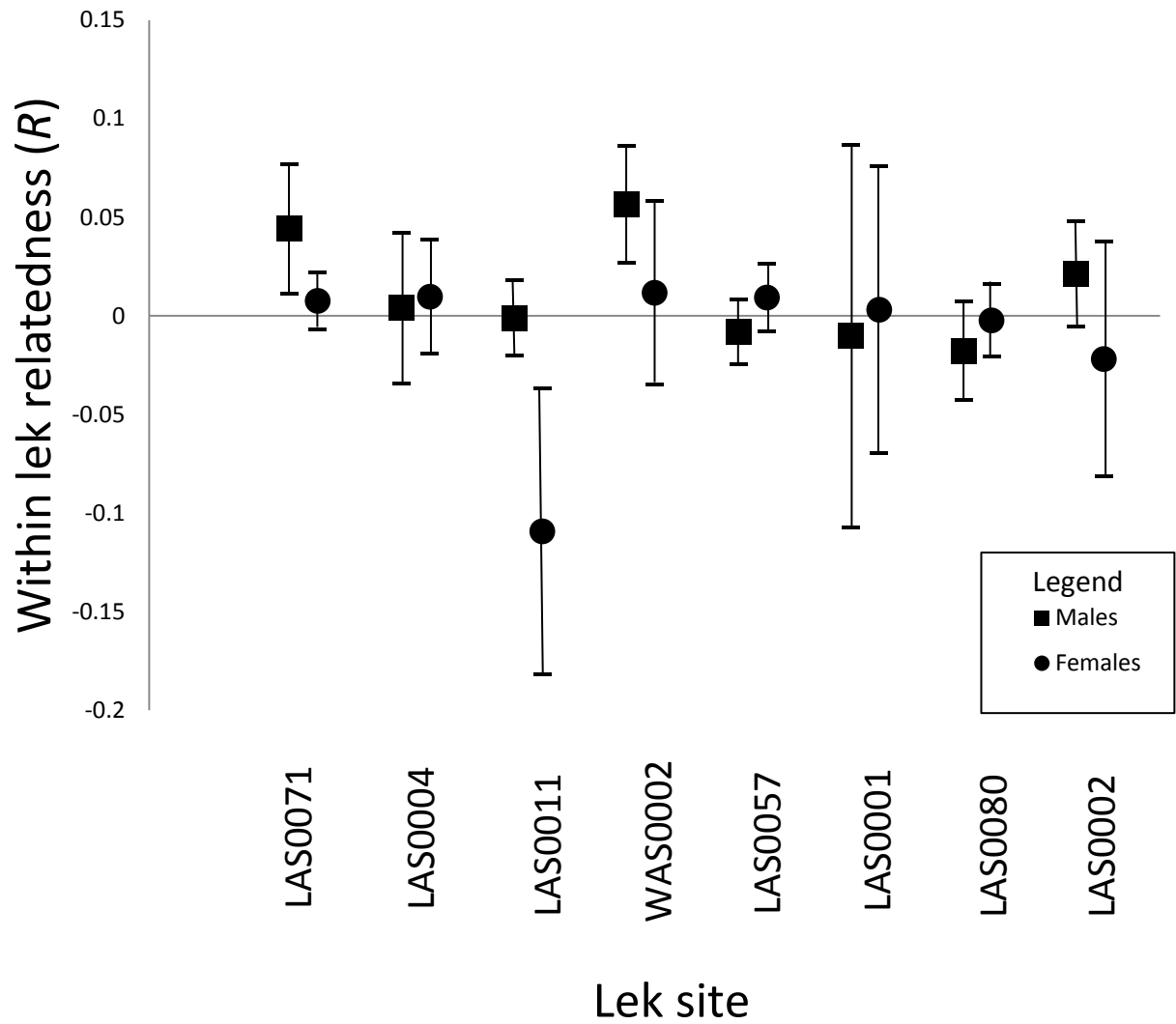


Figure 3. Average within-lek relatedness for greater sage-grouse leks in northeastern California, 2007-2009. Genetic relatedness within each lek is presented as the average relatedness for males (squares) and females (dots), respectively. Bars indicate SE.

**CHAPTER 5. INTEGRATING MOLECULAR DATA TO DETECT PATTERNS OF SEX-BIASED DISPERSAL AND BARRIERS TO GENE FLOW IN GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*)**

**ABSTRACT** – I assessed patterns of dispersal among greater sage-grouse (*Centrocercus urophasianus*) in northeastern California using 19 polymorphic microsatellite loci. My results showed a significant pattern of isolation-by-distance among males, suggesting that male greater sage-grouse are the more philopatric sex and that females have a greater predisposition to disperse. Furthermore, spatial autocorrelation analysis revealed stronger spatial structuring for males than for females. The results from the corrected Assignment Index (A<sub>IC</sub>) also confirmed female-biased dispersal, although differences between genders were not significant. My results indicate molecular data can provide insights into underlying dispersal patterns even when direct observations of dispersal events are lacking. Although more research is needed on the proximate and ultimate causes behind the patterns I observed, my results serve as an important step towards understanding patterns of sex-biased dispersal in greater sage-grouse.

**KEYWORDS:** *Centrocercus urophasianus*, dispersal, isolation-by-distance, sage-grouse, spatial autocorrelation

**INTRODUCTION**

Among avian species where natal dispersal has been documented, a common finding is that females are less philopatric than males (see review in Greenwood 1980). However, few data on dispersal are available for species with lek mating systems (Clarke et al. 1997) and among grouse species in which natal dispersal has been investigated, only 2 studies (e.g., Dunn and

Braun 1985, Thompson 2012) have examined sex-specific movement patterns of juvenile greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) during natal dispersal.

The long-term viability of sage-grouse populations depends, in part, on the effects of landscape level habitat stability on dispersal rates and distances (Dale 2001). Grouse populations are particularly vulnerable to fragmentation of native rangelands (Woodward et al. 2001, Fuhlendorf et al. 2002, Schroeder and Robb 2003), and the ability of sage-grouse to move among suitable patches of habitat depends not only on the juxtaposition of such patches but also on the dispersal behavior of the species (Fahrig and Merriam 1994).

Dispersal also appears to be an important demographic factor in maintaining genetically viable grouse populations (Caizergues et al. 2003a, b; Johnson et al. 2004, Höglund et al. 2007, Segelbacher et al. 2008). 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 might significantly impact the fitness and viability of remaining grouse populations (Bouzat et al. 1998a, b; Segelbacher and Storch 2002, Caizergues et al. 2003b, Segelbacher et al. 2003, Johnson et al. 2004, Höglund et al. 2007, Bech et al. 2009).

Although management of wildlife species threatened by habitat fragmentation has traditionally been based on demographic studies, the use of molecular markers has been increasingly accepted as a tool for describing dispersal and to assist demographic studies (DeWoody 2005, DeYoung and Honeycutt 2005). Dispersal is of particular interest in

conservation genetics because it results in gene flow, the exchange of genes from one population to another. Gene flow not only affects the rate of genetic drift and the expression of deleterious alleles, it determines the genetic structure of populations.

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 might lead to discrepancies between genetic and demographic estimates. 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. Thus, genetic-based estimates offer a temporal perspective on dispersal that is not often available from direct observations.

In California, sage-grouse populations occupy the western periphery of the species' geographic range. The current sage-grouse population structure in northeastern California is thought to consist of spatially discrete lek complexes where connectivity is unknown. At current population levels and distribution, movement between subpopulations by natal dispersal is necessary to facilitate population persistence and genetic variability. A range-wide genetic survey of sage-grouse found gene flow is likely limited to movements by sage-grouse between neighboring populations and not likely the result of long-distance movements of individuals across large portions of the species range (Oyler-McCance et al. 2005). However, the connectivity of habitats suitable for sage-grouse has not been studied in California and little is known about the population genetic structure or how sage-grouse

respond to habitat fragmentation. Because the relationship between dispersal, gene flow, and genetic structure are interrelated and affect the long-term persistence of sage-grouse in California, the objectives of this study were to: 1) describe population genetic structure of sage-grouse in northeastern California; 2) identify putative barriers to gene flow which might influence dispersal; and 3) evaluate patterns of dispersal to assess whether there is evidence for any sex-specific differences.

## **METHODS**

### Study Area and Sample Collection

I assessed patterns of dispersal and gene flow 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 include Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), and little sagebrush (*A. arbuscula*).

I trapped sage-grouse opportunistically on or near lek sites using spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) from March through April 2007-2009. I classified gender and age of captured birds by plumage characteristics and wing molt (Crunden 1963, Dalke et al. 1963). Blood samples were collected from sage-grouse at 13 known, active lek sites within the Buffalo-Skedaddle PMU in northeastern California. I acquired a genetic sample by collecting approximately 3 drops of blood from a slightly over-clipped hallux nail, which was stored 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. Because

sampling juveniles can reduce the ability of genetic tests to detect sex-biased dispersal (Prugnolle and de Meeus 2002), only yearling and adult birds were included in my 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-year sampling period (Chapter 2), which could potentially alter allele frequency, so samples were combined across all years. In addition, individual sage-grouse were marked with a serially-numbered aluminum leg band at capture, to ensure blood samples collected across different years did not include duplicate samples.

#### DNA Extraction and Microsatellite Genotyping

DNA was extracted using DNeasy Tissue Kits (Qiagen, Inc.), following manufacturer's protocols and incorporating modifications from Bush et al. (2005). Individual samples were genotyped for every bird captured at 19 polymorphic microsatellites as described in Chapter 4. Amplification products were run against a LIZ 500 size standard on an ABI 3130xl automated sequencer (Applied Biosystems). I used GENEMAPPER version 3.7 (Applied Biosystems) software, followed by visual inspection and verification, to genotype all samples. I calculated expected ( $H_E$ ) and observed ( $H_O$ ) heterozygosity for each locus and tested for deviations from Hardy-Weinberg equilibrium (HWE) for each locus separately and over all loci and linkage disequilibrium between all pairs of loci using GENEPOP on the web (Raymond and Rousset 1995; <http://wbiomed.curtin.edu.au/genepop/>). In addition, I used the program Micro-Checker 2.2.3 (van Oosterhout et al. 2004) to check for the presence of null alleles, scoring errors due to stuttering, and allelic dropout across all loci.

#### Isolation-by-Distance and Barriers to Gene Flow

I calculated the straight-line Euclidean distance from the geographic coordinates between known, active lek sites within my study area. To test for isolation-by-distance (IBD) across the sampled region, I applied a Mantel test (Mantel 1967) using the program 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). I assessed IBD of males and females separately to identify sex-specific differences in dispersal. Only data from lek sites with sample sizes  $>5$  individuals ( $n = 8$  leks) were retained for the analysis.

Although topographic features are not likely to limit sage-grouse movements, sage-grouse are less tolerant of landuse activities that alter habitats such as roads, which might act as putative barriers to gene flow. Therefore, I examined the possible impact of U.S. Highway 395, which bisects my study area, on the patterns of genetic differentiation in my sampled region by conducting a partial Mantel test (Smouse et al. 1986, Legendre et al. 2002). To investigate population genetic structure and levels of genetic differentiation, I first obtained pairwise  $F_{ST}$  estimates (Weir and Cockerham 1984) from GENEPOP. Second, to assess whether  $F_{ST}$  values among leks sites located west of Highway 395 were significantly different from  $F_{ST}$  values among leks east of Highway 395, I constructed a dissimilarity matrix with 0 in the within group matrices and 1 in the between group submatrix. Only data from lek sites with sample sizes  $>5$  individuals ( $n = 8$  leks) were retained for analysis, resulting in an uneven sample distribution on each side of the highway (65 and 96 individuals sampled on the west and east side of U.S. Highway 395, respectively).

### Sex-biased Dispersal

I used 2 approaches to assess patterns of dispersal in northeastern California. First, analysis of spatial genetic structure at the individual level were conducted 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). I carried out these analyses by calculating pairwise squared genetic distance and geographical matrices, which were used to generate an autocorrelation coefficient ( $r$ ) for each distance class and was presented as a correlogram. The autocorrelation coefficient ranges from 1 (positive autocorrelation) to -1 (negative autocorrelation) with  $r$ -values = 0 indicating no spatial genetic structure. The geographic distances were calculated as the straight-line Euclidian distance between known, active lek sites. I performed separate analyses for males and females. Spatial distances were divided into even distance classes (i.e., 5 km and 20 km for males and females, respectively). For each analysis, I 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 geographical 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). Second, I calculated a separate corrected Assignment Index (A<sub>IC</sub>) for male and female sage-grouse, respectively, using the approach by Favre et al. (1997) implemented in GenAlEx 6.3 (Peakall and Smouse 2006). The A<sub>IC</sub>



calculates the probability that a genotype originated in the population from which it was sampled (Paekall et al. 1995, Favre et al. 1997, Waser and Strobeck 1998). A negative AIC value characterizes dispersing individuals; whereas, a positive AIC value infers philopatry (Mossman and Waser 1999).

## **RESULTS**

### Sample Collection and Hardy-Weinberg Proportions

I collected blood samples from 167 sage-grouse (99 males; 68 females) from 13 known, active lek sites in the spring of 2007-2009. Sixteen of 19 loci were in Hardy-Weinberg disequilibrium at the population level after the significance level was adjusted for the number of comparisons with Bonferroni techniques (Ury 1976). At the lek level, 9 of 247 pairwise comparisons deviated from HWE. Five of 171 comparisons at the population level were in linkage disequilibrium but I could not detect linkage disequilibrium between loci at the lek level after corrections for multiple comparisons. Two loci (SGCA9 and TUD3) were out of HWE due to heterozygote deficiencies. However, there was no evidence that any locus was out of equilibrium consistently, therefore, I believe the frequency of allelic dropout and null alleles was low. Further, the observed deviations from HWE might be due to the patterns of spatial autocorrelation observed across my study area (see Results below; Guillot et al. 2009, Frantz et al. 2010). In addition, no loci were in disequilibrium at the lek level after adjusting for the number of comparisons with Bonferroni (Dunn-Šidák) techniques (Ury 1976), I 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 SGCA and TUD3

(see Bush et al. 2010, 2011), therefore, all loci were considered unlinked and retained for analysis.

#### Isolation-by-distance and Barriers to Gene Flow

A significant positive relationship between genetic and geographic distance was found among leks, indicating high gene flow among neighboring lek sites ( $r = 0.655$ ,  $P = 0.002$ ). In addition, I assessed IBD of males and females separately to identify sex-specific differences in dispersal (Figure 2). My results indicate that IBD was detected in males ( $r = 0.656$ ,  $P = 0.003$ ) but not females ( $r = 0.029$ ,  $P = 0.499$ ), suggesting male sage-grouse are the more philopatric sex and that females may have a greater predisposition to disperse.

The partial Mantel test failed to detect a significant effect on the differentiation between leks separated by U.S Highway 395, which bisects my study area. Therefore, U.S. Highway 395 did not appear to act as a barrier to gene flow for sage-grouse in northeastern California ( $r = -1.00$ ,  $P = 0.475$ ).

#### Sex-biased Dispersal

Maximum distance between known, active lek sites in my sampled region was 82 km (mean =  $34.8 \text{ km} \pm 18.4$  (SD); range = 4.6 to 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 were females at distances  $< 35$  km (Figure 3). However, patterns of genetic structure were similar between the genders at distances of 75-80 km. Geographic distances  $< 20$  km contained no observations for female sage-grouse (Figure 3). Although females had significant genetic similarities at the 80-km distance class, I failed to detect spatial genetic

structure in female sage-grouse. Overall, I believe the higher genetic similarity among males indicates relatively stronger male philopatry and sex-biased dispersal in females.

Female-biased dispersal also was evident from the mean assignment values of sage-grouse sampled from my 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 AIC (mAIC = 0.144) in contrast to the negative mean AIC for females (mAIC = - 0.123). Negative AIC values indicate genotypes less likely than average to occur in the sample (i.e., it characterize individuals with a higher probability of being immigrants because they have less chance of being assigned to the population from which they were sampled); whereas, a positive AIC value indicates a genotype more likely than average to occur in a sample and characterizes individuals with lower probability of being migrants (Mossman and Waser 1999). Moreover, females had proportionally more negative AIC values, although the variance between males and females was not significantly different, indicating a tendency towards higher dispersal in females.

## **DISCUSSION**

Overall, male and female sage-grouse in my study displayed different gene flow patterns across the sampled region, indicating higher rates of gene flow and longer dispersal distances in females. Male sage-grouse showed significant IBD suggesting that male dispersal is restricted to shorter distances. In contrast, I did not observe significant IBD for females, which suggests that females are dispersing farther than males or alternatively, females are migrating beyond the spatial scale of my genetic sampling. Additionally, I detected significant spatial autocorrelation among males but no such pattern was evident among

females. This implies that females are more likely to disperse than males, which is consistent with the pattern observed in birds (Greenwood 1980). Female-biased dispersal has been reported in other grouse species (Hines 1986, Schroeder 1986, Martin and Hannon 1987, Small and Rusch 1989, Giesen and Braun 1993, Smith 1997, Caizergues and Ellison 2002, Warren and Baines 2002, Caizergues et al. 2003a, Segelbacher et al. 2008) and is consistent with field observations for sage-grouse (Dunn and Braun 1985). Thus, it is not surprising that sage-grouse in my study exhibited the typical avian pattern of female-biased dispersal.

In contrast to my results, a recent study by Thompson (2012) found that female sage-grouse were the more philopatric sex. Among grouse species, the non-typical pattern of male-biased dispersal has only been documented in 1 other species, the hazel grouse (*Bonasa bonasia*; Swenson 1991, Montadert and Lèonard 2006, Rhim and Sun 2009, Montadert and Lèonard 2011). Thompson (2012) speculated that the natal dispersal patterns he observed were due, in part, to the complex spatial and temporal patterns found in sagebrush-steppe communities. Dispersal is not necessarily a species-specific fixed trait (Baguette and Van Dyke 2007), therefore, the differences in dispersal behavior I observed were likely due to differences in landuse history, spatial variation in landscape structure, and associated selection pressure on movement behavior (e.g., Clobert et al. 2004, Van Dyck and Baguette 2005). Intraspecific variation in dispersal behavior has been observed among populations living under different environmental regimes (e.g., Hanski et al. 2004) and also among different individuals (e.g., Doerr and Doerr 2005), suggesting comparisons across studies could possibly lead to different conclusions.

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 my study, the AIC confirmed female-biased dispersal although differences between genders 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 AIC values and a higher variance, the difference might not be significant. Exhaustive sampling efforts are necessary to detect sex-biased dispersal using assignment indices (Goudet et al. 2002). Thus, my failure to detect significant differences in mAIC values between genders 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 (Chapter 4) making it difficult to detect significant patterns of sex-biased dispersal using assignment indices. Whether the lack of significance in my results reflects the low power of assignment indices to assess differences in dispersal bias (Goudet et al. 2002), insufficient sample size, or lack of genetic differentiation between lek sites is unknown. However, I believe that other types of analysis presented (e.g., IBD, spatial autocorrelation) provide a more robust test than more conventional methods such as assignment indices. Despite the limitations of assignment indices, my results suggest a pattern of female-biased dispersal in my sampled population of sage-grouse.

Habitat fragmentation likely contributed to the pattern of isolation-by-distance I observed (Alda et al. 2011, Vázquez et al. 2012). Fragmentation is assumed to cause a reduction in the exchange of individuals between habitat patches, which eventually leads to lower colonization probabilities and gene flow rates and, ultimately, isolation for some

species (Hanski and Gilpin 1997). This difference stems from the effects of reduced mean patch size and decreased connectivity across the landscape (i.e., the rate of successful dispersal; Venier and Fahrig 1996).

Spatial autocorrelation analysis showed that significant spatial genetic structuring was detectable within distances of 15 km for males. These results reflect the approximate size of the area occupied by related individuals, i.e., the “genetic patch size.” However, no such pattern was evident in female sage-grouse. Knick and Hanser (2011) found that leks separated by distances greater than 13 to 18 km could be isolated due to decreased probability of dispersal from neighboring leks. Lek sites within my study area boundary were considerably farther apart ( $\text{Mean}_{\text{nearest neighbor}} = 10.9 \text{ km}$ ; Davis unpublished data) than has been reported across the geographic range of sage-grouse (range = 1.1 km to 4.0; 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 my study, and substantial population declines were associated with habitat fragmentation. The dispersal abilities of sage-grouse are assumed to be low (e.g.,  $3.8 \pm 1.3 \text{ km}$  and  $2.7 \pm 0.3 \text{ km}$ , for males and females, respectively; Thompson 2012). Thus, my results indicate movement between adjacent leks likely exceeds the dispersal ability of sage-grouse, suggesting movement between occupied habitat patches could be challenging in northeastern California. Consequently, sage-grouse populations in northeastern California, which occupy increasingly disjunct portions of the occupied range, have a higher risk of extinction compared with larger, core populations (Wisdom et al. 2011).

My results indicate that molecular data can provide valuable insights into underlying dispersal patterns even when direct observations of dispersal events are unavailable. Direct measures of dispersal are lacking in my study, but I have demonstrated through genetic methods a pattern of female-biased dispersal in sage-grouse. Although more research is needed on the proximate and ultimate causes behind the patterns I observed, my results serve as an important step towards understanding patterns of sex-biased dispersal in sage-grouse.

## LITERATURE CITED

- Alda, F., P. Sastre, P. J. De La Cruz-Cardiel, and I. Doadrio. 2011. Population genetics of the endangered Cantabrian capercaillie in northern Spain. *Animal Conservation* 14:249-260.
- Baguette, M., and H. Van Dyck. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecology* 22:1117-1129.
- Bech, N., J. Boissier, S. Drovetski, and C. Novoa. 2009. Population genetic structure of rock ptarmigan in the 'sky islands' of French Pyrenees: implications for conservation. *Animal Conservation* 12:138-145.
- Bouzat, J. L., H. H. Cheng, H. A. Lewin, R. I. Westemeier, J. D. Brawn, and K. N. Paige. 1998a. Genetic evaluation of a demographic bottleneck in the greater prairie-chicken. *Conservation Biology* 12:836-849.
- Bouzat, J. L., H. A. Lewin, and K. N. Paige. 1998b. The ghost of genetic diversity past: historical DNA analysis of the greater prairie-chicken. *American Naturalist* 152:1-6.
- Bush, K. L., C. L., Aldridge, J. E. Carpenter, C. A. Paszkowski, M. S. Boyce, and D. W. Coltman. 2010. Birds of a feather do not always lek together: genetic diversity and kinship structure of greater sage-grouse (*Centrocercus urophasianus*) in Alberta. *Auk* 127:343-353.
- Bush, K. L., C. K. Dyte, B. J. Moynahan, C. L. Aldridge, H. S. Sauls, A. M. Battazzo, B. L. Walker, K. E. Doherty, J. Tack, J. Carlson, D. Eslinger, J. Nicholson, M. S. Boyce, D. E. Naugle, C. A. Paszkowski, and D. W. Coltman. 2011. Population structure and genetic diversity of greater sage-grouse (*Centrocercus urophasianus*) in fragmented landscapes at the northern edge of their range. *Conservation Genetics* 12:527-542.

- Bush, K. L., M. D. Vinsky, C. L. Aldridge, and C. A. Paszkowski. 2005. A comparison of sample types varying in invasiveness for use in DNA sex determination in an endangered population of greater sage-grouse (*Centrocercus urophasianus*). *Conservation Genetics* 6:867-870.
- Caizergues, A., and L. N. Ellison. 2002. Natal dispersal and its consequences in black grouse *Tetrao tetrix*. *Ibis* 144:478-487.
- Caizergues, A., A. Bernard-Laurent, J. F. Brenot, L. Ellison, and J. -Y. Rasplus. 2003a. Population genetic structure of rock ptarmigan *Lagopus mutus* in northern and western Europe. *Molecular Ecology* 12:2267-2274.
- Caizergues, A., O. Rätti, P. Helle, L. Rotelli, L. Ellison, and J.-Y. Rasplus. 2003b. Population genetic structure of male black grouse (*Tetrao tetrix* L.) in fragmented vs. continuous landscapes. *Molecular Ecology* 12:2297-2305.
- Casgrain P., and P. Legendre. 2001. The R Package for Multivariate and Spatial Analysis, version 4.0. User's Manual. Department des Sciences Biologiques, Université de Montreal. [Online]. Available at [www.bio.umontreal.ca/casgrain/en/labo/R/index.html](http://www.bio.umontreal.ca/casgrain/en/labo/R/index.html).
- Clarke, A. L., B. E. Saether, and E. Roskaft. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429-438.
- Clobert J., R. A. Ims, and F. Rousset. 2004. Causes, mechanisms and consequences of dispersal. Pages 307-335 in I. Hanski I and O. E. Gaggiotti, editors. *Ecology, genetics, and evolution of metapopulation*, Academic, Amsterdam.
- Crunden, C.W. 1963. Age and sex of sage grouse from wings. *Journal of Wildlife Management* 27:846-850.
- Dale, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small isolated bird populations. *Oikos* 92:344-356.
- Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. *Journal of Wildlife Management* 27:811-841.
- DeWoody, J. A. 2005. Molecular approaches to the study of parentage, relatedness, and fitness: practical applications for wild animals. *Journal of Wildlife Management* 69:1400-1418.
- DeYoung, R. W., and R. L. Honeycutt. 2005. The molecular toolbox: genetic techniques in wildlife ecology and management. *Journal of Wildlife Management* 69:1362-1384.



- Doerr, E. D., and V. A. J. Doerr. 2005. Dispersal range analysis: quantifying individual variation in dispersal behaviour. *Oecologia* 142:1–10.
- Dunn, P. O., and C. E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. *Auk* 102:621–627.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50–59.
- Favre, F., F. Balloux, J. Goudet, and N. Perrin. 1997. Female-biased dispersal in the monogamous mammal *Crocodylus russula*: evidence from field data and microsatellite patterns. *Proceedings of the Royal Society of London B* 264:127–132.
- Frantz, A. C., L. C. Pope, T. R. Etherington, G. J. Wilson, and T. Burke. 2010. Using isolation-by-distance-based approaches to assess the barrier effect of linear landscape elements on badger (*Meles meles*) dispersal. *Molecular Ecology* 19:1663–1674.
- Fuhlendorf, S. D., A. J. W. Woodward, D. M. Leslie Jr., and J. S. Shackford. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. *Landscape Ecology* 17:617–628.
- Giesen, K. M., and C. E. Braun. 1993. Natal dispersal and recruitment of juvenile white-tailed ptarmigan in Colorado. *Journal of Wildlife Management* 57:72–77.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224–231.
- Goudet, J., N. Perrin, and P. Waser. 2002. Tests for sex-biased dispersal using bi-parentally inherited genetic markers. *Molecular Ecology* 11:1103–1114.
- Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- Guillot, G. R. Leblois, A. Coulon, and A. C. Frantz. 2009. Statistical methods in spatial genetics. *Molecular Ecology* 18:4734–4756.
- Goudet, J., N. Perrin, and P. Waser. 2002. Tests for sex-biased dispersal using bi-parentally inherited genetic markers. *Molecular Ecology* 11:1103–1114.
- Hanf, J. M., P. A. Schmidt, and E. B. Groshens. 1994. Sage grouse in the high desert of central Oregon: results of a study, 1988–1993. U.S. Department of Interior, Bureau of Land Management, Prineville District, Oregon, USA.

- Hanski, I., C. Eralahti, M. Kankare, O. Ovaskainen, and H. Sirén. 2004. Variation in migration propensity among individuals maintained by landscape structure. *Ecology Letters* 7:958–966.
- Hanski, I., and M. E. Gilpin. 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Hines, J. E. 1986. Survival and reproduction of dispersing blue grouse. *Condor* 88:43–49.
- Höglund, J., J. K. Larsson, H. A. H. Jansman, and G. Segelbacher. 2007. Genetic variability in European black grouse (*Tetrao tetrix*). *Conservation Genetics* 8:239–243.
- Johnson, J. A., M. R. Bellinger, J. E. Toepfer, and P. Dunn 2004. Temporal changes in allele frequencies and low effective population size in greater prairie-chickens. *Molecular Ecology* 13:2617–2630.
- Knick, S. T., and S. E. Hanser. 2011. Connecting patterns and process in greater sage-grouse populations and sagebrush landscapes. *In* Knick, S. T., and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution* 11:514–517.
- Legendre, P., M. R. T. Dale, M. –J. Fortin, J. Gurevitch, M. Hawn, and D. Meyers. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25:601–615.
- Mantel, N. 1967. The detection of disease clustering and generalized regression approach. *Cancer Research* 27:209–220.
- Martin, K., and S. J. Hannon. 1987. Natal philopatry and recruitment of willow ptarmigan in north central and northwestern Canada. *Oecologia* 71:518–524.
- Montedert, M., and P. Lèonard. 2006. Post-juvenile dispersal of hazel grouse *Bonasa bonasia* population in the southeastern French Alps. *Wildlife Biology* 9:357–364.
- Montedert, M., and P. Lèondard. 2011. Natal dispersal affects population dynamics of hazel grouse in heterogeneous landscapes. Pages 89–103 *in* B. K. Sandercock, K. Martin, and G. Segelbacher, editors. *Ecology, conservation, and management of grouse*. Studies in Avian Biology (vol. 39), University of California Press, Berkeley, California, USA.

- Mossman, C. A., and P. M. Waser. 1999. Genetic detection of sex-biased dispersal. *Molecular Ecology* 8:1063-1067.
- Oyler-McCance, S. J., N. W. Kahn, K. P. Burnam, C. E. Braun, and T. W. Quinn. 1999. A population genetic comparison of large- and small-bodied sage grouse in Colorado using microsatellite and mitochondrial DNA markers. *Molecular Ecology* 8:1457-1465.
- Oyler-McCance, S. J., S. E. Taylor, and T. W. Quinn. 2005. A multilocus population genetic survey of the greater sage-grouse across their range. *Molecular Ecology* 14:1293-1310.
- Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6:288-295.
- Peakall R., M. Ruibal, and D. B. Lindenmeyer. 2003 Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. *Evolution* 57:1182-1195.
- Prugnolle, F., and T. de Meeus. 2002. Inferring sex-biased dispersal from population genetic tools: a review. *Heredity* 88:161-165.
- Raymond, M., and F. Rousset. 1995. GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86:248-249.
- Rhim, S. -J., and S. -H. Sun. 2009. Natal dispersal of hazel grouse *Bonasa bonasia* in relation to habitat in a temperate forest of south Korea. *Forest Ecology and Management* 258:1055-1058.
- Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics* 145:1219-1228.
- Schroeder, M. A. 1986. The fall phase of dispersal in juvenile spruce grouse. *Canadian Journal of Zoology* 64:16-20.
- Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. *Wildlife Biology* 9:291-299.
- Segelbacher, G., J. Höglund, and I. Storch. 2003. From connectivity to isolation: genetic consequences of population fragmentation in capercaillie across Europe. *Molecular Ecology* 12:1773-1780.

- Segelbacher, G., S. Manel, and J. Tomiuk. 2008. Temporal and spatial analyses disclose consequences of habitat fragmentation on the genetic diversity in capercaillie (*Tetrao urogallus*). *Molecular Ecology* 17:2356-2367.
- Segelbacher, G., and I. Storch. 2002. Capercaillie in the Alps: the genetic evidence of metapopulation structure and population decline. *Molecular Ecology* 11:1669-1677.
- Seutin, G., B. N. White, and P. T. Boag. 1991. Preservation of avian blood and tissue samples for DNA analyses. *Canadian Journal of Zoology* 69:82-90.
- Small, R. J., and D. H. Rusch. 1989. The natal dispersal of ruffed grouse. *Auk* 106:72-79.
- Smith, A. A. 1997. Dispersal and movements in a Swedish willow grouse *Lagopus lagopus* population. *Wildlife Biology* 3:279.
- Smouse, P. E., J. C. Long, and R. R. Sokal. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology* 35:627-632.
- Smouse, P. E., and P. Peakall. 1999. Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. *Heredity* 82:561-573.
- Swenson, J. E. 1991. Is the hazel grouse a poor disperser? *Transactions of the Congress of the International Union of Game Biologists* 20:347-352.
- Thompson, T. R. 2012. Dispersal ecology of greater sage-grouse in northwestern Colorado: evidence from demographic and genetic methods. Dissertation. University of Idaho, Moscow, Idaho, USA.
- Ury, H. K. 1976. A comparison of four procedures for multiple comparison among means (pairwise contrasts) for arbitrary sample sizes. *Technometrics* 18:89-97.
- Van Dyck, H., and M. Baguette. 2005. Dispersal behaviour in fragmented landscapes: routine or special movements? *Basic Applied Ecology* 6:535-545.
- van Oosterhout, C., W. F. Hutchinson, D. P. M. Wills, and P. Shipley. 2004. Micro-checker: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology* 4:535-538.
- Vázquez, J. F., T. Pèrez, F. Quirós, J. R. Obeso, J. Albornoz, and A. Domínguez. 2012. Population genetic structure and genetic diversity of the endangered Cantabrian capercaillie. *Journal of Wildlife Management* 76:957-965.
- Venier, L. A., and L. Fahrig. 1996. Habitat availability causes the species-abundance distribution. *Oikos* 76:564-570.

- Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. *Wildlife Society Bulletin* 20: 425-426.
- Wallestad, R. O. 1975. Life history and habitat requirements of sage grouse in central Montana. Game Management Division, Montana Department of Fish and Game, Helena, Montana, USA.
- Warren, P. K., and D. Baines. 2002. Dispersal, survival and causes of mortality in black grouse *Tetrao tetrix* in northern England. *Wildlife Biology* 8:91-97.
- Waser, P. M., and C. Strobeck. 1998. Genetic signature of inter-population dispersal. *Trends in Ecology and Evolution* 13:43-44.
- Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38:1358-1370.
- Wisdom, M. J., C. W. Meinke, S. T. Knick, and M. A. Schroeder. 2011. Factors associated with extirpation of sage-grouse. Pages 451-472 in Knick, S. T., and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. *Studies in Avian Biology Series* (vol. 38), University of California Press, Berkeley, California, USA.
- Woodward, A. J. W., S. D. Fuhlendorf, D. M. Leslie Jr., and J. Shackford. 2001. Influence of landscape composition and change on lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations. *American Midland Naturalist* 145:261-274.

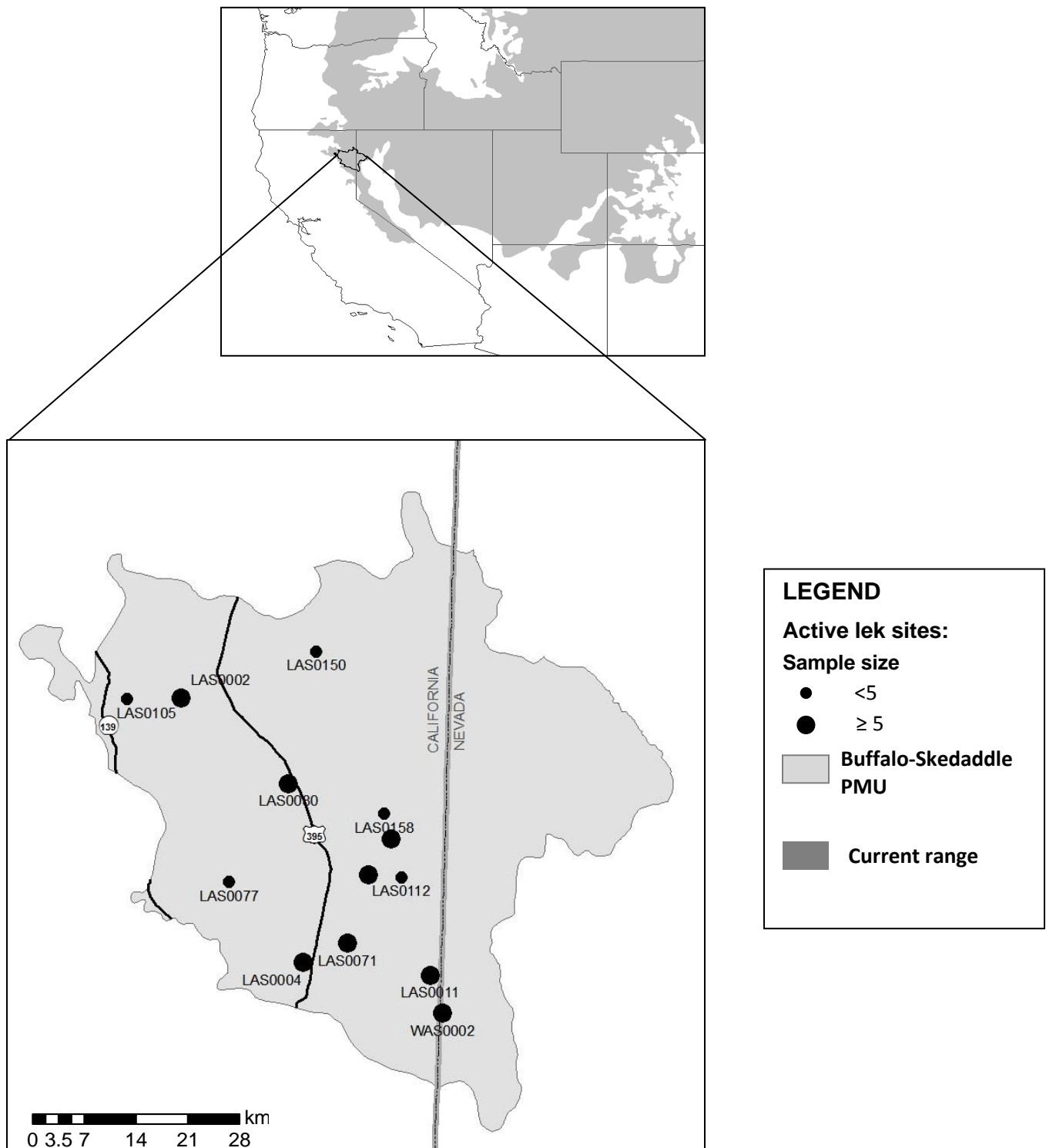


Figure 1. Map of the study area in northeastern California and geographical location of sampled greater sage-grouse leks (black circles).

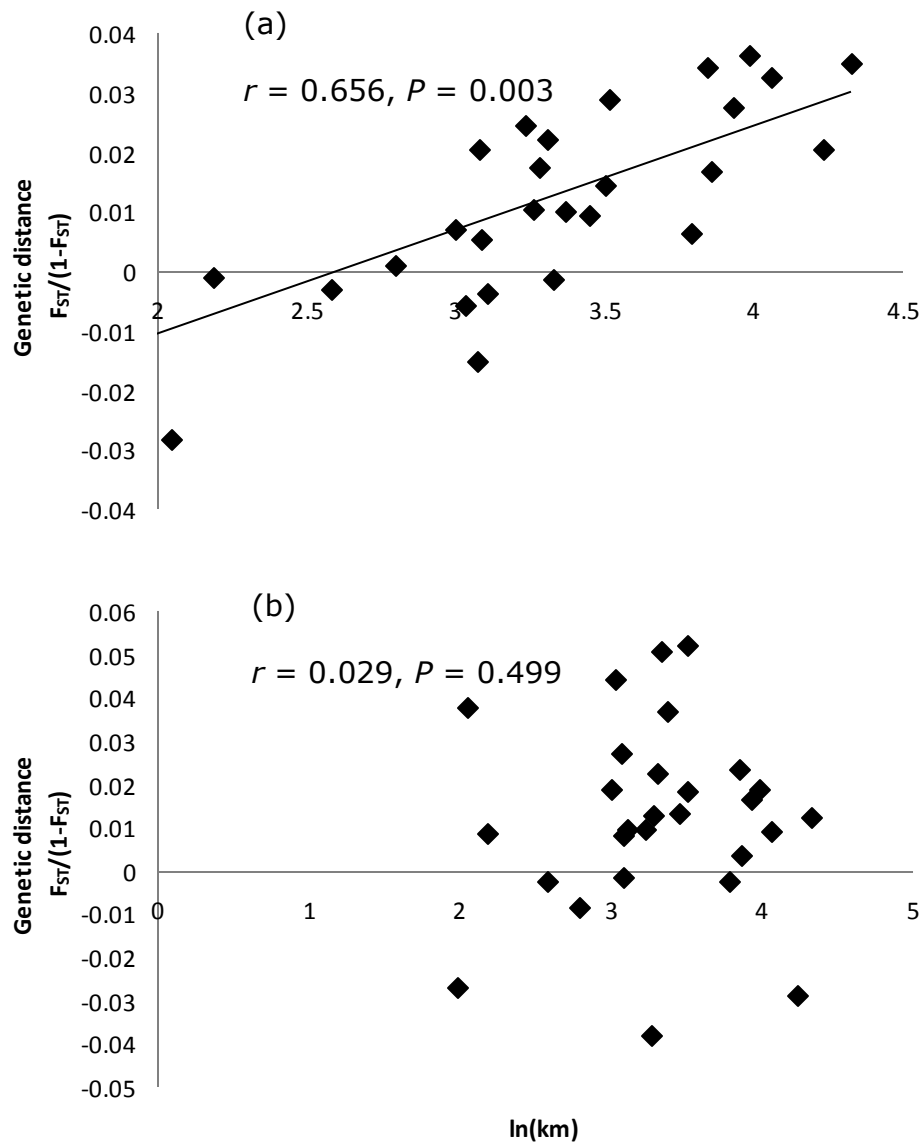
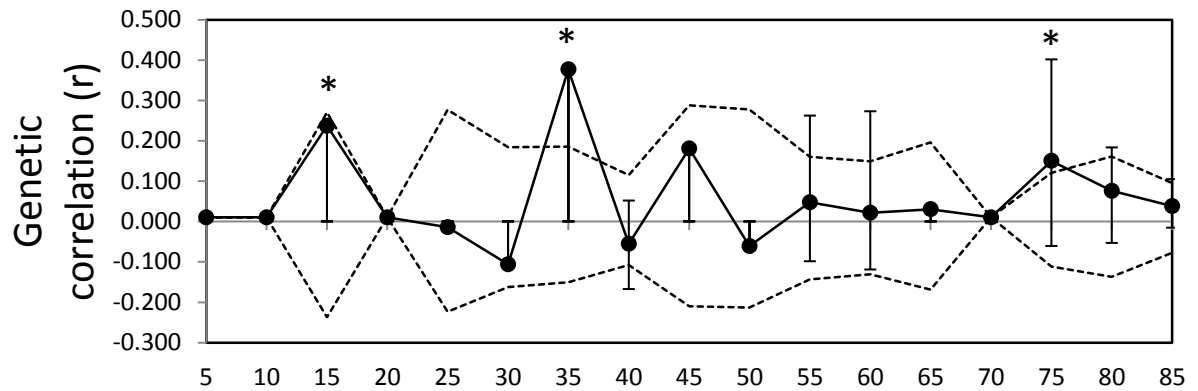


Figure 2. Analysis of isolation by distance for (a) males and (b) females, respectively. Genetic distance ( $F_{ST}/(1-F_{ST})$ ) are plotted against geographic distance for pairwise comparisons of 8 lek sites of greater sage-grouse in northeastern California, 2007-2009.

(a) Male



(a) Female

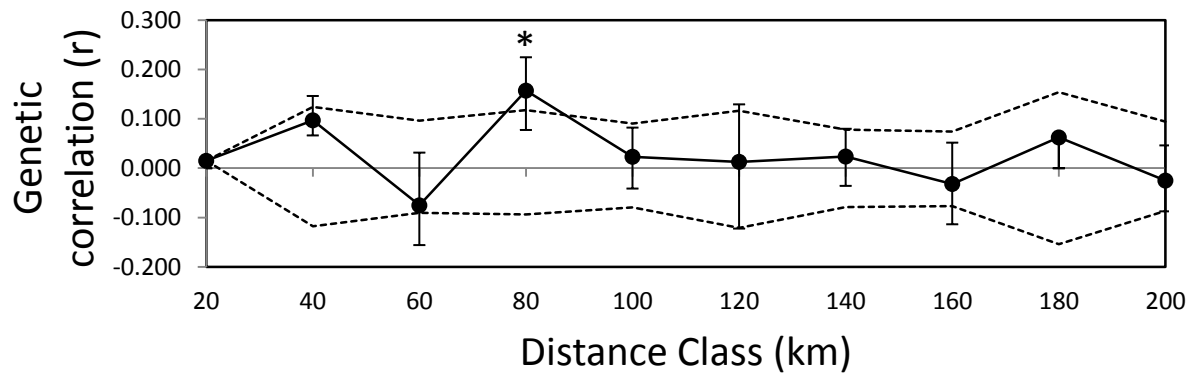


Figure 3. Spatial genetic structure of (a) male and (b) female greater sage-grouse in northeastern California, 2007-2009. The permutation 95% confidence interval (dashed lines) and the bootstrapped 95% confidence error bars are shown. Stars indicated significant positive spatial autocorrelation values.



**CHAPTER 6. ASSESSING THE GEOGRAPHIC DISTRIBUTION OF NESTING  
AND BROOD-REARING HABITAT FOR GREATER SAGE-GROUSE IN  
NORTHEASTERN CALIFORNIA: IMPLICATIONS FOR CONSERVATION AT  
THE WESTERN PERIPHERY OF THE SPECIES RANGE**

**ABSTRACT** – Understanding habitat selection across multiple scales and identifying the environmental variables that influence the geographic distribution of greater sage-grouse (*Centrocercus urophasianus*) breeding habitats (i.e., nesting and brood-rearing) is critical for conservation planning and long-term population persistence. I used a 2-step approach to identify nesting and brood-rearing habitat for greater sage-grouse in northeastern California. First, I used spatial autoregressive models to examine local scale habitat characteristics to describe the distribution of nest sites and brood-rearing locations. Second, I used Geographic Information System analysis and maximum entropy techniques to develop a spatially explicit model to identify nesting and brood-rearing habitat at a landscape scale. My findings were consistent with previous research on greater sage-grouse nest and brood ecology. At the local scale, females selected sagebrush (*Artemisia* spp.) landcover types with increased grass height and visual obstruction for nesting. The amount of sagebrush canopy cover was also important in explaining greater sage-grouse brood habitat use. The primary difference between brood-rearing locations within sagebrush-dominated habitats and paired random locations was grass height and visual obscurity in the surrounding sagebrush-steppe community. My landscape scale model indicated greater sage-grouse nesting and brood-rearing habitat were limited across my study area. Loss and degradation of existing sagebrush habitats and conversion of large tracts of sagebrush to other vegetation, such as

annual grasslands and juniper (*Juniperus occidentalis*) woodlands, in northeastern California will likely result in declining greater sage-grouse populations because of reduced nesting success and decreased productivity. Given the limited amount of suitable nesting and brood-rearing habitat, my results suggest conservation efforts focused on these scarce resources will be important for effective management of breeding season habitat for greater sage-grouse in northeastern California.

**KEY WORDS:** *Centrocercus urophasianus*, brood-rearing, maximum entropy, nesting, sage-grouse, spatial autoregressive model

Assessing the geographic distribution of plant and/or animal species is essential for informed conservation planning to create management strategies with the goal of maintaining viable populations. This is particularly true for species of concern, however, survey data are rarely available to describe species presence at every location across the geographic range of the species. Thus, methods that predict species distributions from presence-only data (e.g., Hirzel et al. 2002, Pearce and Boyce 2006) have been used to extrapolate beyond known species occurrences, by relating known occurrences with environmental variables that are relevant to habitat suitability (Phillips and Dudík 2008).

Numerous authors have reviewed and compared methods that rely on presence-only data (e.g., see Elith et al. 2006), however, Phillips et al. (2004, 2006) recently introduced the use of the maximum entropy method (MaxEnt) for modeling species geographic distributions with presence-only data. MaxEnt is a machine-learning technique founded on the principle of maximum entropy (Jaynes 1957), which builds on Hutchinson's ecological niche theory (Hutchinson 1957). Ecological niche theory rests on the premise that the species'

fundamental niche consists of the set of all conditions that allow for the species' survival, whereas its realized niche is that subset of the fundamental niche that the species actually occupies (Hutchinson 1957). Thus, geographic areas that satisfy the environmental conditions of a species' fundamental niche represent its potential distribution, whereas the geographic area known to be occupied by the species constitutes its realized distribution (Phillips et al. 2006). Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) are ideal for modeling the geographic distribution of breeding season (i.e., nest and brood-rearing) habitats using maximum entropy methods, in part, because sage-grouse populations inhabit large, interconnected expanses of sagebrush (*Artemisia* spp.), and consequently have been characterized as a landscape scale species (Connelly et al. 2004). In addition, sage-grouse are considered an umbrella species (Rowland et al. 2006), thus, management to benefit sage-grouse likely benefits passerine birds associated with sagebrush communities (Hanser and Knick 2011) and other species dependent upon sagebrush-steppe habitats.

Several authors have reported on the underlying causes of ongoing population declines across the geographic range of sage-grouse. However, nest success and loss of brood-rearing habitat, resulting in reduced brood survival have been identified as the 2 most critical factors associated with sage-grouse demography and population size (Aldridge and Brigham 2001, Gregg 2006, Beck et al. 2006). While much research has been conducted at local scales, addressing habitat characteristics related to nest success and chick survival (e.g., Aldridge and Brigham 2002, Moynahan et al. 2007, Gregg and Crawford 2009), research to identify and assess critical nesting and brood-rearing habitat for sage-grouse at the landscape

scale is limited (e.g., Wisdom et al. 2002 a, b; Aldridge and Boyce 2007, Yost et al. 2008, Atamian et al. 2010, Doherty et al. 2010, Shepherd et al. 2011). Of these landscape models, few (e.g., Aldridge and Boyce 2007, Doherty et al. 2010) have considered sage-grouse nest and brood-rearing habitat at multiple scales. Moreover, previous landscape-level analyses focused on sage-grouse populations within the core regions of the sage-grouse range.

Species habitat relationships can vary between geographic regions (Wiens et al. 1987) and focusing on peripheral populations is important given the vulnerability of these populations to extinction (Lande 1993). Declining, peripheral populations of sage-grouse in northeastern California, which occupy the western fringe of the species range and are separated from larger core populations, fit these conditions (Wisdom et al. 2011). Peripheral populations are important to maintain connectivity among populations. Moreover, the loss of small, isolated populations has likely contributed to declines in sage-grouse populations across the core of the geographic range (Knick and Hanser 2011).

Understanding habitat selection across multiple scales has important implications for explaining the geographic distribution of sage-grouse in northeastern California. Previous studies describing habitat selection of sage-grouse have evaluated the importance of selection at multiple scales across various life history stages (Aldridge and Boyce 2007, Carpenter et al. 2010, Doherty et al. 2008; 2010), suggesting it will likely require a combination of scales to completely understand how sage-grouse respond to their environment. Although local scale attributes of sagebrush communities influence within-season movements, such as choice of nesting or brood-rearing locations (Connelly et al. 2000), environmental variables other than vegetation might influence nest site selection at broader scales. For example, in

the Powder River Basin of southeast Montana, sage-grouse selected for less rugged patches of sagebrush habitat for nest sites with little tolerance for juniper (*Juniperus* spp.), grassland, and riparian habitats at landscape scales (Doherty et al. 2010). Similarly, results from Jensen (2006) showed that the landscape characteristics of surface roughness and ruggedness, elevation, and slope potentially influenced nest site selection in central Wyoming.

Knowledge of both local and landscape scale habitat characteristics is fundamental for preserving the viability of sage-grouse populations and can also inform management decisions and provide crucial information to wildlife managers to identify the most appropriate locations for conservation and management of sagebrush habitats to benefit sage-grouse. Thus, the goal of this study was to use a 2-step approach to identify nesting and brood-rearing habitats for sage-grouse in northeastern California. First, I used spatial autoregressive models (SAR) to examine local scale habitat characteristics that cannot currently be mapped in Geographic Information System (GIS) to describe the distribution of nest sites and brood-rearing locations in northeastern California. Second, I used GIS analysis and maximum entropy techniques to study the environmental factors that influence the spatial distribution of nest sites and brood-rearing locations in northeastern California and to produce habitat suitability maps that describe the potential geographic distribution of nesting and brood-rearing habitats at the landscape scale. Specifically, the objectives of this study were to: 1) examine the effects of local scale habitat features on sage-grouse nest site and brood-rearing habitat use; 2) identify nesting and brood-rearing habitats at the landscape scale in northeastern California; 3) map the geographic distribution of nesting and brood-

rearing habitat critical to the long-term persistence of sage-grouse in northeastern California; and 4) assess the predictive capacity of these models using independent data.

## **STUDY AREA**

This study was conducted in a 597,116 ha region of sagebrush-steppe habitat that included portions of the Buffalo-Skedaddle Population Management Unit (PMU) in Lassen County, California, where sage-grouse populations occupy the western periphery of the species' geographic range. Elevation ranged from 1,400 to 2,400 m. The predominant sagebrush types included Wyoming big sagebrush (*A. tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), and little sagebrush (*A. arbuscula*). Other common vegetation communities included annual grasslands and juniper (*J. occidentalis*) dominated woodlands. The study area was primarily composed of 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 as irrigated alfalfa (*Medicago* spp.).

## **MATERIALS AND METHODS**

### **Trapping and Radiomarking**

I trapped sage-grouse opportunistically using spotlighting techniques (Giesen et al. 1982, Wakkinen et al. 1992) on or near 13 lek sites from March through April 2007-2009. I classified gender and age of captured birds by plumage characteristics and wing molt (Crunden 1963, Dalke et al. 1963). Female sage-grouse were fitted with a serially-numbered aluminum leg band and a  $\leq 20$ -g necklace-mounted ATS radio transmitter (Advanced Telonics Systems, Inc., Insanti, MN, USA). Females were monitored 1-3 times per week

with a hand-held Yagi antenna and portable receiver throughout the breeding season to determine nesting chronology and ascertain habitats used for nesting. Positions of radio-collared females were determined by circling the estimated location of the female, indicated by the loudest signal strength (Springer 1979). When monitoring revealed a female had initiated a nest (i.e., 2-3 locations near the same spot), I approached the female until I observed the female on the nest and I recorded the nest location in Universal Transverse Mercator (UTM) coordinates using a Global Positioning System (GPS) unit. Nesting females were monitored remotely (>60 m) to avoid disturbance (Holloran and Anderson 2005). Once monitoring revealed a female had moved away from the nest and incubation had likely ceased, I examined the nest to ascertain fate. I classified nests as successful if  $\geq 1$  egg hatched. Depredated nests were distinguished from successful nests by the presence of a firmly attached shell membrane in broken eggs (Wallestad and Pyrah 1974). In addition, I monitored broods every 1-3 days with a hand-held Yagi antenna and portable receiver until a breakdown in brood integrity or if the brood was lost. Brood locations were determined by locating the radiomarked female and circling within 25 m to avoid disturbance.

### **Local Scale Analysis**

I defined local scale habitat features as those vegetative attributes measured at nest sites and brood-rearing locations. I applied basic exploratory spatial data analysis (ESDA) to assess the spatial structure of the data, explore spatial dependence, and measure heterogeneity (Wilhelm and Steck 2006). I used global tests (e.g., a univariate Moran scatterplot was constructed for each vegetative attribute measured at nest sites and brood locations) to provide insight into what types of patterns could be expected from the nest and brood-rearing

data sets. Additionally, local statistics (e.g., local measures of spatial autocorrelation) were used to detect local patterns in nest and brood-rearing data and to quantify the extent of dependency and heterogeneity that were present in the data. All local scale spatial analyses were conducted using GeoDa 0.9.5.i5 software for geodata analysis (Anselin et al. 2006).

### **Habitat Structure and Stand Characteristics**

Stand characteristics that cannot currently be mapped in GIS were described at selected nest sites and brood-rearing locations within my study area. Habitat sampling at nest sites was performed after hatching for successful nests and after the predicted hatch date for depredated or abandoned nests. Because of logistical constraints, not all brood locations were sampled. Vegetative attributes at nest sites and brood locations were measured along two, 10-m perpendicular transects intersecting at the nest bowl or center of use. Species composition and percent cover of grasses, forbs, bare ground, and litter were estimated at five, 50- x 50-cm quadrat frames spaced equidistantly along each transect (Daubenmire 1959). Within each quadrat frame, cover was ranked into 6 classes (e.g., 1: 0-1%; 2: 1.1-5%; 3: 5.1-25%; 4: 25.1-50%; 5 = 50.1-75%; 6: 75.1-100%) following Connelly et al. (2003). In addition, the height of the live shrub (excluding seed heads), forb, and tallest droop height of the grass plant (excluding flower stalks), nearest the outside right corner of the frame were measured along each 10-m transect. Visual obstruction readings (VORs) were recorded along each 10-m transect. VORs were measured at a height of 1 m from a distance of 5 m (Robel et al. 1970). VORs provided an index of visual obstruction of all vegetation (not just grass and/or herbaceous cover). Live shrub canopy cover was quantified using the line intercept method (Canfield 1941). Vegetative attributes were measured at paired random



points within an arbitrary distance of 500 m of each nest site or brood location using the techniques just described. Random points within 100 m of nests and brood locations were excluded to reduce the potential of dependence among samples. To ensure continuity over the course of the 3 year study, I used the same observer to measure and record stand characteristics

### **Moran's I**

To assess the effects of habitat structure on the distribution of nest sites and brood-rearing locations within my study area, I first examined spatial autocorrelation to determine if the inclusion of the spatial term was necessary in my regression models. Spatial autocorrelation was measured using the Moran's I statistic (Moran 1948, 1950), defined as:

$$I = \frac{N \sum_i \sum_j W_{i,j} (X_i - \bar{X})(X_j - \bar{X})}{(\sum_i \sum_j W_{i,j}) \sum_i (X_i - \bar{X})^2}$$

Where  $N$  is the number of cases;  $X_i$  is the variable of interest at a particular location;  $X_j$  is the variable value at another location;  $\bar{X}$  is the mean of the variable; and  $W_{ij}$  is a weight applied to the comparison between location  $i$  and location  $j$ .

Before selecting a spatial weight matrix, I first constructed and compared weighting matrices for lags 1 to 5 using the Queen contiguity (Anselin 2002) and selected the spatial lag that achieved both a high coefficient of spatial autocorrelation and was statistically significant (Voss and Chi 2006). The spatial lags were compared to their unlagged counterparts in a scatter plot. Significance declined with increasing lag for almost all variables examined. In addition, the first order contiguity explained most of the spatial structure, thus, the first order weighting function was used in the spatial analysis of the nest

site and brood-rearing location data. A univariate Moran scatter plot was constructed for each explanatory variable and significance was assessed using the empirical distribution of the statistic under the null hypothesis of no spatial autocorrelation (999 permutations) for the nest site and brood-rearing location data sets.

### **Local Indicators of Spatial Autocorrelation (LISA)**

I implemented local measures of spatial autocorrelation as LISA maps (cluster and significance) for both the nest site and brood-rearing location data. The LISA statistic is an indicator of spatial heterogeneity, which identifies local pockets of non-stationarity referred to as “hot spots” (i.e., sets of contiguous locations for which LISA is significant; Anselin 1995).

### **Regression Analysis**

Following the exploratory spatial data analysis (ESDA), I fit a normal regression model by Ordinary Least Squares (OLS) to the nest site and brood-rearing location data sets. I assessed multicollinearity using variance inflation factors (VIF), removing any variables with VIF scores >10 (Marquardt 1970, Mason et al. 1989, Neter et al. 1989:409; Hair et al. 1995, Menard 1995:66). Examination of the residuals was used to assess the overall fit of the model and to test for spatial dependence. In addition, a Breusch-Pagan test (Breusch and Pagan 1979) for heteroscedastic variance of error was conducted. The normal regression model was respecified as both the linear regression model with a spatially lagged response and spatial error. Because  $R^2$  is not a meaningful metric for comparing spatial autoregressive and OLS models (Jetz et al. 2005), Akaike’s Information Criterion (AIC; Akaike 1973) was

used to distinguish between regression models and to select the best candidate model (i.e., the model with the lowest AIC value).

In the case of linear regression with normally distributed responses, the classical normal regression model is expressed as:

$$\mu(i) = \beta_0 + \beta_1 X_1(i) + \beta_2 X_2(i) + \dots \beta_K X_K(i)$$

where  $\beta_0$  denotes the intercept parameter and  $\beta_1, \beta_2, \dots, \beta_K$  denotes the regression parameters of the model, which are the parameters of interest (Haining 2003: Eq. 9.29). Ordinary least squares is used to estimate the parameters of the mean ( $\beta_1, \beta_2, \dots, \beta_K$ ) and the errors ( $\sigma^2$ ) (Haining 2003). This model will be appropriate as a model for spatial variation if the value of the response at location  $i$  is only a function of predictor levels in  $i$  and the errors in the model  $\{e(i)\}$  can be assumed to be independent (Haining 2003). The latter implies there is no spatially correlated measurement error and any unmeasured predictors excluded from the model specification are also spatially uncorrelated.

An important consideration in spatial modeling is that the model residuals are not spatially autocorrelated (Haining 2003). Simple OLS regression models provide insight into the overall relationships and spatial trends, but the classical approach to regression modeling assumes that there is only first-order variation and no second-order variation in the process (Bailey and Gatrell 1995). This assumption is typically violated with most real data sets and residuals are often spatially autocorrelated. Fitting a regression model by OLS when the residuals are spatially correlated results in a biased estimate of  $\sigma^2$ . As a result, the observed goodness of fit (i.e.,  $R^2$ ) is inflated and tests of the hypothesis have a higher Type I error (Haining 2003). Consequently, the model might not be doing as good of a job in explaining

the variation in the response variable as implied by the goodness of fit measure and there is likely information in the residuals about the behavior of the response variable that is not being used (Haining 2003).

In cases where there is spatially correlated measurement error (i.e., non-constant variance or heteroscedasticity), the normal regression model can be respecified as a linear regression model with a spatial lagged predictor variable, specified as:

$$Y = \rho WX + X\beta + \epsilon$$

where  $Y$  denotes the vector of response variables,  $X$  denotes the matrix of explanatory variables,  $W$  denotes the spatial weight matrix, and  $\epsilon$  denotes the vector of error terms that are independent but not necessarily identically distributed.

A second approach to SAR modeling is the spatial error model. This model is applied when there appears to be significant autocorrelation, but tests for spatial lag do not suggest inclusion of the latter will provide significant improvement to the model. The spatial error model is written as:

$$Y = X\beta + \lambda WY - \lambda WX\beta + \epsilon.$$

where the terms are defined in the same way as the spatial lag model.

The addition of the SAR component to the standard linear regression model incorporates spatial autocorrelation into the model, resulting in significant improvement over the standard OLS model.

## **Landscape Scale Analysis**

### **GIS Database and Environmental Variables**

Available spatial data derived from previous studies of sage-grouse nesting and brood-rearing habitat selection (e.g., Aldridge and Boyce 2007, Yost et al. 2008, Atamian et al. 2010, Doherty et al. 2010), variables related to anthropogenic disturbance (e.g., Wisdom et al. 2011), and fire history were incorporated into a GIS database (Table 1). Most spatial data used in my study were available for download on the SAGEMAP website (<http://sagemap.wr.usgs.gov>; USDI 2001). Regional spatial data were derived from the U.S. Census Bureau's TIGER data to describe roads, U.S. Geological Survey (USGS) digital elevation models (DEMs) to describe topographical data (elevation, slope, aspect), and Landfire Existing Vegetation Map (LANDFIRE 2006). Slope values were derived from the 30 m DEM data and reclassified as <10%, 11-20%, >20%. Similarly, aspect values were obtained from the DEM and re-classified as flat (< 44°), north (316° to 45°), east (46° to 135°), south (136° to 225°) and west (226° to 315°) following Yost et al. (2008). In addition, to evaluate food resources during brood-rearing, I used the DEM of the study area to calculate a Compound Topographic Index (CTI) using AML (Arc Macro Language) script run in ArcInfo Workstation for ArcGIS 9.3 (see Evans 2002). CTI was expressed as:

$$\ln[As/\tan\beta]$$

where  $As$  represents the catchment area per pixel calculated as  $(\text{flow accumulation} + 1) * (\text{pixel area m}^2)$  and  $\beta$  refers to the slope expressed in radians. The CTI models soil water content (Moore et al. 1991) as a function of both the slope and the upstream contributing area per unit width orthogonal to the flow direction and can be used as a substitute for vegetation

productivity (Gessler et al. 1995). Low values of the CTI represent steep slopes or hills and areas with high CTI values represent places with gentle slopes, depressions, or plains.

Vegetation in LANDFIRE (2006) was classified from Landsat Thematic Mapper satellite imagery taken in 2002 ( $\pm 2$  yr) and consisted of 210 ecological systems of which 61 occurred in my study area. I developed 8 landcover classes from the original ecological systems mapped by LANDFIRE (2006): all sagebrush, agriculture (cultivated crops, pasture, and hayland), riparian, western juniper, grassland, other shrubs and/or woodland types (e.g., shrub or forest landcover types other than sagebrush and juniper), open water, and developed (urban and suburban areas). Pooling closely related landcover data increases the classification accuracy of the map (Beier et al. 2008). Because of the inaccuracies that can occur when classifying satellite imagery (Lillesand and Kiefer 2000, Gallant 2009), mapping different sagebrush species (Knick and Hanser 2011), and because little sagebrush comprised only 1% of the sagebrush landcover classes within my study area, all sagebrush landcover classes were combined into 1 composite sagebrush landcover.

A 500-m buffer was generated around anthropogenic features (roads, transmission lines, communication towers) to characterize the effect of human disturbance on sage-grouse (i.e., avoidance area) or modifications to landuse that result in the loss of sage-grouse habitat. Most of the currently available information on impacts of anthropogenic features on sage-grouse populations is focused on lek abandonment and changes in male lek attendance (e.g., Walker et al. 2007). However, to my knowledge, no published studies have examined nest and/or brood success, survival, or habitat selection as they relate to behavioral avoidance of roads and various forms of infrastructure that affect habitat use by sage-grouse. Because the

behavioral response of sage-grouse is likely similar to that of other prairie grouse, and given the paucity of published data specific to sage-grouse, the extent of the buffer surrounding structures and roads was adapted from recent work on prairie grouse (e.g., Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011).

Maps were prepared in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA) for use in the program MaxEnt version 3.3.3 (Phillips et al. 2006, Phillips and Dudík 2008). All GIS data layers were transformed into ASCII format with matching cell size (30 m), extent, and projection system. All data were set to the projected coordinate system of North American Datum 1983, Universal Transverse Mercator Zone 10 North (NAD83, UTM Zone 10N).

### **MaxEnt and Habitat Suitability**

In a highly vagile species with landscape scale spatial requirements, such as sage-grouse, reliable information on species occurrence is often lacking. I used the program MaxEnt version 3.3.3 (Phillips et al. 2006, Phillips and Dudík 2008) to assess the geographic distribution of sage-grouse nest and brood-rearing habitat in northeastern California. MaxEnt is a species distribution modeling approach that relies on presence-only data (Phillips et al. 2006), performs well with small data sets (Phillips and Dudík 2008, Wisz et al. 2008), is robust in the presence of spatial autocorrelation (Segurado et al. 2006), and frequently outperforms alternative niche-based modeling approaches (Elith et al. 2006, Wisz et al. 2008).

MaxEnt functions on the concept of maximum entropy, in which the distribution of a given population will tend toward uniform distribution after all ecologically important

parameters are taken into account (Phillips et al. 2004). MaxEnt uses a maximum-likelihood method to measure correlation between environmental layers and presence point locations and generate a spatial probability distribution. This can be interpreted as a probability of occurrence or suitability for that species (Phillips et al. 2006). The probability of the model is displayed in terms of “gain,” which is equal to the log of the total number of grid cells minus log loss (the average negative log probability across the sample locations). As the model efficiency is incrementally improved, the overall gain increases until a minimum cumulative threshold is reached (point at which additional gain per iteration falls below a preset value) or a maximum number of iterations is reached. Once the probability distribution is assigned, it is possible to assess which habitat variables have the most predictive power. A detailed statistical explanation of the MaxEnt program and modeling procedure is given by Phillips et al. (2006) and Elith et al. (2011).

A total of 8 environmental layers (landcover type, elevation, slope, aspect, roads, communication towers, transmission lines, and fire history) were entered into a preliminary analysis of the geographic distribution on sage-grouse nesting habitat and 9 environmental variables (landcover type, elevation, slope, aspect, CTI, roads, communication towers, transmission lines, and fire history) were entered into a preliminary analysis of the geographic distribution of sage-grouse brood-rearing habitat. MaxEnt’s jackknife test of variable importance was run for each variable to evaluate the relative strengths of each predictor variable. Because the presence of primary roads (e.g., interstate highways and paved roads) did not appear to influence habitat use, I did not distinguish between road types (primary versus secondary unpaved roads) in further analysis. The final reduced model of



sage-grouse nesting and brood-rearing habitat retained 6 and 5 environmental variables, respectively (see Results below). As recommended by Phillips and Dudík (2008), I ran the program MaxEnt under its default parameter settings to analyze all models. Models were parameterized with a background sample of 10,000 points, a default convergence threshold of  $10^{-5}$ , maximum iterations of 1,000, and the regularization parameter was set to the default value of 1. Model performance was evaluated by setting aside a subset of presence data for training and using the remaining observation records to test the resulting model. I made 15 random partitions of the occurrence localities. Each partition was created by randomly selecting 75% of the presence records ( $n = 56$  nests and 355 brood locations, respectively) as training data and the remaining 25% of presence records ( $n = 18$  nests and 118 brood locations, respectively) were reserved for testing the model. In addition, the full set of presence records was used to build the final reduced model to obtain the best estimate of the geographic distribution of nesting and brood-rearing habitat in northeastern California.

Model performance was evaluated using receiver operating characteristic (ROC) analysis, which characterizes the performance of a model at all possible thresholds by a single number; i.e., the area under the ROC curve (AUC) (Phillips et al. 2006). The advantage of ROC analysis is that the area under the ROC curve provides a single measure of model performance (Phillips et al. 2006). The AUC is the probability that a randomly chosen presence site will be ranked above a randomly chosen absence site and measures the ability of the model to discriminate between sites where a species is present versus sites where the species is absent (Hanley and McNeil 1982). The value of the AUC typically ranges between 0.5, indicating that model performance is not better than random and a perfect ranking of 1.0

(Swets 1988, Elith et al. 2006). Models with values  $>0.75$  signify better model performance (Elith 2002) and indicate that predictions are sufficiently accurate to be used in conservation planning (Pearce and Ferrier 2000). Additionally, I also assessed the importance of the environmental predictors using a jackknife test of variable importance that quantified AUC and gain changes when excluding a variable (Phillips et al. 2006). The jackknife test of variable importance shows the training gain of each variable if the model was run in isolation and compares it to the training gain with all the variables (Phillips et al. 2006). This is useful to identify those predictor variables which contribute the most individually (Elith et al. 2010). Once habitat suitability maps were derived, I converted the probability distribution map into raster format and created probability classes ranking from unsuitable to optimal habitat: Unsuitable (0–25%), Marginal (26–50%), Suitable (51–75%), and Optimal (76–100%).

### **Model Validation**

I validated the predictive capacity of my spatial models with an independent data set (Popham 2000) from prior research in northeastern California (1998-2000), using an independent sample of 84 nests and 79 brood locations from 20 different sage-grouse broods.

## **RESULTS**

### **Local Scale Analysis: ESDA and Regression Analysis**

Over 3 breeding seasons (2007-2009), I located and measured stand characteristics at 63 nest sites and at 63 paired random points during the nesting period. Additionally stand characteristics were measured during the 2007 and 2008 field seasons at 30 brood-rearing locations and at 30 paired random points.

### **Nest Sites**

Univariate analysis of the Lassen County nest data confirmed there was strong evidence of both positive spatial autocorrelation (as indicated by the Moran's I) as well as spatial heterogeneity in the form of distinct spatial regimes for 6 variables including live sagebrush and shrub canopy cover, percent cover of grasses and bare ground, and nest bowl shrub and forb height (Table 2). There was no indication of significant spatial clustering for cover of forbs and litter, nest bowl grass height, and visual obstruction readings (Table 2).

The spatial pattern of nest sites is illustrated by the LISA maps (cluster and significance; Figure 1), which shows the significant locations by type and association. For example, the dark red locations are indications of spatial clusters with the dark red and blue shades corresponding to high surrounded by high and low surrounded by low, respectively. Conversely, the light red and light blues are indications of spatial outliers (low surround by high and high surrounded by low, respectively). The accompanying LISA significance map shows the locations with a significant local Moran in different shades of green, depending on the degree of significance. Local statistics detected local patterns in the nest site data and quantified the extent of the dependency and heterogeneity that were present. Inhomogeneous data points showed there was no overall tendency to clustering, although there might have been local clusters. Thus, the structure of dependency for nest site locations was heterogeneous (i.e., the relationship was non-stationary) across my study area.

The results from fitting a standard linear regression model indicated grass height at the nest and visual obstruction had a significant positive influence on the distribution of nest sites, whereas live sagebrush and shrub canopy cover, percent cover of grasses and bare

ground, and nest bowl shrub and forb height had no significant effect on nest distribution. However, the measure of overall goodness of fit provided by the coefficient of determination ( $R^2$ ) for the OLS model was 0.22, indicating much of what determined nest site distribution went unexplained by this model. Moreover, the global Moran's I test on the residuals after fitting the standard linear regression suggests that there was strong evidence of spatial autocorrelation among the residuals (Moran's I = -2.673;  $p$ -value = 0.008). Thus, the independence assumption of the error term appeared to be violated and I, therefore, proceeded to fit spatial linear regression models in order to account for the spatial autocorrelation.

AIC confirmed that both spatial linear regression models outperformed the normal regression model that ignored space to describe nest distribution within my study area (Table 3). Between the spatial lag model and the spatial error model, I selected the former as the best-approximating model of my data because of a slightly smaller AIC value. Grass height and visual obstruction remained significant in the spatial lag (Table 4). Compared to the corresponding OLS regression model, the explanatory power of the spatial autoregressive model increased over the OLS regression with an  $R^2$  of 0.39. These results suggest model improvement using spatial components to assess the importance of local scale habitat variables on the distribution of nest sites within my study area. While I chose to compare results from spatial linear regression models with those from the standard OLS model, I recognize the spatial patterns of non-stationarity I observed warrants further attention. Techniques such as geographically weighted regression (GWR; Fotheringham et al. 2002)

can compensate for the non-stationarity in the data and future analysis should make use of likelihood-based GWR for structural regression analysis.

### **Brood-Rearing Locations**

Univariate analysis of the Lassen County brood-rearing location data confirmed there was strong evidence of both positive spatial autocorrelation (as indicated by the Moran's I) as well as spatial heterogeneity in the form of distinct spatial regimes for 7 variables including forb height and canopy cover, grass canopy cover, shrub height and canopy cover, bareground, and litter (Table 5). There is no indication of significant spatial clustering for grass height and visual obstruction (Table 5). Local statistics indicated that the structure of dependency of the brood location point data varied across my study area, suggesting the structure of dependency for vegetative attributes related to habitat structure were heterogeneous or non-stationary.

Shrub canopy cover had a significant positive influence on the distribution of brood-rearing locations as indicated from fitting a standard linear regression model to the data set. Conversely, visual obstruction had a significant negative influence on the distribution of brood sites. The remaining vegetative attributes had no significant effect on the distribution of brood-locations across my study area. However, the measure of overall goodness of fit provided by the coefficient of determination ( $R^2$ ) for the OLS model was 0.34, indicating much of what determined brood-rearing locations went unexplained by this model.

Grass height and visual obstruction remained significant in the spatial lag and spatial error model. Although the global Moran's I test on the residuals after fitting the standard linear regression suggests there was no evidence of spatial autocorrelation among the

residuals (Moran's  $I = -1.116$ ;  $p$ -value = 0.2643), AIC confirmed that both spatial linear regression models outperformed the normal regression model to describe the distribution of brood-rearing locations within my study area (Table 6). Between the spatial lag model and the spatial error model, I selected the latter as the best-approximating model of my data, because of a slightly smaller AIC value. Table 7 summarizes the regression parameter estimates of the spatial error model for Lassen County brood-rearing locations. The explanatory power of the model increased over the OLS regression with an  $R^2$  of 0.45. These results demonstrated that the addition of the SAR component resulted in an improvement over the standard OLS model. Thus, it is likely that the results of the global OLS regression model, which assumes spatial stationarity, likely failed to explain local variation in vegetative attributes measured at brood-rearing locations.

### **Landscape Scale Analysis: MaxEnt and Habitat Suitability**

The habitat suitability maps of nest and brood-rearing habitat in northeastern California consisted of sage-grouse records collected during 2007 through 2009, representing 74 nest sites and 476 brood locations. MaxEnt relies on an unbiased sample of presence records cleaned for duplicates (Elith et al. 2010, Newbold 2010), however, during brood-rearing some radiomarked females were observed together in mixed flocks. To avoid the possibility of dependency in the brood-rearing location data, duplicate brood locations ( $n = 3$ ) were not retained and the final data set contained 473 brood locations.

### **Nest Sites**

Model performance, based on 8 predictor variables, which included landcover type, aspect, elevation, fire (prescribed and natural), roads, slope, transmission lines, and communication

towers, had a high goodness of fit (average test AUC for the replicate runs = 0.748, SD = 0.058). Transmission lines and communication towers did not appear to influence habitat use (contributing <1% to the model) and were not included in my reduced model, which increased model fit (average test AUC for the replicate runs = 0.758, SD = 0.027). The regularized training gain for the final reduced model using the full set of presence records was 0.785.

Models based on replicate runs and using the full set of occurrence locations produced similar predictions for the geographic distribution of nesting habitat in northeastern California. Based on the predictive contribution of each variable, landcover type was the most important environmental variable in the MaxEnt models of sage-grouse nest sites within my study area (30.6% contribution). The relative importance of the remaining predictors variables for the reduced 6-variable model were aspect (25.7% contribution), elevation (20.2% contribution), fire (13.4% contribution), and roads (9.1% contribution). Slope was a weak predictor variable, contributing only 1% to the model.

The results of the jackknife test of variable importance indicated the environmental variable with highest gain when used in isolation was elevation, followed by landcover type. The environmental variable that decreases the gain the most when it is omitted was aspect, which therefore appears to have the most information that is not present in the other variables.

My findings suggest that the most suitable nesting habitat was characterized by flat areas or north-facing slopes within mid-elevation range (mean = 1,607 m  $\pm$  14.2 SE; range =

1,350-1,943 m) and associated with sagebrush cover. Sage-grouse avoided steep slopes and demonstrated avoidance of easterly, southerly, and westerly aspects for nest sites.

My final model of the geographic distribution of sage-grouse nesting habitat in northeastern California indicated that < 2% of the study area was classified in the Optimal habitat suitability class (Figure 2), suggesting optimal nesting habitat represents a small proportion of the overall landscape within my study area. Further, my findings indicate that the majority of the study area (46%) was classified as Unsuitable nesting habitat (Figure 2). Although suitable nesting habitat was limited across the study area, a relatively high proportion of nest sites (~59%) occurred in habitat patches classified as Optimal (14%) and Suitable (45%) nesting habitat. Apparent nest success was not affected by whether a nest occurred within an area classified as suitable (Optimal = 67%; Suitable = 47%) or unsuitable habitat classifications (Marginal = 64%; Unsuitable = 57%); where apparent nest success was calculated by dividing the number of successful nests (including renests) divided by the total number of radiomarked females alive at the onset of the nesting season.

### **Brood-rearing**

Model performance, based on 9 predictor variables, which included landcover type, aspect, elevation, CTI, fire (prescribed and natural), roads, slope, transmission lines, and communication towers, had a high goodness of fit (average test AUC for the replicate runs = 0.806, SD = 0.014). Transmission lines, communication towers, fires, and roads did not appear to influence habitat use (contributing <1% to the model) and were not included in my reduced model which increased model fit (average test AUC for the replicate runs = 0.815,



SD = 0.013). The regularized training gain for the final reduced model using the full set of presence records was 0.830.

Models based on replicate runs and using the full set of occurrence locations produced similar predictions for the geographic distribution of brood-rearing habitat in northeastern California. Based on the predictive contribution of each variable, elevation was the most important environmental variable in the MaxEnt models of sage-grouse brood-rearing locations within my study area (39% contribution). The relative importance of the remaining predictors variables for the reduced 5-variable model were aspect (32.5% contribution), CTI (11% contribution), landcover (9.2% contribution), and slope (8.3% contribution).

The results of the jackknife test of variable importance indicated the environmental variable with highest gain when used in isolation was elevation, followed by aspect. The environmental variable that decreases the gain the most when it is omitted is elevation, which therefore appears to have the most information that is not present in the other variables.

My findings suggest that areas with high CTI uplands classification values (e.g., see Cress et al. 2009), which represent places with mesic ( $12 \leq \text{CTI} < 18.5$ ) and dry uplands ( $\text{CTI} < 12$ ), provided the most suitable brood-rearing habitat. Brood-rearing locations were characterized by flat areas within mid-elevation range (mean = 1,622 m  $\pm$  6.8 SE; range = 1,357-2,085 m) and associated with sagebrush cover followed by a decrease in habitat suitability across steeper terrain.

My final model of the geographic distribution of sage-grouse brood-rearing habitat in northeastern California indicated that approximately 1% of the study area was classified in

the Optimal habitat suitability class (Figure 3), suggesting optimal brood-rearing habitat represents a small proportion of the overall landscape within my study area. My findings indicate that the majority of the study area (67%) was classified as Unsuitable brood-rearing habitat (Figure 3). Sage-grouse broods used lower ranked habitat classes (Marginal = 49%; Unsuitable = 16%) more frequently, whereas a small proportion of broods (35%) occurred in high quality habitat patches (i.e., classified as either Suitable or Optimal habitat), which comprised only 8% of my study area.

### **Model Validation**

My landscape scale model classified approximately 39% of independent sage-grouse nests and brood-rearing locations into Suitable or Optimal habitats. I assumed that sage-grouse would be unlikely to occur in Marginal or Unsuitable habitat classes, however, 61% of the independent breeding season locations (i.e., nesting and brood-rearing) used for model validation occurred in those 2 probability classes. Because a higher proportion of the independent sample occurred in Marginal or Unsuitable habitats, I determined the proportion of independent sage-grouse nest and brood-rearing locations used for model validation that occurred in each of the 4 probability classes and compared the proportions to the frequency of occurrence of nest and brood locations used for model development. The proportion of nest and brood locations were similar for 3 probability classes (Unsuitable, Marginal, Suitable), suggesting that my model correctly identified landscapes for nesting and brood-rearing habitat for sage-grouse in northeastern California (Figure 4). Only the Optimal habitat class had a higher proportion of nest and brood locations for data sets used for model development (29%) compared to independent samples used for model validation (4%).

## **DISCUSSION**

Previous studies describing habitat selection of sage-grouse have evaluated the importance of selection at multiple scales across various life history stages (Aldridge and Boyce 2007, Carpenter et al. 2010, Doherty et al. 2008; 2010), suggesting it will likely require a combination of scales to completely understand how sage-grouse respond to their environment. Accordingly, I used a 2-step approach to identify nesting and brood-rearing habitats for sage-grouse in northeastern California. First, I used SAR models to examine local scale habitat characteristics that cannot currently be mapped in GIS to describe the distribution of nest sites and brood-rearing locations in northeastern California. I then used GIS analysis and maximum entropy techniques to study the environmental factors that influence the spatial distribution of nest sites and brood-rearing locations in northeastern California and to produce habitat suitability maps that describe the potential geographic distribution of nesting and brood-rearing habitats at the landscape scale. My results are consistent with other studies (e.g., Aldridge and Boyce 2007, Doherty et al. 2010), demonstrating both local and landscape scale habitat features were important in sage-grouse nesting and brood-rearing habitat use.

The selection of local scale habitat features and stand characteristics by females, and the relationship of nest site and brood-rearing characteristics with habitat availability has been previously described (see Schroeder et al. 1999). A meta-analysis of sage-grouse nesting habitat data indicated sagebrush cover and grass height were greater at nest sites than at random locations (Hagen et al. 2007). Additional findings from the meta-analysis concluded sage-grouse brood-rearing habitat had less sagebrush cover, taller grass, greater

forb cover, and greater grass cover than random sites. Hagen et al. (2007) concluded that overall estimates of vegetative structure at nest sites and brood-rearing locations were consistent with published guideline requirements for managing sage-grouse habitats (Connelly et al. 2000). My findings were consistent with previous research on sage-grouse nest and brood ecology. At the local scale, females selected sagebrush landcover types with increased grass height and visual obstruction for nesting. The primary difference between brood-rearing locations within sagebrush-dominated habitats and paired random locations was grass height (15.2 versus 16.2 cm) and visual obscurity (1.2 versus 2.4 dm) in the surrounding sagebrush-steppe community. The amount of sagebrush canopy was also important in explaining brood-rearing habitat use. Compared to nesting habitat, brood-rearing locations measured across my study area typically had less live shrub canopy cover (8.0 versus 11.3%), less herbaceous forb cover (7.8 versus 9.9%), and lower visual obstruction (1.2 versus 4.6 dm).

Although sage-grouse are considered a landscape-scale species which require vast expanses of contiguous sagebrush-steppe habitats across all life history stages (Connelly et al. 2004), the published guidelines for the management of sage-grouse (Connelly et al. 2000) describe local scale habitat requirements but do not include landscape or multi-scale management recommendations. My landscape scale model indicated sage-grouse nesting habitat was limited across my study area, with optimal and suitable nesting habitat ranging from only 2% to 17%, respectively. Although optimal habitat was important for sage-grouse nest success in northeastern California, approximately 42% of nests sites were in areas of marginal or unsuitable habitat. Similarly, my results suggest optimum and suitable habitat

classes for brood-rearing were also uncommon on the landscape (1% and 7% of the study area, respectively), suggesting loss of quality brood-rearing habitat is limiting sage-grouse populations in northeastern California. Other landscape-level assessments of sage-grouse brood-rearing habitat also reported high quality brood-rearing habitat was highly restricted (Aldridge and Boyce 2007, Atamian et al. 2010), limiting sage-grouse populations in other parts of the species' range.

The habitat structure of sagebrush-steppe ecosystems are shaped by various factors, including climate, soil, topography and landuse history. The landscape scale features that had the most influence on nest site selection in my study included landcover type, aspect, and elevation. Fire history and roads were also strong predictors of nest-site suitability for female sage-grouse. Approximately 93% of nests were within sagebrush landcover types, while 4% occurred in juniper woodlands. Approximately 3% of the nest sites were located in non-sagebrush landcover types. My results indicate sage-grouse avoid steep slopes for nest sites and conform to previous reports of sage-grouse nest site selection (Yost et al. 2008). In addition, results from my study indicated that suitable nesting habitat was characterized by flat areas or northerly aspects. In contrast, Yost et al. (2008) found sage-grouse in Oregon showed a slight avoidance of north- and west-facing slopes for nests sites, inferring the thermal benefit of early morning exposure to solar radiation to nest success had some driving force on nest site selection. While it is widely accepted that in the northern hemisphere south-facing slopes receive more solar radiation than north-facing slopes (Holland and Steyn 1975), south-facing slopes are typically characterized by xeric environments that are more sparsely vegetated than moister north-facing slopes. Consequently, it is possible that

vegetation characteristics required for successful sage-grouse nesting, such as canopy cover of sagebrush, grass, and forbs, were greater on north-facing slopes and, therefore, influenced nest site selection in northeastern California.

Fires, both prescribed and natural, are important drivers of vegetation structure and composition within sagebrush communities (Miller et al. 2011). My landscape scale model indicated 24% (18/74) of nest sites occurred in areas with a known history of fire disturbance. Studies have demonstrated that fire can have long-term effects (>10 years) on sagebrush-steppe communities (Nelle et al. 2000, Beck et al. 2009). Moreover, in Oregon, Byrne (2002) found female sage-grouse continued to avoid burned areas even after sagebrush recovered to pre-burn levels. Historical fire records indicate that since 1907, approximately 11% of my study area has been disturbed by fire. Individual fire events across my study area have increased over time with over 60% of the fires occurring after 1980. Of those nests located in burned areas, 83% (15/18) were located in a 2001 wildfire, which burned approximately 26,144 ha and removed much of the total sagebrush cover, leaving few unburned islands of surviving shrubs. The characteristics of this individual fire event indicates sage-grouse were likely unable to modify habitat use within this area, particularly since sage-grouse are known to use traditional nesting areas across multiple years (e.g., Fischer et al. 1993). Although female sage-grouse still occupied those habitat patches, apparent nest success (initial and renests) overall was low (44%). The reduced proportion of successful nests might be due to changes in structure, composition, and abundance of vegetation within sagebrush-steppe habitat following fire. In Idaho, Shepherd et al. (2011) found more open, fragmented, and therefore less suitable sagebrush communities, increased

visual nest detection by predators resulting in an increase in the amount or type of nest predation.

It is possible that the number of nest sites I observed in areas associated with fire disturbance was an artifact of which leks were sampled over the course of my study. Of the 13 known, active lek sites in my study area, 4 occurred within the 2001 wildfire site. Nest-site fidelity by female sage-grouse was apparent in my study (Chapter 3). Moreover, given the high fidelity of sage-grouse to nest sites (Berry and Eng 1985, Fischer et al. 1993, Schroeder and Robb 2003, Holloran and Anderson 2005, Herman-Brunson 2007, Moynahan et al. 2007, Kaczor 2008), sage-grouse might persist in marginal or unsuitable habitats. However, these habitats likely will not result in successful nesting attempts and, ultimately, could contribute to decreases in productivity. Because the landscapes sage-grouse occupy can change rapidly, site fidelity could possibly result in a lag period between the time of landscape degradation and habitat abandonment or local extinction. Thus, sage-grouse continue to select nest sites and brood-rearing locations in attractive sink habitats before the population is eventually extirpated. For example, Aldridge and Boyce (2007) found that >50% of the nesting habitat and 75% of the brood-rearing habitat in the northern fringe of the sage-grouse range in Canada occurred in high-risk areas, resulting in a demographic sink.

Landscape scale environmental variables were also important to brood-rearing habitat use. Topography (elevation, slope, aspect), food resources indexed as CTI, and landcover type all helped to explain the geographic distribution of brood-rearing habitat in northeastern California. Mesic habitats provided the most suitable brood-rearing habitat in my study, presumably because forb and insect abundance was higher. Similarly, in southeastern

Alberta brood-rearing habitat selection was strong for mesic habitats, with broods selecting for higher wetness values and higher mean CTI scores (Aldridge and Boyce 2007). Earlier studies also reported habitat structural characteristics and availability of insects and succulent forbs as primary determinants of brood-rearing habitat selection by sage-grouse (Klebenow 1969, Peterson 1970, Wallestad 1971, Autenrieth 1981). In east-central Nevada, sage-grouse broods also used riparian shrublands and higher elevation sites characterized by moister and greener vegetation (Atamian et al. 2010).

Although broods in my study primarily occupied sagebrush landcover types (87%) with reduced grass height and lower visual obstruction, 8% of brood-rearing locations occurred in juniper woodlands or exotic annual grasslands. Of the 597,116 ha of potential sagebrush habitat within my study area, >46% of the area currently has a high percentage of exotic annual grasses or juniper encroachment (Armentrout and Hall 2005). Further, approximately 19% of the sagebrush community within the study area has crossed a threshold to being dominated by annual grasslands or western juniper (Armentrout and Hall 2005), suggesting suitable sagebrush availability was low across my study area.

Numerous studies have demonstrated cover of sagebrush and the associated herbaceous understory decrease with increasing tree dominance (Miller et al. 2000, Roberts and Jones 2000, Schaefer et al. 2003). Elimination of sagebrush and associated shrub species might be more permanent in sagebrush-steppe communities dominated by annual grasses than if the herbaceous understory consisted of native perennial bunchgrasses and forbs (Miller et al. 2011). Results from Doherty et al. (2010) suggest that juniper invasion could displace nesting sage-grouse. Nest site fidelity might lower nest success and population



viability if this structural alteration negatively impacts sage-grouse nesting habitat. Further, Shepherd et al. (2011) found that grass-forb dominated land cover was an important variable in explaining brood success in Idaho, with successful broods having less grass-forb dominated habitat in the surrounding landscape. In addition, Shepherd et al. (2011) speculated grass-forb dominated habitats influenced brood success through increased visibility and was a primary factor in brood depredation. Although the relationship between habitat fragmentation and its effects on sage-grouse populations dynamics are poorly understood, invasion of western juniper and exotic grass species have resulted in loss and degradation of sagebrush habitats and are considered the primary reason for the population decline and range contraction of sage-grouse in northeastern California (S. C. Gardner, personal communication).

Recent research has shown that sage-grouse are sensitive to habitat fragmentation caused by anthropogenic features and human activity can affect habitat selection (Aldridge and Boyce 2007, Doherty et al. 2010) and nesting activities (Lyon and Anderson 2003, Holloran et al. 2010). Of the 3 anthropogenic features I evaluated, only roads appeared related to the geographic distribution of nest sites. Distances from nests to the nearest road was highly variable and ranged from 16 to 2,195 m. Fifty percent of all sage-grouse nests were found within 500 m of secondary roads, which did not appear to influence nest-site selection. In addition, the presence of primary and secondary roads did not appear to influence sage-grouse brood habitat use. Similarly, Atamian et al. (2010) found sage-grouse broods in east-central Nevada were unaffected by location of roads during the late brood-rearing period. Although sage-grouse nests occurred close to roads in some cases, this

relationship was due, in part, because most roads in my study area were rarely travelled secondary dirt roads. While sage-grouse in my study did not appear to avoid roads during nesting and brood-rearing, data from several studies indicate that prairie grouse, including sage-grouse, avoid or nest at reduced rates in areas near roads (Lyon and Anderson 2003, Robel et al. 2004, Pitman et al. 2005, Aldridge et al. 2012). Moreover, the noise and disturbance associated with roads can alter nest site selection, habitat use, and lek persistence (Lyon and Anderson 2003, Holloran et al. 2010, Hagen et al. 2011). Direct mortality associated with vehicle collisions can occur but is a relatively small percentage of overall mortality in sage-grouse (Aldridge and Boyce 2007). How sage-grouse respond to roads likely depends on the amount of available suitable habitat adjacent to roads, road configuration, and the road type (Frair et al. 2008). Thus, sage-grouse response to anthropogenic disturbance is likely different where those features are more pervasive within the occupied range of the species.

While anthropogenic features such as transmission lines and communication towers did not appear to influence habitat use and were not included in my final models of nest and brood-rearing habitat in northeastern California, these features were not pervasive across my study area. Although these features were largely absent in my study area, transmission lines and cellular towers were strongly associated with sage-grouse extirpation, where these anthropogenic features were common in occupied sage-grouse range (Wisdom et al. 2011). The behavioral response of sage-grouse is likely similar to that of other prairie grouse species, such as the lesser prairie-chicken (*Tympanuchus pallidicinctus*), and research has suggested that both species will avoid transmission lines during the breeding season (Braun

1998, Hagen 2003, Pitman et al. 2005). In addition, collisions with overhead transmission lines can cause direct mortality to sage-grouse (Beck et al. 2006, Aldridge and Boyce 2007), further limiting sage-grouse populations.

Construction of transmission lines also provides perches for various raptor species, which could potentially increase the mortality rate of sage-grouse (Connelly et al. 2000). What is more, the presence of transmission lines might fragment sage-grouse habitats even if raptors are not present (Hagen et al. 2011) and cause sage-grouse avoidance of otherwise suitable nesting and brood-rearing habitat and further restrict the sage-grouse range. Wisdom et al. (2011) speculated that collisions with cellular towers also cause sage-grouse injury and mortality. In addition, sage-grouse avoidance of vertical structures could influence sage-grouse movements and habitat use, however, no research has investigated these issues. Whether cellular towers reflects sensitivity to visual obstruction or some other form of disturbance associated with human development (e.g., interstate highways, urban development), or is a response to other detrimental factors, remains unknown (Wisdom et al. 2011). However, recent studies emphasize the importance of taking behavioral avoidance into consideration when assessing anthropogenic impacts on grouse habitat (Pitman et al. 2005, Hagen et al. 2011).

Although the effects of anthropogenic features on sage-grouse demography and habitat use have received little attention, impacts of fragmentation are cumulative and often result in behavioral responses to whatever changes are occurring on the landscape. The distribution of optimal and suitable nesting and brood-rearing habitat in northeastern California were rare across the landscape. As a sagebrush obligate, sage-grouse are

dependent on sagebrush to maintain long-term population persistence. Viable sage-grouse populations require large landscapes (Patterson 1952, Connelly et al. 2000). Thus, landscape fragmentation leads to increasingly unsuitable conditions for sage-grouse (Schroeder et al. 2004, Aldridge et al. 2008) and, ultimately, could lead to population declines which might in turn affect extinction risk (Johnson et al. 2011). In northeastern California, loss and degradation of existing sagebrush habitats and conversion of large tracts of sagebrush to other vegetation (e.g., annual grasslands, juniper woodlands) will likely result in declining sage-grouse populations because of reduced nesting success and decreased productivity.

While the underlying causes for ongoing population declines in northeastern California are poorly understood, they are likely related to changes in landcover types. Even though sage-grouse occupied marginal habitat within my study area, unsuitable nesting and brood-rearing habitat might be contributing to decreases in productivity and population declines in northeastern California. Sagebrush habitats are severely altered across much of my study area and the sagebrush community structure and ecological function will continue to decline as a result of invasive species, juniper encroachment, altered fire regimes, and climate change. Given the limited amount of suitable nesting and brood-rearing habitat, my results suggest conservation efforts focused on these scarce resources will be important for effective management of breeding season habitat for sage-grouse in northeastern California.

## **MANAGEMENT IMPLICATIONS**

Numerous studies have recommended that sage-grouse populations should be managed across multiple spatial scales (e.g., Aldridge and Boyce 2007, Carpenter et al. 2010, Doherty et al. 2008; 2010). Although my landscape model identified landscapes for nesting and

brood-rearing habitat for sage-grouse in northeastern California, careful attention still needs to be given to managing sagebrush-steppe habitats during other life history stages. My results indicate that sage-grouse nesting and brood-rearing habitat were limited across my study area and, ultimately, might contribute to decreases in nest success and productivity in northeastern California. To make certain that critical sage-grouse habitat is not lost, seasonal use areas for nesting, brood-rearing, and migration routes must be identified and managed appropriately to ensure that these habitats are available. Likewise, maintaining connectivity between habitats will be important to the recovery and long-term persistence of sage-grouse populations occurring on the geographic periphery of the species' distribution.

## LITERATURE CITED

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. *Ecological Applications* 17:508-526.
- Aldridge, C. L., and R. M. Brigham. 2001. Nesting and reproductive activities of greater sage-grouse in a declining northern fringe population. *Condor* 103:537-543.
- Aldridge, C. L., and R. M. Brigham. 2002. Sage-grouse nesting and brood habitat use in southern Canada. *Journal of Wildlife Management* 66:433-444.
- Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. *Diversity and Distributions* 14:983-994.
- Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for Gunnison sage-grouse: a spatially explicit hierarchical approach. *Journal of Wildlife Management* 76:391-406.

- Anselin, L. 1995. Local indicators of spatial association – LISA. *Geographical Analysis* 27:93-115.
- Anselin, L. 2002. Under the hood: issues in the specification and interpretation of spatial regression models. *Agricultural Economics* 27:247–267.
- Anselin, L., I. Syabri, and K. Youngihn. 2006. GeoDa: an introduction to spatial data analysis. *Geographical Analysis* 38:5-22.
- Armentrout, D. J., and F. Hall. 2005. Conservation strategy for sage-grouse (*Centrocercus urophasianus*) and sagebrush ecosystems within the Buffalo-Skedaddle population management unit. Bureau of Land Management, Eagle Lake Field Office, Susanville, California, USA.
- Atamian, M. T., J. S. Sedinger, J. S. Heaton, E. J. Blomberg. 2010. Landscape-level assessment of brood-rearing habitat for greater sage-grouse in Nevada. *Journal of Wildlife Management* 74:1533-1543.
- Autenrieth, R. E. 1981. Sage grouse management in Idaho. Idaho Department of Fish and Game. *Wildlife Bulletin* 9.
- Bailey, T. C., and A. C. Gatrell. 1995. Interactive spatial data analysis. John Wiley and Sons, Inc., New York, New York, USA.
- Beck, J. L., J. W. Connelly, and K. P. Reese. 2009. Recovery of greater sage-grouse habitat features in Wyoming big sagebrush following prescribed fire. 2009. *Restoration Ecology* 17:393-403.
- Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of greater sage-grouse in southeastern Idaho. *Wildlife Society Bulletin* 34:1070-1078.
- Berry, J. D., and R. L. Eng. 1985. Interseasonal movements and fidelity to seasonal use areas by female sage grouse. *Journal of Wildlife Management* 49:237-240.
- Beier, P., D. R. Majka, and W. D. Spencer. 2008. Forks in the road: choices and procedures for designing wildlife linkages. *Conservation Biology* 22:836-851.
- Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? *Proceedings of the Western Association State Fish and Game Wildlife Agencies* 78:139-156.
- Breusch, T., and A. Pagan. 1979. A simple test for heteroscedasticity and random coefficient variation. *Econometrica* 47:1287-1294.

- Byrne, M. W. 2002. Habitat use by female greater sage-grouse in relation to fire at Hart Mountain National Antelope Refuge, Oregon. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. *Journal of Forestry* 39:388-394.
- Carpenter, J. E., C. L. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. *Journal of Wildlife Management* 78:1806-1814.
- Connelly, J. W., and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. *Wildlife Biology* 3:229-234.
- Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Western Association of Fish and Wildlife Agencies. Unpublished report, Cheyenne, Wyoming, USA.
- Connelly, J. W., K. P. Reese, and M. A. Schroeder. 2003. Monitoring of greater sage-grouse habitats and populations. College of Natural Resources Experiment Station Bulletin 80, University of Idaho, Moscow, Idaho, USA.
- Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. *Wildlife Society Bulletin* 28:967:985.
- Cress, J. J., R. Sayre, P. Comer, and H. Warner. 2009. Terrestrial ecosystems – topographic moisture potential of the conterminous United States: U.S. Geological Survey Scientific Investigations Map 3086, scale 1:5,000,000, 1 sheet.
- Crunden, C. W. 1963. Age and sex of sage grouse from wings. *Journal of Wildlife Management* 27:846-850.
- Dalke, P. D., D. B. Pyrah, D. C. Stanton, J. E. Crawford, and E. F. Schlatterer. 1963. Ecology, productivity, and management of sage grouse in Idaho. *Journal of Wildlife Management* 27:811-841.
- Daubenmire, R. F. 1959. A canopy coverage method of vegetation analysis. *Northwest Science* 33:224-227.
- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2008. Greater sage-grouse winter habitat selection and energy development. *Journal of Wildlife Management* 72:187-195.

- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. *Journal of Wildlife Management* 74:1544-1553.
- Elith, J. 2002. Quantitative methods for modeling species habitat: comparative performance and application to Australian plants. Pages 39-58 *in* S. Ferson and M. Burgman, editors. *Quantitative methods for conservation biology*, Springer-Verlag, New York, USA.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Elith, J., M. Kearney, and S. J. Phillips. 2010. The art of modeling range-shifting species. *Methods in Ecology and Evolution* 1:330-342.
- Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17:43-57.
- Evans, J. 2002. Compound topographic index, AML script. ESRI Support Center Downloads. ESRI, Redlands, California, USA.  
<<http://arcscripts.esri.com/details.asp?dbid=11863>>.
- Fischer, R. A., A. D. Apa, W. L. Wakkinen, K. P. Reese and J. W. Connelly. 1993. Nesting-area fidelity of sage-grouse in southeastern Idaho. *Condor* 95:1038-1041.
- Fotheringham, A. S., C. Brunsdon, and M. Charlton. 2002. *Geographically weighted regression: the analysis of spatially varying relationships*. Wiley, Chichester.
- Frair, J. L., E. H. Merrill, H. L. Beyer, and J. M. Morales. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. *Journal of Applied Ecology* 45:1504–1513.
- Gallant, A. L. 2009. What you should know about land-cover data. *Journal of Wildlife Management* 73:796-805.
- Gessler, P. E., I. D. Moore, N. J. McKenzie, and P. J. Ryan. 1995. Soil-landscape modeling and spatial prediction of soil attributes. *International Journal of GIS* 9:421-432.
- Giesen, K. M., T. J. Schoenberg, and C. E. Braun. 1982. Methods for trapping sage grouse in Colorado. *Wildlife Society Bulletin* 10:224-231.



- Gregg, M. A. 2006. Greater sage-grouse reproductive ecology: linkages among habitat resources, maternal nutrition, and chick survival. Dissertation. Oregon State University, Corvallis, USA.
- Gregg, M. A., and J. A. Crawford. 2009. Survival of greater sage-grouse chicks and broods in the northern Great Basin. *Journal of Wildlife Management* 73:904-913.
- Hagen, C. A. 2003. A demographic analysis of Lesser Prairie-Chicken populations in southwestern Kansas: survival, population viability, and habitat use. Dissertation. Kansas State University, Manhattan, Kansas, USA.
- Hagen, C. A., J. W. Connelly, and M. A. Schroeder. 2007. A meta-analysis for greater sage-grouse nesting and brood rearing habitats. *Wildlife Biology* 13:42-50.
- Hagen, C. A., J. C. Pitman, T. M. Loughin, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2011. Impacts of anthropogenic features on habitat use by lesser prairie-chickens. Pages 63-76 in B. K. Sandercock, K. Martin, and G. Segelbacher, editors. *Ecology, conservation, and management of grouse. Studies In Avian Biology* (no. 39), University of California Press, Berkeley, California, USA.
- Haining, R. 2003. *Spatial data analysis: theory and practice*. Cambridge University Press, Cambridge, UK.
- Hair, J. F. Jr., R. E. Anderson, R. L. Tatham, and W. C. Black. 1995. *Multivariate data analysis*. Third edition. Macmillan, New York, New York, USA.
- Hanley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a Receiver Operating Characteristic (ROC) curve. *Radiology* 143:29-36.
- Hanser, S. E., and S. T. Knick. 2011. Greater Sage-Grouse as an umbrella species for shrubland passerine birds: a multiscale assessment. Pages 473-487 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology* (vol. 38), University of California Press, Berkeley, California, USA.
- Herman-Brunson, K. M. 2007. Nesting and brood-rearing success and habitat selection of greater sage-grouse and associated survival of hens and broods at the edge of their historic distribution. Thesis. South Dakota State University, Brookings, South Dakota, USA.
- Hirzel, A. H., J. Hausser, D. Chessel, and N. Perrin. 2002. Ecological-niche factor analysis: how to compute habitat suitability maps without absence data? *Ecology* 83:2027-2036.

- Holloran, M. J., and S. H. Anderson. 2005. Spatial distribution of greater sage-grouse nests in relatively contiguous habitats. *Condor* 107:742-752.
- Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. *Journal of Wildlife Management* 74:68-72.
- Holland, P. G., and D. G. Steyn. 1975. Vegetational responses to latitudinal variations in slope, angle, and aspect. *Journal of Biogeography* 2:179-183.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology* 22:415-427.
- Jaynes, E. T. 1957. Information theory and statistical mechanics. *Physical Review* 106:620-630.
- Jensen, B. M. 2006. Migration, transition range and landscape use by greater sage-grouse (*Centrocercus urophasianus*). Thesis. University of Wyoming, Laramie, Wyoming, USA.
- Jentz, W., B. Rahbek, J. W. Lichstein. 2005. Local and global approaches to spatial data analysis in ecology. *Global Ecology and Biogeography* 14:97-98.
- Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997-2007. Pages 407-450 in S. T. Knick and J. W. Connelly, editors. *Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38)*, University of California Press, Berkeley, California, USA.
- Kaczor, N. W. 2008. Nesting and brood-rearing success and resource selection of greater sage-grouse in northwestern South Dakota. Thesis. South Dakota State University, Brookings, South Dakota, USA.
- Klebenow, D.A. 1969. Sage grouse nesting and brood habitat in Idaho. *Journal of Wildlife Management* 33:649-661.
- Knick, S. T., and S. E. Hanser. 2011. Connecting pattern and process in greater sage-grouse populations and sagebrush landscapes. Pages 383-405 in S. T. Knick and J. W. Connelly, editors. *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38)*, University of California Press, Berkeley, California, USA.

- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- LANDFIRE. 2006. National existing vegetation type layer. USDI Geological Survey. <<http://gisdata.usgs.net/website/landfire/>>. Accessed 12 October 2011.
- Lillesand, T. M., and R. W. Kiefer. 2000. Remote sensing and image interpretation. John Wiley and Sons, New York, New York, USA.
- Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:1943-1967.
- Marquardt, D. W. 1970. Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics* 12:591-612.
- Mason, R. L., R. F. Gunst, and J. L. Hess. 1989. Statistical design and analysis of experiments: Applications to engineering and science. New York: Wiley.
- Menard, S. 1995. Applied logistic regression analysis: Sage University series on quantitative applications in the social sciences. Thousand Oaks, California: Sage.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145-184 in S. T. Knick and J. W. Connelly, editors. Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Miller, R. F., T. Svejcar, and J. A. Rose. 2000. Impacts of western juniper on plant community composition and structure. *Journal of Range Management* 53:574–585.
- Moore, I. D., R. B. Grayson, and A. R. Ladson. 1991. Digital terrain modeling: a review off hydrological, geomorphological, and biological applications. *Hydrological Process* 5:3-30.
- Moran, P. 1948. The interpolation of statistical maps. *Journal of the Royal Statistical Society B* 10:243–251.
- Moran, P. 1950. Notes on continuous stochastic phenomena. *Biometrika* 37:17-23
- Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2007. Factors affecting nest survival of greater sage-grouse in north central Montana. *Journal of Wildlife Management* 71:1773-1783.
- Nelle, P. J., K. P. Reese, and J. W. Connelly. 2000. Long-term effects of fire on sage grouse

- habitat. *Journal of Range Management* 53:586-591.
- Neter, J. W. Wasserman, and M. H. Kutner. 1989. *Applied linear regression models*. Homewood, Illinois: Irwin.
- Newbold, T. 2010. Applications and limitations of museum data for conservation ecology, with particular attention to species distribution models. *Progress in Physical Geography* 34:3-22.
- Patterson, R. L. 1952. *The sage grouse in Wyoming*. Sage Books Inc., Denver, Colorado, USA.
- Pearce, J. L., and M. S. Boyce. 2006. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology* 43:405-412.
- Pearce, J. and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133:225-245.
- Peterson, J.G. 1970. The food habitats and summer distribution of juvenile sage grouse in central Montana. *Journal of Wildlife Management* 34:147-155.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231-259.
- Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161-175.
- Phillips, S. J., M. K. Dudík, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. Pages 655-662 *in* Proceedings of the twenty-first international conference on machine learning. ACM. Banff, Alberta, Canada.
- Pitman, J. C., C. A. Hagen, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2005. Location and success of lesser prairie-chicken nests in relation to vegetation and human disturbance. *Journal of Wildlife Management* 69:1259-1269.
- Popham, G. P. 2000. *Sage grouse nesting habitat in northeastern California*. Thesis. Humboldt State University, Humboldt, California, USA.
- Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009. Avoidance behavior of prairie grouse: implications for wind and energy development. *Conservation Biology* 23:1253-1259.
- Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295-297.

- Robel, R. J., J. A. Harrington Jr., C. A. Hagen, J. C. Pitman, and R. R. Reker. 2004. Effect of energy development and human activity on the use of sand sagebrush habitat by lesser prairie-chickens in southwestern Kansas. *Transactions of the North American Wildlife and Natural Resources Conference* 69:251-266.
- Roberts, C., and J. A. Jones. 2000. Soil patchiness in juniper-sagebrush communities of central Oregon. *Plant and Soil* 223:45-61.
- Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. *Biological Conservation* 129:323-335.
- Schaefer, R. J., D. J. Thayer, and T. S. Burton. 2003. Forty-one years of vegetation change on permanent transects in northeastern California: implications for wildlife. *California Fish and Game* 89:55-71.
- Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardner, M. A. Hilliard, G. D. Kobriger, S. M. Mcadam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Rickerson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. *Condor* 106:363-376.
- Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. *Wildlife Biology* 9:291-299.
- Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage grouse (*Centrocercus urophasianus*). In *The Birds of North America*, No. 425. (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Segurado, P., M. B. Araujo, and W. E. Kunin. 2006. Consequences of spatial autocorrelation for niche-based models. *Journal of Applied Ecology* 43:433-444.
- Shepherd, J. F., J. W. Connelly, and K. P. Reese. 2011. Modeling nest and brood habitats of greater sage-grouse. Pages 137-150 in B. K. Sandercock, K. Martin, and G. Segelbacher, editors. *Ecology, conservation, and management of grouse. Studies in Avian Biology* (no. 39), University of California Press, Berkeley, California, USA.
- Springer, J. T. 1979. Some source of bias and sampling error in radio triangulation. *Journal of Wildlife Management* 43:926-935.
- Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240:1285-1293.
- United States Department of the Interior (USDI). 2001. SAGEMAP: a GIS database for sage grouse and shrub steppe management in the Intermountain West. USDI Geological Survey. <<http://sagemap.wr.usgs.gov>>. Accessed 29 September 2011.

- Voss, P. R., and G. Chi. 2006. Highways and population change. *Rural Sociology*, 71:33–58.
- Wakkinen, W. L., K. P. Reese, J. W. Connelly, and R. A. Fischer. 1992. An improved spotlighting technique for capturing sage grouse. *Wildlife Society Bulletin* 20:425-426.
- Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. *Journal of Wildlife Management* 71:2644-2654.
- Wallestad, R. O. 1971. Summer movement and habitat use by sage grouse broods in Montana. *Journal of Wildlife Management* 35:129-136.
- Wallestad, R. O., and D. Pyrah. 1974. Movement and nesting of sage grouse hens in central Montana. *Journal of Wildlife Management* 38:630-633.
- Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrub steppe birds: the effects of spatial scales. *Oikos* 48:132-147.
- Wilhelm, A., and R. Steck. 2006. Exploring spatial data using interactive graphics and local statistics. *The Statistician* 47:423-430.
- Wisdom, M. J., M. M. Rowland, B. C. Wales, M. A. Hemstrom, W. J. Hann, M. G. Raphael, R. S. Holthausen, R. A. Gravenmier, and T. D. Rich. 2002a. Modeled effects of sage-brush-steppe restoration on greater sage-grouse in the Interior Columbia Basin, USA. *Conservation Biology* 16:1223-1231.
- Wisdom, M. J., B. C. Wales, M. M. Rowland, M. G. Raphael, R. S. Holthausen, T. D. Rich, and V. A. Saab. 2002b. Performance of greater sage-grouse models for conservation assessment in the Interior Columbia Basin, USA. *Conservation Biology* 16:1232-1242.
- Wisdom, M. J., C. W. Meinke, S. T. Knick, and M. A. Schroeder. 2011. Factors associated with extirpation of sage-grouse. Pages 451-472 in S. T. Knick and J. W. Connelly, editors. *Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats*. Studies in Avian Biology (vol. 38), University of California Press, Berkeley, California, USA.
- Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, A. Guisan, and N. P. S. Distribut. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14:763–773.
- Yost, A. C., S. L. Peterson, M. Gregg, and R. Miller. 2008. Predictive modeling and mapping sage grouse (*Centrocercus urophasianus*) nesting habitat using maximum

entropy and a long-term dataset from Southern Oregon. *Ecological Informatics* 3:375-386.

Table 1. Environmental variables used to model the geographic distribution of greater sage-grouse nest and brood-rearing habitat in Lassen County, California.

Environmental variable	Variable description	Data source
TOWERS	Communication towers	SAGEMAP
POWER	Transmission lines	SAGEMAP
ROADS	Primary interstate highways and secondary roads (paved and unpaved)	TIGER
FIRE	Historical fire record (1907-2007) of wildfire and prescribed burns within study area	SAGEMAP
LAND	Landcover reclassified into 8 landcover classes: sagebrush, agriculture (cultivated crops, pasture, and hayland), riparian, juniper, grassland, shrub and/or woodland types (other than sagebrush or juniper), open water, and developed (urban and suburban areas)	LANDFIRE
DEM	Elevation	Digital Elevation Model (DEM)
SLOPE	Slope generated from DEM and reclassified as <10%, 11-20%, >20%	DEM
ASPECT	Aspect generated from DEM and reclassified as flat (< 44°), north (316° to 45°), east (46° to 135°), south (136° to 225°) and west (226° to 315°)	DEM
CTI	Compound Topographic Index calculated from DEM where high values indicate increased moisture	DEM



Table 2. Dataset variables for calculating univariate Moran's I and associated  $p$ -values to assess the effects of habitat structure on the distribution of nest sites in Lassen County, California, USA, 2007-2009.

Variable	Moran's I	$p$ -value
Live sagebrush canopy cover	0.2064	0.001
Live shrub cover	0.0827	0.042
Grass canopy cover	0.2038	0.002
Forb canopy cover	0.0501	0.054
Litter	0.0046	0.398
Bare ground	0.0806	0.049
Shrub height	0.1395	0.006
Grass Height	0.0852	0.051
Forb Height	0.2017	0.001
Visual obstruction reading (VOR)	0.0729	0.060

Table 3. Classical and spatial regression models used to examine the distribution of greater sage-grouse nests sites in Lassen County, California, 2007-2009.

Model	$R^2$	AIC	Schwarz criterion	Spatial dependence <sup>1</sup>	Breusch-Pagan test
Classical	0.22	173.20	203.40	-2.67	6.27*
Spatial Lag	0.39	156.27	190.30	18.93	2.73*
Spatial Error	0.37	157.38	188.58	-5.04	2.15*

<sup>1</sup>Spatial dependence was measured as Moran's I for classical regression models, the likelihood ratio test for spatial lag regression models, and lambda for spatial error regression models.

\*Non-significant.

Table 4. Results of spatial lag model ( $R^2 = 0.39$ ) on the determinants of greater sage-grouse nest site distribution in Lassen County, California, 2007-2009.

Variable	Coefficient	SE	z-value	p-value
Live sagebrush canopy cover	-0.0463	0.283	-0.164	0.870
Live shrub cover	0.3106	0.457	0.680	0.497
Grass canopy cover	-0.1608	0.354	-0.454	0.650
Forb canopy cover	-0.2259	0.307	-0.736	0.461
Litter	0.0034	0.004	0.852	0.394
Bare ground	0.0026	0.004	0.647	0.518
Shrub height	-0.0045	0.002	-1.864	0.062
Grass Height	0.0162	0.008	2.138	0.033
Forb Height	0.0890	0.193	0.459	0.646
Visual obstruction reading (VOR)	0.5561	0.165	3.378	0.001

Table 5. Dataset variables for calculating univariate Moran's I and associated *p*-values to assess the effects of habitat structure on the distribution of brood-rearing locations in Lassen County, California, USA, 2007-2008.

Variable	Moran's I	P-value
Live shrub canopy cover	0.1652	0.002
Grass canopy cover	0.3780	0.001
Forb canopy cover	0.1699	0.015
Litter	0.2252	0.002
Bare ground	0.1345	0.025
Shrub height	0.2388	0.003
Grass height	0.0731	0.130
Forb Height	0.1795	0.008
Visual obstruction reading (VOR)	0.0127	0.328

Table 6. Classical and spatial regression models used to examine the distribution of greater sage-grouse brood-rearing locations in Lassen County, California, 2007-2008.

Model	$R^2$	AIC	Schwarz criterion	Spatial dependence <sup>1</sup>	Breusch-Pagan test
Classical	0.34	82.29	103.23	-1.12*	7.52*
Spatial Lag	0.43	79.36	102.40	4.93	5.49*
Spatial Error	0.45	76.42	97.36	3.46	4.62*

<sup>1</sup>Spatial dependence was measured as Moran's I for classical regression models, the likelihood ratio test for spatial lag regression models, and lambda for spatial error regression models.

\*Non-significant.

Table 7. Results of spatial error model ( $R^2 = 0.45$ ) on the determinants of greater sage-grouse brood-rearing locations in Lassen County, California, 2007-2008.

Variable	Coefficient	SE	z-value	p-value
Live shrub canopy cover	2.0842	0.765	2.722	0.006
Grass canopy cover	-0.0053	0.004	-1.328	0.184
Forb canopy cover	0.02081	0.008	2.502	0.012
Litter	-0.0033	0.005	-0.559	0.575
Bare ground	-0.0047	0.006	-0.763	0.445
Shrub height	0.0051	0.003	1.604	0.108
Grass height	-0.0026	0.013	-0.197	0.843
Forb Height	-0.0100	0.013	-0.727	0.466
Visual obstruction reading (VOR)	-0.2614	0.052	-4.980	0.000

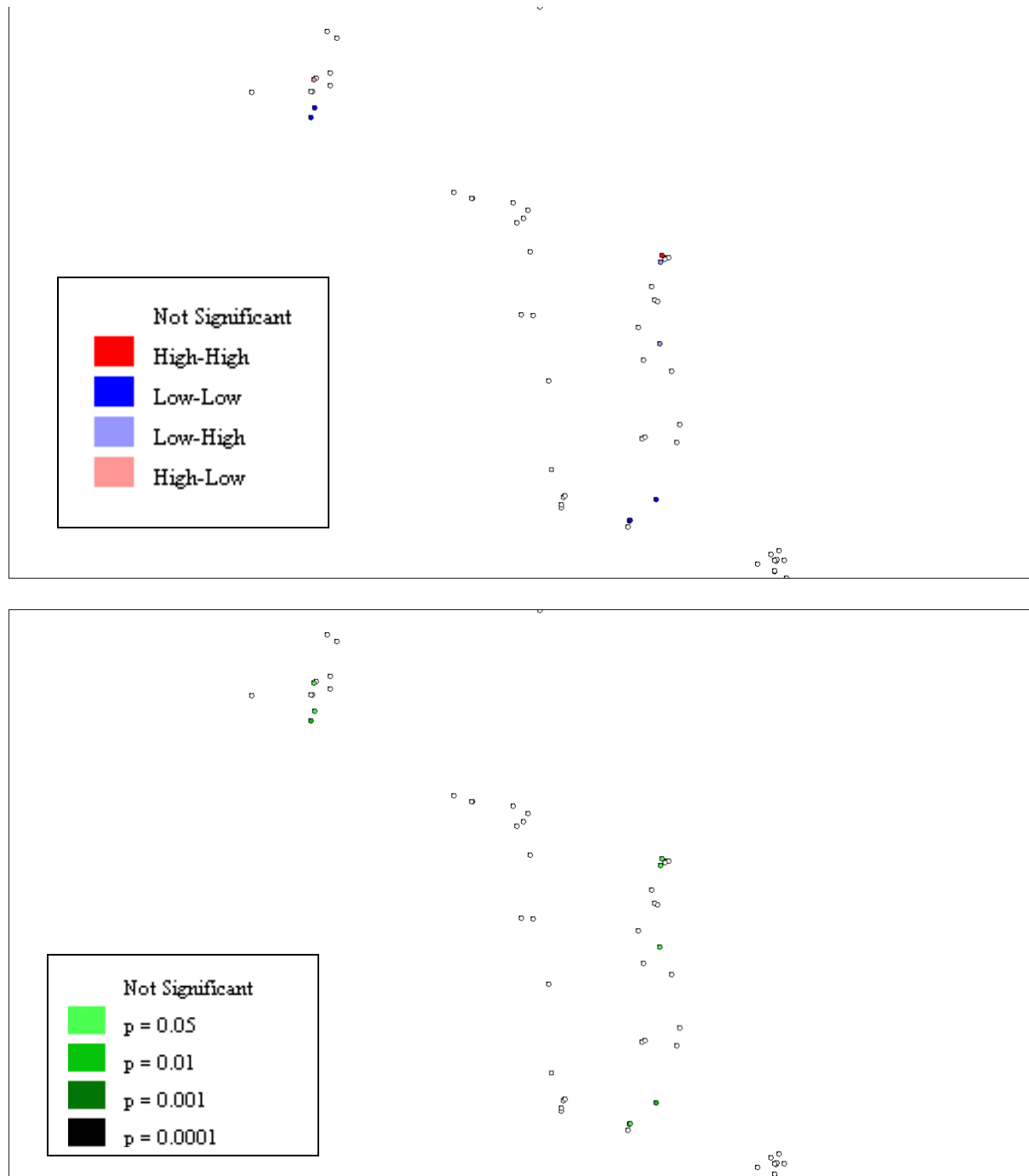


Figure 1. Univariate LISA cluster and significance maps for grass height measured at greater sage-grouse nest sites, Lassen County, California, 2007-2009.

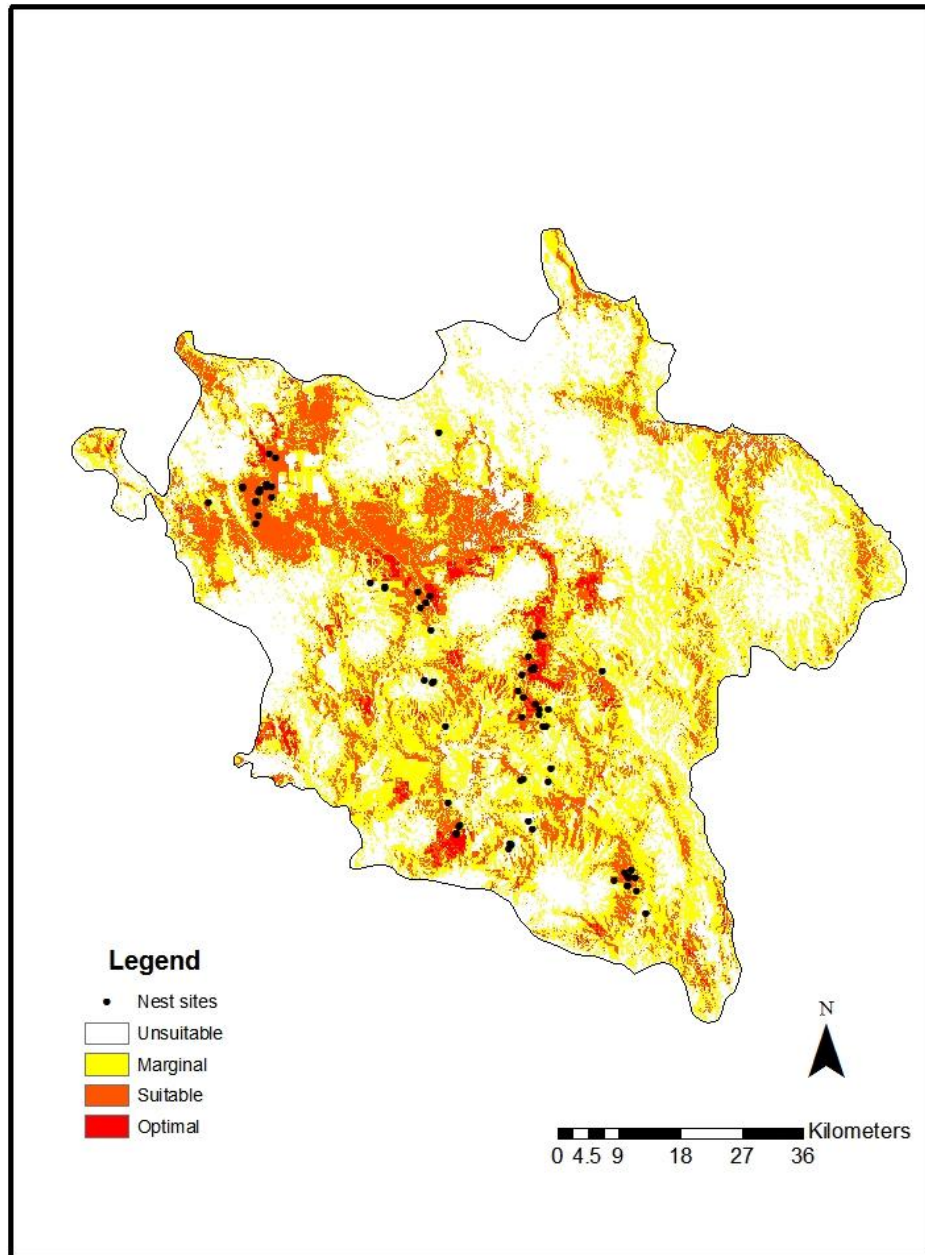


Figure 2. Geographic distribution of greater sage-grouse nesting habitat, Lassen County, California, 2007-2009. Habitat quality is represented by four probability classes ranking from unsuitable to optimal habitat: Unsuitable (representing 46% of the total study area), Marginal (35%), Suitable (17%), and Optimal (2%).

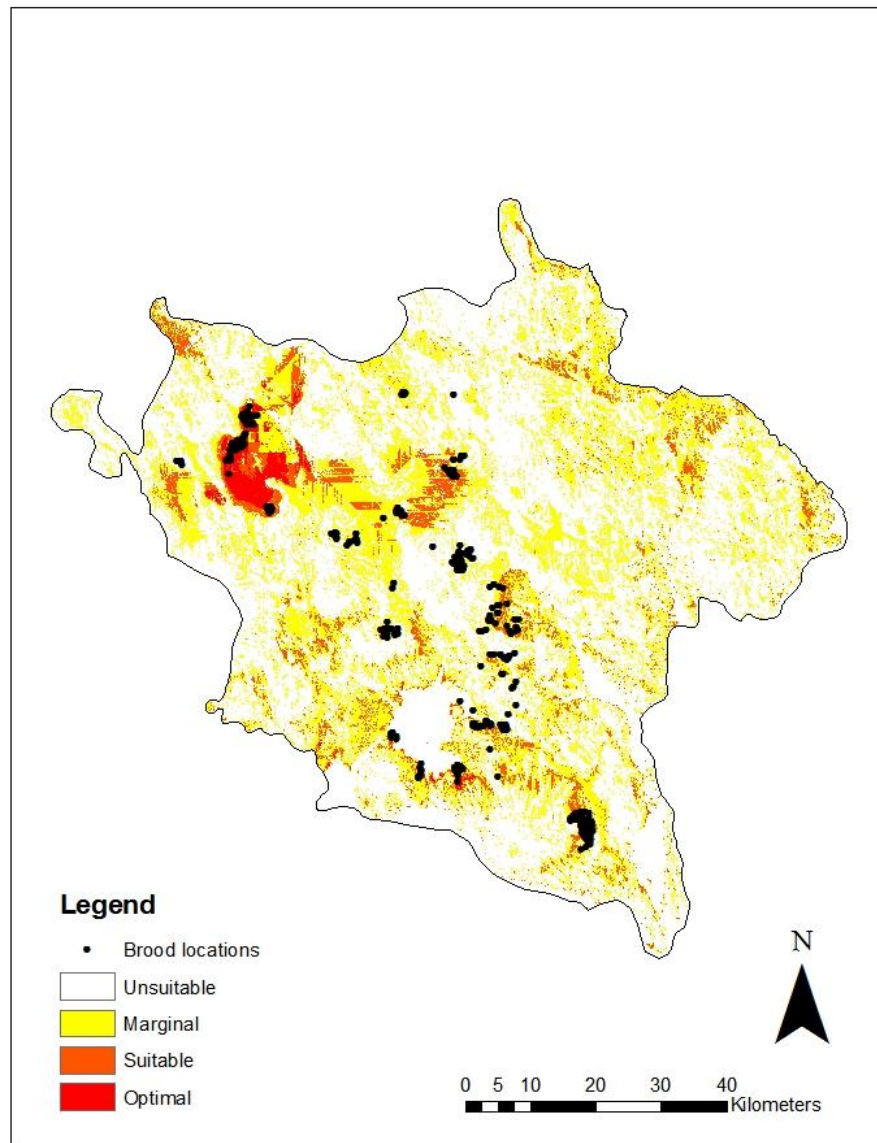


Figure 3. Geographic distribution of greater sage-grouse brood-rearing habitat, Lassen County, California, 2007-2009. Habitat quality is represented by four probability classes ranking from unsuitable to optimal habitat: Unsuitable (representing 67% of the total study area), Marginal (25%), Suitable (7%), and Optimal (1%).

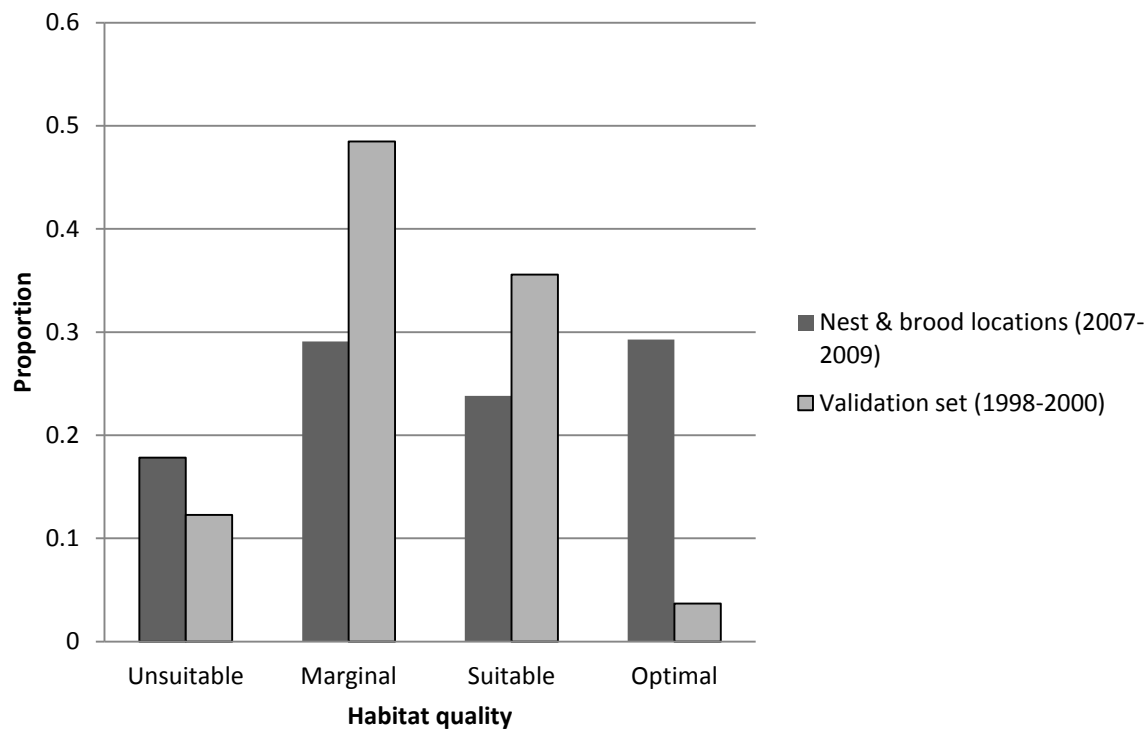


Figure 4. Comparison of habitat quality among an independent sample of greater sage-grouse nest and brood-rearing locations ( $n = 163$ ) used for model validation and nest and brood-rearing locations collected from 2007-2009 across the Lassen County study area for model development ( $n = 550$ ).

## CHAPTER 7. USE OF LEAST-COST PATH MODELING TO ASSESS LANDSCAPE CONNECTIVITY FOR GREATER SAGE-GROUSE IN NORTHEASTERN CALIFORNIA

**ABSTRACT** – I used a habitat suitability model developed from presence-only data to predict the annual geographic distribution of greater sage-grouse (*Centrocercus urophasianus*) in northeastern California. I then incorporated habitat suitability modeling into a least-cost path analysis to assess landscape connectivity for greater sage-grouse and to identify potential dispersal corridors that will facilitate movement of greater sage-grouse between adjacent leks within my study area. My results show that greater sage-grouse were closely associated with high quality habitat patches and that the geographic distribution of greater sage-grouse habitat was strongly affected by topographic complexity. An analysis of lek connectivity indicated that movement corridors between adjacent leks exceeded the dispersal capability of greater sage-grouse, resulting in dispersal routes too long to promote connectivity. Functional connectivity between adjacent leks was likely altered by invasive annual grass species, such as cheatgrass (*Bromus tectorum*) and medusahead rye (*Taeniatherum caput-medusa*), and juniper (*Juniperus occidentalis*) encroachment. The spatial structure of the greater sage-grouse population in northeastern California might not be conducive to long-term persistence. To ensure landscape connectivity, maintenance of large tracts of contiguous sagebrush (*Artemisia* spp.) will be important to sustain demographic and genetic exchange among greater sage-grouse populations occurring on the western periphery of the species geographic range.

**KEY WORDS:** *Centrocercus urophasianus*, dispersal, landscape connectivity, sage-grouse



Reports of local and range-wide declines in greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) populations have traditionally focused attention on factors influencing the distribution and abundance of sage-grouse (Braun 1998, Connelly et al. 2004). These declines are generally attributed to habitat loss and fragmentation, yet, little is known about the effects of habitat fragmentation on sage-grouse populations. Landscape connectivity, defined as the degree to which the landscape facilitates or impedes movements between resource patches (Taylor et al. 1993:571), is species-specific (Goodwin 2003) and is commonly characterized either as structural connectivity (i.e., the distance and spatial configuration of landscape features) or functional connectivity (i.e., the influence on animal movement and the behavior of dispersing individuals; Wiens et al. 1997, Chetkiewicz et al. 2006).

Organisms that have large home ranges and occur in low numbers, such as sage-grouse, are particularly sensitive to habitat fragmentation (Noss et al. 1996). Landscape-level landuse practices can have both direct and indirect effects on sage-grouse habitats and populations. Changes in landuse patterns that affect the ability of individuals to move between local subpopulations could ultimately result in the loss of sage-grouse over a broad geographic area. Seasonal movements and dispersal appear to be facilitated by the size, shape, and quality of habitat, presence of dispersal routes through the landscape, and the spatial configuration of habitat patches on the landscape (Fahrig and Merriam 1994). A lack of connectivity, due to processes such as habitat fragmentation, might lead to modifications of sage-grouse behavior, including changes in home range size and movement patterns

(Trombulak and Frissell 2000) and population structure (e.g., metapopulation dynamics; Anderson and Danielson 1997).

Numerous methods have been developed to quantify landscape connectivity and predict species movements. One of the most popular techniques is least-cost path analysis (Adriaensen et al. 2003), which evaluates landscape connectivity based on the “cost” or effort an individual has to exert to move between habitat(s) used by an organism in heterogeneous landscapes. Traditionally, least-cost path analysis has been used to identify sites that are potentially used as dispersal corridors (e.g., Epps et al. 2007) or alternatively, as a way of evaluating the most likely paths by which genes flow across the landscape (e.g., Storfer et al. 2007, Braunisch et al. 2010).

Exploring how sage-grouse move in response to the spatial structure of their environment is a critical step toward our understanding of the influence of landscape structure on dispersal and seasonal movement patterns. Previous studies have demonstrated the importance of preserving landscape connectivity and several authors have identified the need to understand the effects of habitat fragmentation and the distribution of habitat patches on gene flow to understand the requirements for population persistence. Because sage-grouse are often sensitive to anthropogenic habitat alteration and are facing local and range-wide declines, studies providing information on sustaining sage-grouse populations play a critical role in the species long-term persistence.

Sagebrush (*Artemisia* spp.) habitats are severely altered across much of northeastern California and the sagebrush community structure and ecological function are likely to continue to decline as a result of invasive species, juniper (*Juniperus occidentalis*)

encroachment, altered fire regimes, and climate change. The status of sage-grouse populations in northeastern California is likely dependent upon the spatial scale of interest. Spatial structure influences species viability at 2 scales: within subpopulations and between subpopulations (if more than one exists). Within a subpopulation, managers must consider the spatial arrangement and quality of habitat patches between individual home ranges, dispersal capabilities of the species, mortality risks and dispersal costs, and the annual and lifetime reproductive success of the species (Roloff and Haufler 1997). Between subpopulations, the size, shape, and relative contributions of each subpopulation have important consequences for population persistence and stability (Fahrig and Merriam 1994).

In northeastern California, loss and fragmentation of sagebrush habitats appear to have split sage-grouse populations into smaller, loosely connected lek complexes leading to isolation of local subpopulations that were historically part of a larger metapopulation. Leonard et al. (2000) speculated that at least 2,764 km<sup>2</sup> of habitat was required to sustain a sage-grouse population in southeastern Idaho, suggesting that sage-grouse are associated with landscape-level structure and stability. However, it is not known how spatial arrangement, composition, and change of habitat within home ranges influences sage-grouse populations. The questions facing managers include whether these subpopulations interchange, the contribution of individual subpopulations to overall population structure and stability, and the resiliency of the system to anthropogenic habitat deterioration and fragmentation (Roloff and Haufler 1997). To preserve landscape connectivity and, ultimately, the ability to support sage-grouse movement and gene flow, wildlife managers need to identify areas that provide the best remaining sagebrush habitat. Habitat modeling

would provide managers a practical tool to identify and prioritize sage-grouse habitats, guide conservation planning, and mitigate impacts of anthropogenic disturbance and other landscape alterations on sagebrush-steppe communities.

Several characteristics of sage-grouse ecology make sage-grouse an ideal focal species to model habitat use and delineate potential dispersal corridors. First, sage-grouse have large home ranges and are relatively sensitive to landscape fragmentation. Second, sage-grouse are sagebrush obligates and indicators of sagebrush-steppe quality and abundance across the landscape. Also, sage-grouse are considered an umbrella species (Rowland et al. 2006, Hanser and Knick 2011). Thus, conservation strategies will likely benefit other species dependent on sagebrush-steppe communities. Finally, as a consequence of their lek mating system, lek sites form natural networks and are well suited for least-cost path analysis. Thus, the objectives of this study were to: 1) identify and map the geographic distribution of sage-grouse habitat critical to the long-term persistence of sage-grouse in northeastern California; 2) assess the predictive capacity of the habitat suitability model using independent data; and 3) assess landscape connectivity, identify potential movement pathways, and model dispersal corridors between occupied leks by incorporating a habitat suitability map into least-cost path analysis.

## **STUDY AREA**

This study was conducted in a 597,116 ha region of sagebrush-steppe habitat that included portions of the Buffalo-Skedaddle Population Management Unit (PMU) in Lassen County, California, where sage-grouse populations occupy the western periphery of the species' geographic range. Elevation ranged from 1,400 to 2,400 m. The predominant sagebrush

types included Wyoming big sagebrush (*A. t. wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), and little sagebrush (*A. arbuscula*). Other common vegetation communities included annual grasslands and juniper-dominated woodlands. The study area was primarily composed of public lands (>60%) administered by the Bureau of Land Management. The primary landuse was domestic livestock grazing including both sheep and cattle. Other land uses included agricultural crops, primarily as irrigated alfalfa (*Medicago* spp.).

## **MATERIALS AND METHODS**

### **GIS Database and Environmental Variables**

Available spatial data derived from previous studies of sage-grouse habitat selection (e.g., Aldridge and Boyce 2007, Yost et al. 2008, Atamian et al. 2010, Carpenter et al. 2010, Doherty et al. 2008; 2010) and suitable for characterizing sage-grouse habitat quality, variables related to anthropogenic disturbance (e.g., Wisdom et al. 2011), and fire history were incorporated into a Geographical Information System (GIS) database (Table 1). Most spatial data used in this study are available for download on the SAGEMAP website (<http://sagemap.wr.usgs.gov>; USDI 2001). Regional spatial data were derived from the U.S. Census Bureau's TIGER data to describe roads and Landfire Existing Vegetation Map (LANDFIRE 2006). I used the topographic ruggedness index (TRI) developed by Riley et al. (1999) to quantify topographic heterogeneity across my study area. The TRI values were derived from 30 m U.S. Geological Survey (USGS) digital elevation models (DEMs) and reclassified as: level terrain surface (0-80 m), nearly level surface (81-116 m), slightly rugged surface (117-161 m), intermediately rugged surface (162-239 m), moderately rugged (240-497 m), highly rugged (498-958 m), and extremely rugged (959-5,000m) following

recommendations from Riley et al. (1999). In addition, to evaluate food resources, I used the DEM of the study area to calculate a Compound Topographic Index (CTI; Evans 2002). CTI was expressed as:

$$\text{Ln}[A_s/\tan\beta]$$

where  $A_s$  represents the catchment area per pixel calculated as (flow accumulation + 1) \* (pixel area  $\text{m}^2$ ) and  $\beta$  refers to the slope expressed in radians. The CTI models soil water content (Moore et al. 1991) as a function of both the slope and the upstream contributing area per unit width orthogonal to the flow direction and can be used as a substitute for vegetation productivity (Gessler et al. 1995). Low values of the CTI represent steep slopes or hills and areas with high CTI values represent places with gentle slopes, depressions, or plains.

Vegetation in LANDFIRE (2006) was classified from Landsat Thematic Mapper satellite imagery taken in 2002 ( $\pm 2$  yr) and consisted of 210 ecological systems of which 61 occurred in my study area. I developed 8 landcover classes from the original ecological systems mapped by LANDFIRE (2006): all sagebrush, agriculture (cultivated crops, pasture, and hayland), riparian, western juniper, grassland, other shrub and/or woodland types (e.g., landcover classes other than sagebrush or juniper and including woodland and forest landcover types), open water, and developed (urban and suburban areas). Pooling closely related landcover data increases the classification accuracy of the map (Beier et al. 2008). Because of the inaccuracies that can occur when classifying satellite imagery (Lillesand and Kiefer 2000, Gallant 2009), mapping different sagebrush species (Knick and Hanser 2011), and because little sagebrush comprised only 1% of the sagebrush landcover classes within

my study area, all sagebrush landcover classes were combined into 1 composite sagebrush landcover.

A 500-m buffer was generated around anthropogenic features (roads, transmission lines, communication towers) to characterize the effect of human disturbance on sage-grouse (i.e., avoidance area) or modifications to land use that result in the loss of sage-grouse habitat. Most of the currently available information on impacts of anthropogenic features on sage-grouse populations is focused on lek abandonment and changes in male lek attendance (e.g., Walker et al. 2007). However, to my knowledge, no published studies have examined sage-grouse habitat selection as they relate to behavioral avoidance of roads and various forms of infrastructure that might affect habitat use by sage-grouse. Because the behavioral response of sage-grouse is likely similar to that of other prairie grouse, and given the paucity of published data specific to sage-grouse, the extent of the buffer surrounding structures and roads was adapted from recent work on prairie grouse (e.g., Pitman et al. 2005, Pruett et al. 2009, Hagen et al. 2011).

Maps were prepared in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA) for use in the program MaxEnt version 3.3.3 (Phillips et al. 2006, Phillips and Dudík 2008). All GIS data layers were transformed ASCII format with matching cell size (30 m), extent, and projection system. All data were set to the projected coordinate system of North American Datum 1983, Universal Transverse Mercator Zone 10 North (NAD83, UTM Zone 10N).

### **MaxEnt and Habitat Suitability**

In a highly vagile species with landscape scale spatial requirements, such as sage-grouse, reliable information on species occurrence is often lacking. I used the program MaxEnt version 3.3.3 (Phillips et al. 2006, Phillips and Dudík 2008) to predict the annual geographic distribution of sage-grouse habitat in northeastern California. Maxent is a species distribution modeling approach that relies on presence-only data (Phillips et al. 2006), performs well with small data sets (Phillips and Dudík 2008, Wisz et al. 2008), is robust in the presence of spatial autocorrelation (Segurado et al. 2006), and frequently outperforms alternative niche-based modeling approaches (Elith et al. 2006, Wisz et al. 2008). MaxEnt functions on the concept of maximum entropy, in which the distribution of a given population will tend toward a uniform distribution after all ecologically important parameters are taken into account (Phillips et al. 2004). MaxEnt uses a maximum-likelihood method to measure correlation between environmental layers and presence point locations and generate a spatial probability distribution. This can be interpreted as a probability of occurrence or suitability for that species (Phillips et al. 2006). The probability of the model is displayed in terms of “gain,” which is equal to the log of the total number of grid cells minus log loss (the average negative log probability across the sample locations). As the model efficiency is incrementally improved, the overall gain increases until a minimum cumulative threshold is reached (point at which additional gain per iteration falls below a preset value) or a maximum number of iterations is reached. Once the probability distribution is assigned, it is possible to assess which habitat variables have the most predictive power. A detailed



statistical explanation of the MaxEnt program and modeling procedure is given by Phillips et al. (2006) and Elith et al. (2011).

A total of 7 environmental layers (landcover type, TRI, CTI, roads, communication towers, transmission lines, and fire history) were entered into a preliminary analysis of the annual geographic distribution on sage-grouse habitat. MaxEnt's jackknife test of variable importance was run for each variable to evaluate the relative strengths of each predictor variable. Because the presence of primary roads (e.g., interstate highways and paved roads) did not appear to influence habitat use I did not distinguish between road types (primary versus secondary unpaved roads) in further analysis. The final reduced model of sage-grouse habitat retained 4 environmental variables (see Results below). As recommended by Phillips and Dudík (2008), I ran the program MaxEnt under its default parameter settings to analyze all models. Models were parameterized with a background sample of 10,000 points, a default convergence threshold of  $10^{-5}$ , maximum iterations of 1,000, and the regularization parameter was set to the default value of 1. Model performance was evaluated by setting aside a subset of presence data for training and using the remaining observation records to test the resulting model. I made 15 random partitions of the occurrence localities. Each partition was created by randomly selecting 75% of the presence records ( $n = 1,784$ ) as training data and the remaining 25% of presence records ( $n = 594$ ) were reserved for testing the model. In addition, the full set of presence records were used to build the final reduced model to obtain the best estimate of the geographic distribution of sage-grouse habitat in northeastern California.

Model performance was evaluated using receiver operating characteristic (ROC) analysis, which characterizes the performance of a model at all possible thresholds by a single number; i.e., the area under the ROC curve (AUC) (Phillips et al. 2006). The advantage of ROC analysis is that the area under the ROC curve (AUC) provides a single measure of model performance (Phillips et al. 2006). The AUC is the probability that a randomly chosen presence site will be ranked above a randomly chosen absence site and measures the ability of the model to discriminate between sites where a species is present versus sites where the species is absent (Hanley and McNeil 1982). The value of the AUC typically ranges between 0.5, indicating that model performance is not better than random and a perfect ranking of 1.0 (Swets 1988, Elith et al. 2006). Models with values  $> 0.75$  indicate better model performance (Elith 2002) and indicate that predictions are sufficiently accurate to be used in conservation planning (Pearce and Ferrier 2000). Additionally, I also assessed the importance of the environmental predictors using a jackknife test of variable importance that quantified AUC and gain changes when excluding a variable (Phillips et al. 2006). The jackknife test of variable importance shows the training gain of each variable if the model was run in isolation and compares it to the training gain with all the variables (Phillips et al. 2006). This is useful to identify those predictor variables which contribute the most individually (Elith et al. 2010).

### **Model Validation**

I validated the predictive capacity of my spatial model with an independent data set from prior research in northeastern California (1998-2000), using an independent sample of 1,426 sage-grouse locations (Popham 2000).

### **Least-Cost Path Analysis**

Lek locations are useful for spatial modeling of landscape connectivity (e.g., Knick and Hanser 2011), and numerous studies have used lek-based landscape analyses to study the spatial ecology of prairie grouse (Merrill et al. 1999, Niemuth 2000, Woodward et al. 2001), including sage-grouse (Knick and Hanser 2011). I assessed connectivity of the current distribution of sage-grouse in northeastern California and examined how habitat suitability influenced seasonal movement patterns and potential dispersal corridors. I restricted my analysis of connectivity to known, occupied leks ( $n = 13$ ) surveyed from 2007-2009 across my study area and assumed the distribution of lek sites represented the spatial structure of sage-grouse populations in northeastern California.

Because uncertainty in a model makes continuous habitat suitability values too accurate to reflect actual habitat conditions (Hirzel et al. 2006), I reclassified habitat suitability into 4 probability classes ranking from unsuitable to optimal habitat: Unsuitable (0–25%), Marginal (26–50%), Suitable (51–75%), and Optimal (76–100%). The reclassified annual habitat suitability map was then incorporated into least-cost path analysis prepared in Linkage Mapper 0.7 BETA (McRae and Kavenagh 2011). The primary input of a least-cost model is a resistance surface, which accounts for variation in the ease of movement or “cost” of travel within each grid cell based on an organisms habitat requirements or different landuse types. The output layer is a cost raster in which the value for each cell represents the lowest possible cumulative cost of moving to that cell from the nearest source cell. Most least-cost modeling relies on expert opinion to parameterize the model and develop the cost surface (Beier et al. 2008). However, habitat suitability models

provide a data-based alternative for achieving this (Chetkiewicz and Boyce 2009). Other studies have demonstrated that the integration of habitat suitability models with least-cost path models provide a rigorous, empirically-based method to reflect species-specific variation in resource selection (Manly et al. 2002, Noss and Daly 2006, Chetkiewicz and Boyce 2009). In accordance with Beier et al. (2008), I generated a cost distance raster for the study area proportionate to the inverse of the predicted probabilities calculated from the habitat suitability model (i.e., low resistance reflected high habitat quality and high resistance reflected low habitat quality).

For each least-cost path, Linkage Mapper provided the Euclidean distance between adjacent leks, the total length of the path, and the total cost of the path. Cost distance is considered a more accurate measure than Euclidean distance because it takes into account the landscape configuration and structure from a species point of view (Richard and Armstrong 2010). Accordingly, I also calculated cost-weighted distances and developed a least-cost path map (i.e., the potential dispersal route which the least resistance is accumulated) from known, occupied leks to assess landscape connectivity, identify potential movement pathways, and model dispersal corridors between occupied leks in northeastern California.

## **RESULTS**

### **MaxEnt and Habitat Suitability**

The annual habitat suitability map consisted of sage-grouse records collected during 2007 through 2009, representing 3,071 locations (Figure 1). Maxent relies on an unbiased sample of presence records cleaned for duplicates (Elith et al. 2010, Newbold 2010), however, during the course of my study some radiomarked sage-grouse were observed together in

mixed flocks. To avoid the possibility of dependency in the sage-grouse location data, duplicate locations ( $n = 628$ ) were not retained. In addition, radiomarked sage-grouse locations observed outside my study area ( $n = 2$ ) were omitted from analysis. The final data set contained 2,441 locations for building the habitat suitability model.

Model performance, based on 7 predictor variables, which included landcover type, TRI, CTI, fire (prescribed and natural), roads, transmission lines, and communication towers, had a high goodness of fit (average test AUC for the replicate runs = 0.788, SD = 0.008). Exclusion of anthropogenic features (roads, transmission lines, communication towers), which did not appear to influence habitat use (contributing <1% to the model) did not improve model fit (average test AUC for the replicate runs = 0.783, SD = 0.010). Although model performance remained largely unchanged when excluding anthropogenic features, I considered the reduced 4-variable model to be the most parsimonious model and, therefore, the best-approximating model supported by the data. The regularized training gain for the final reduced model using the full set of presence records was 0.783.

Models based on replicate runs and using the full set of occurrence locations produced similar predictions for the geographic distribution of sage-grouse habitat in northeastern California. Based on the predictive contribution of each variable, TRI was the most important environmental variable in the reduced 4-variable MaxEnt model of sage-grouse habitat use within my study area (75.8% contribution), followed by landcover type (16.8% contribution). Fire and CTI were relatively weak predictors, contributing only 4.4% and 3.1% to the model, respectively.

The results of the jackknife test of variable importance indicated the environmental variable with highest gain when used in isolation was TRI. Similarly, the environmental variable that decreases the gain the most when it is omitted was TRI, which therefore appears to have the most information that is not present in the other variables.

My findings suggest that the most suitable sage-grouse habitat was characterized by flat, level terrain associated with sagebrush cover. My final model of the geographic distribution of sage-grouse habitat in northeastern California indicated that approximately 7% of the study area was classified in the Optimal habitat suitability class, suggesting optimal sage-grouse habitat represents a small proportion of the overall landscape within my study area. Further, my results indicate that the majority of the study area (60%) was classified as Unsuitable sage-grouse habitat. Although suitable sage-grouse habitat was limited across the study area, a relatively high proportion of sage-grouse (~60%) occupied habitat patches classified as Optimal (36%) or Suitable (24%) habitat.

### **Model Validation**

My habitat suitability model classified approximately 45% of independent sage-grouse locations into Suitable or Optimal habitats. I assumed that sage-grouse would be unlikely to occur in Marginal or Unsuitable habitats, however, 55% of the independent sage-grouse locations used for model validation occurred in those two probability classes. Because a higher proportion of the independent sample occurred in Marginal or Unsuitable habitat classes, I determined the proportion of independent sage-grouse locations used for model validation that occurred in each of the 4 probability classes and compared the proportions to the frequency of occurrence of sage-grouse locations used for model development. The

proportion of sage-grouse locations were similar for 3 probability classes (Unsuitable, Marginal, Suitable), suggesting that my model correctly identified sage-grouse habitat critical to the long-term persistence of sage-grouse in northeastern California (Figure 2). Only the Optimal habitat class had a higher proportion of sage-grouse locations for the data set used for model development (36%) compared to independent samples used for model validation (15%).

### **Least-Cost Path Analysis**

The least-cost path analysis map for sage-grouse illustrates patterns of movement potential for sage-grouse in northeastern California (Figure 3). The least-cost path analysis identified 29 linkages between the 13 known, occupied lek sites in northeastern California. On average each lek site had 4 connections (range = 2–7 connections). Least-cost paths between leks deviated from the straight-line Euclidean distance between adjacent sage-grouse lek sites (Figure 3). The Euclidean distance of linkages between leks ranged from 4.9 km up to 38.5 km (mean = 19.5 km  $\pm$  9.1 (SD)). Comparatively the mean (non-weighted) least-cost path was 24.6 km  $\pm$  12.2 (SD) and the mean cost-weighted distance between lek sites was 43 km  $\pm$  21.9 (SD). Knick and Hanser (2011) speculated that leks separated by distances >13-18 km could be isolated due to decreased probability of dispersal from neighboring leks. The number of linkages between lek sites is reduced to 7 if I restricted linkages to those with a (non-weighted) least-cost path of 13 km or less, and only 2 had a cost-weighted distance  $\leq$ 13 km (Figure 4).

## DISCUSSION

I used a habitat suitability model developed from presence-only data to predict the annual geographic distribution of sage-grouse in northeastern California. I then incorporated habitat suitability modeling into a least-cost path analysis to assess landscape connectivity for sage-grouse in northeastern California and identify potential dispersal corridors that will facilitate the movement of sage-grouse between leks. Although GIS-based models have been used elsewhere to examine dispersal and landscape connectivity in heterogeneous landscapes and to identify wildlife corridors, to my knowledge, there are no current data on the geographic distribution of sage-grouse habitat in my study area and my analysis provides the first description of potential routes of dispersal for sage-grouse in northeastern California.

Sage-grouse were closely associated with high-quality habitat patches. My results showed that the geographic distribution of sage-grouse habitat was strongly affected by topographic heterogeneity. Topographic complexity likely affected sage-grouse habitat use by determining landcover type or by influencing the thermal environment of the species. Larsson et al. (*in press*) also speculated that the role of vegetative cover in habitat selection was important for thermal regulation in the lesser prairie-chicken (*Tympanuchus pallidicinctus*). Landcover type was another important component of the annual habitat suitability model, emphasizing the value of relatively large tracts of contiguous sagebrush. Maintenance of these landscape conditions and measures to mitigate putative barriers due to habitat loss and fragmentation will be important to sustain demographic and genetic exchange among sage-grouse populations occurring on the western periphery of the species' geographic range.



Recent research has shown sage-grouse are sensitive to habitat fragmentation caused by anthropogenic features (Braun 1986, Lyon and Anderson 2003, Connelly et al. 2004, Aldridge 2005, Johnson et al. 2011, Knick and Hanser 2011, Wisdom et al. 2011) and human activity can affect sage-grouse habitat selection (Aldridge and Boyce 2007, Doherty et al. 2010). My results suggest that anthropogenic features such as roads, transmission lines, and communication towers were not be a reliable metric to measure the impacts of anthropogenic disturbance on sage-grouse in this landscape. While anthropogenic features did not appear to influence habitat use and were not included in my final model of sage-grouse habitat in northeastern California, these features were not pervasive across my study area and limited my ability to effectively model the impacts of these features on habitat use. While sage-grouse in my study did not appear to avoid roads, data from several studies indicate that prairie grouse, including sage-grouse, avoid or nest at reduced rates in areas near roads (Lyon and Anderson 2003, Robel et al. 2004, Pitman et al. 2005, Aldridge et al. 2012). Moreover, the noise and disturbance associated with roads can alter nest site selection, habitat use, and lek persistence (Lyon and Anderson 2003, Holloran et al. 2010, Hagen et al. 2011). Direct mortality associated with vehicle collisions can occur but is a relatively small percentage of overall mortality in sage-grouse (Aldridge and Boyce 2007). How sage-grouse respond to roads likely depends on the amount of available suitable habitat adjacent to roads, road configuration, and the road type (Frair et al. 2008). Thus, sage-grouse response to anthropogenic disturbance is likely different where those features are more pervasive within the occupied range of the species.

Even though transmission lines and cellular towers were largely absent in my study area, these anthropogenic features were strongly associated with sage-grouse extirpation, where these features were common in occupied sage-grouse range (Wisdom et al. 2011). The behavioral response of sage-grouse is likely similar to that of other prairie grouse species, such as the lesser prairie-chicken, and research has suggested that both species will avoid transmission lines during the breeding season (Braun 1998, Hagen 2003, Pitman et al. 2005). In addition, collisions with overhead transmission lines can cause direct mortality to sage-grouse (Beck et al. 2006, Aldridge and Boyce 2007), further limiting sage-grouse populations. Construction of transmission lines also provides perches for various raptor species, which could potentially increase the mortality rate of sage-grouse (Connelly et al. 2000). What is more, the presence of a transmission lines might fragment sage-grouse habitats even if raptors are not present (Hagen et al. 2011), potentially causing sage-grouse avoidance of otherwise suitable sage-grouse habitat and thus further restrict the sage-grouse range. Wisdom et al. (2011) speculated that collisions with cellular towers also cause sage-grouse injury and mortality. In addition, sage-grouse avoidance of vertical structures likely influences sage-grouse movements and habitat use, however, no research has investigated these issues. Whether cellular towers reflects sensitivity to visual obstruction or some other form of disturbance associated with intensive human development (e.g., interstate highways, urban development), or is a response to other detrimental factors, remains unknown (Wisdom et al. 2011). However, recent studies emphasize the importance of taking behavioral avoidance into consideration when assessing anthropogenic impacts on grouse habitat (Pitman et al. 2005, Hagen et al. 2011).

Fragmentation of sagebrush-steppe ecosystems is not limited to human-induced alterations, and over 46% of the landscape in my study area had a high percentage of exotic annual grasses such as cheatgrass (*Bromus tectorum*) and medusahead rye (*Taeniatherum caput-medusa*) or juniper encroachment (Armentrout and Hall 2005). Moreover, approximately 19% of the sagebrush community within the study area has crossed a threshold to being dominated by annual grasslands or western juniper (Armentrout and Hall 2005), suggesting sagebrush availability was low across my study area. Habitat fragmentation and conversion of sagebrush-steppe communities could alter the movement of individuals between local subpopulations, playing a role in shaping the population structure of sage-grouse in northeastern California. Despite being sagebrush obligates, sage-grouse have persisted across fragmented landscapes. Through habitat suitability modeling and least-cost path analysis, I have demonstrated that habitat degradation and fragmentation might limit dispersal of sage-grouse. Without efforts to halt on-going habitat modifications or restoration of unsuitable habitat that could potentially impede movements, it is possible that isolation among this population will continue or increase, likely with negative consequences for the persistence of sage-grouse in northeastern California.

Understanding how individuals disperse through heterogeneous landscapes is essential for predicting the impact that landscape alterations (e.g., habitat fragmentation) have on populations (Fahrig 2007), however, information for dispersal patterns is lacking for sage-grouse. In Colorado, juvenile females ( $n = 12$ ) moved an average 8.8 km and males ( $n = 12$ ) moved 7.4 km (Dunn and Braun 1985). These distances are greater than natal dispersal distances reported by Thompson (2012), where the median dispersal distance for juvenile

sage-grouse was  $3.84 \pm 1.26$  km and  $2.68 \pm 0.30$  km for males and females, respectively. Direct observations of dispersal from radio telemetry data or indirect measures of gene flow were not incorporated in my model. However, in a range-wide analysis assessing the spatial connectivity of sage-grouse lek sites, Knick and Hanser (2011) estimated the mean nearest-neighbor lek distance was  $5.2 \text{ km} \pm 0.05 \text{ km}$  (SE,  $n = 4,838$ ) and suggested that leks separated by distances  $>13\text{-}18$  km could be isolated due to decreased probability of dispersal from neighboring leks. As a consequence, some of the delineated dispersal routes between adjacent leks identified by my least-cost path model are more limited with regard to their actual use by sage-grouse than others. In cases in which the movement corridor between adjacent leks exceeds the estimated dispersal ability of sage-grouse, the linkage design probably would not provide meaningful connectivity for dispersing sage-grouse (Beier et al. 2008). In my study, the lengths of potential dispersal corridors often exceeded the dispersal capability of sage-grouse, resulting in corridors too long to promote connectivity (e.g., mean Euclidean distance = 19.5 km; mean cost-weight distance = 43.0 km). An analysis of habitat connectivity for sage-grouse in the Columbia Plateau Ecoregion of eastern Washington also found the cost-weight distances were at the upper end of recorded dispersal distances for sage-grouse (range = 91.3 to 123.5 km, mean =  $103.3 \pm 17.4$  (SD)), suggesting movement between occupied habitat patches could be challenging (WHCWG 2012). Knick and Hanser (2011) speculated that sage-grouse populations will decrease with the loss of larger leks, highly connected leks, or leks that serve as key stepping stones by connecting core regions. Sage-grouse populations occurring on the periphery of the range-wide distribution, such as those in northeastern California, likely depend on dispersal from connecting leks (Knick and

Hanser 2011). Thus, maintaining connectivity with larger populations from the core of the occupied range in Nevada would likely help reverse and/or stabilize the process of range reduction that have resulted in population declines in northeastern California.

While the landscape in northeastern California is well-connected for sage-grouse based on Euclidean distance, the estimated landscape resistance suggests functional connectivity between adjacent leks is dramatically altered. Linkages between leks were limited, with most leks linked to only 4 other lek sites. In northeastern California, leks separated by marginal or unsuitable habitat that restricts connectivity elevates the risk of extirpation. The linkage patterns I modeled for sage-grouse suggest that the spatial structure of populations in northeastern California is not conducive to long-term persistence. At least 4 of the leks I identified were isolated (<4 lek connections), presumably with a very low likelihood of successful immigration or recolonization if extirpation occurred. These disconnected leks likely have a reduced probability of long-term persistence, assuming they support relatively small populations. Of the 13 known, occupied lek sites within my study area, 2 of the smallest, peripheral leks (i.e., the mean number of males attending these leks was 2 and 4 males, respectively) were inactive by 2008 and remained abandoned through 2009. Thus, conservation efforts in northeastern California should focus on maintaining population connectivity by identifying and preserving larger, more highly connected leks that are associated with lower levels of habitat fragmentation and/or anthropogenic disturbance.

Whether or not a landscape is fragmented depends on how species are able to use and move through a heterogeneous landscape effectively. In contrast to ground-dispersing species, more vagile organisms, such as sage-grouse, are less restricted by physical barriers.

Radio telemetry data were insufficient to document natal dispersal within my study area, however, 1 yearling female that was radiomarked as a chick in 2007 was monitored during the 2008 breeding season and initiated a nest within 9.87 km of the natal nest site but was not successful (Davis, unpublished data). A telemetry study in the same area demonstrated diurnal space use and seasonal movement patterns exceeded estimates of home range size reported in previous investigations and extensive unidirectional movements (e.g., up to 53.3 km) between seasonal ranges were not uncommon (Chapter 3). Similarly, in Washington, females routinely moved 13 km between leks sites during a single breeding season and in at least 2 cases, females moved 27 km and 34 km between nest locations within the same nesting season (Schroeder and Robb 2003). These distances are considerably greater than what has been recorded for dispersing sage-grouse in Colorado (Dunn and Braun 1985, Thompson 2012).

Dispersal appears to be an important demographic factor in maintaining genetically viable grouse populations (Caizergues et al. 2003a, b; Johnson et al. 2004, Höglund et al. 2007, Segelbacher et al. 2008). 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 impact the fitness and viability of remaining grouse populations (Bouzat et al. 1998a, b; Segelbacher and Storch 2002, Caizergues et al. 2003b, Segelbacher et al. 2003, Johnson et al. 2004, Höglund et al. 2007, Bech et al. 2009). Areas that are not connected by direct movements might still experience high rate 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 up to 316 km for sage-grouse in northern Montana. Furthermore, Bush et al. (2011) suggested that patches of habitat in northern Montana were large enough for leks to form a stepping stone network across that landscape that would allow dispersal, in spite of extensive fragmentation. 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.

Although sage-grouse are declining and have lost a significant portion of their range in northeastern California, sage-grouse in my study exhibited high genetic diversity (Chapter 4). However, the long-term persistence of this population is limited by the availability of suitable habitat. Whether or not sage-grouse dispersal capabilities are adequate to ensure species persistence in the current landscape will depend on the rate of landscape change relative to the rate at which sage-grouse can adapt in response to that change. Often, changes to the landscape structure occur too quickly for evolution of animal movement behavior to effectively respond, limiting the species' ability to evolve in response to landscape change (Remeš 2000, Thomas 2000, Pulido 2007). For example, simulation studies indicate that the more fragmented the habitat is, the longer it takes for adaptations in animal movement parameters to evolve (Paradis 1998). Further, fragmentation causes a reduction in the exchange of organisms between habitat patches, which eventually leads to lower colonization

probabilities and gene flow rates and, ultimately, isolation for some species (Hanski and Gilpin 1997). This difference stems from the effects of reduced mean patch size and decreased connectivity in the landscape (i.e., the rate of successful dispersal; Venier and Fahrig 1996). The results from my study suggest suitable sagebrush-steppe habitat will likely continue to decline in northeastern California and consequently, sage-grouse will find proportionally less suitable habitat over time. The decline in sage-grouse habitat I observed is similar to other findings within the geographic range of sage-grouse (Leonard et al. 2000, Connelly et al. 2004, Shepherd et al. 2011). Ultimately, the ongoing declines of sagebrush-steppe communities will likely affect productivity, survival, and the long-term persistence of sage-grouse populations in northeastern California.

## **MANAGEMENT IMPLICATIONS**

Landscape features have important consequences for movement patterns and it is increasingly clear that the conservation of remaining sage-grouse populations in northeastern California requires conservation strategies that not only maintain sage-grouse habitat, but also support landscape connectivity. Understanding how sage-grouse respond to landscape heterogeneity and landscape structure is critical if we are to succeed in mitigating both historical and recent habitat loss and predict the potential effects of future landuse practices on sage-grouse populations. Least-cost path analysis provides an important tool for improving our understanding of the movement of sage-grouse across heterogeneous landscapes, which can be used to guide landscape and species management. While my results provided information for local wildlife managers, similar efforts are needed throughout the extant range of sage-grouse to guide conservation planning across the



geographic range of the species. Although integrating habitat suitability models with least-cost path analysis addressed functional connectivity within my study area, there is no guarantee that linkages between leks will ensure population persistence (Taylor et al. 2006). Nor does it guarantee that potential routes for dispersal will maintain or restore connectivity through landscapes threatened by habitat loss and fragmentation. To offset the effects of habitat fragmentation and maintain landscape connectivity across the geographic distribution of sage-grouse, the challenge will be linking lek-based, landscape-scale analyses with regional conservation planning to identify the contribution of dispersal corridors to population persistence. How landscape composition and configuration influences patterns of dispersal and, ultimately, gene flow has important implications for explaining the distribution of sage-grouse and is essential for the viability of the species. To ensure landscape connectivity and the ability to support sage-grouse movement and gene flow in northeastern California, conservation efforts should concentrate on maintaining large tracts of contiguous sagebrush habitat and enhancing the quality and connectivity of those patches (e.g., see Aldridge et al. 2008).

Although habitats used during the breeding season differ from non-breeding habitat, my habitat suitability model predicted annual habitat selection and did not take seasonality into account. In addition to this short-coming, Malczewski (2000) warned model insufficiency can affect reliability of a linkage design to the extent it does not encompass all the factors that contribute to resistance. For example, a recent study of sage-grouse indicated males avoid leks with experimentally-elevated noise (Blickley et al. 2012). Fences might also contribute to resistance as both fence collisions and mortality have been documented in

prairie grouse (Patten et al. 2005, Wolfe et al. 2007), including sage-grouse (Scott 1942, Flake et al. 2010, Stevens et al. 2012). My model did not include fences, wind power, and other factors for which I lacked spatial data. In addition, factors that influence landscape resistance, such as anthropogenic noise and climate change, were not considered in my model.

Global climate change could also pose a significant threat to sage-grouse through a variety of mechanisms. In particular, global climate change models predict more variable and extreme weather events, higher temperatures, drier summer soil conditions, and wetter winters (Miller et al. 2011). Though research demonstrating how sage-grouse will respond to these regional anthropogenic-driven climatic shifts is lacking, models predict climate change and associated consequences will likely interact, and potentially magnify, limiting factors such as disease (Walker and Naugle 2011) and habitat loss and degradation, which are already impacting sage-grouse across the species geographic distribution (USDI 2010, 75FR:13910-14014). Thus, it is possible that the environmental variables I used to model the geographic distribution of sage-grouse habitat in northeastern California were insufficient to describe habitat suitability or are better explained by covariates not included in my analysis. Despite these limitations, my model provides the first conceptual framework for prioritizing sage-grouse habitat in northeastern California, contributes to our understanding of the factors that determine sage-grouse distribution over large geographic extents, and currently represents the only dataset to base management decisions regarding landscape connectivity in northeastern California. Future research should consider sage-grouse ecology during different times in the life history of the species or during different seasons. To ensure long-

term population persistence, conservation strategies should focus on conserving existing habitats, retaining the spatial structure of leks and/or habitat patches, and restoring large tracts of contiguous sagebrush habitat within the estimated dispersal ability of the species.

## LITERATURE CITED

- Adriaensen, F., J. P. Chardon, G. Deblust, E. Swinnen, S. Villalba, H. Gulinck, and E. Matthysen. 2003. The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning* 64:233–247.
- Aldridge, C. L. 2005. Identifying habitats for persistence of greater sage-grouse (*Centrocercus urophasianus*). Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Aldridge, C. L., and M. S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. *Ecological Applications* 17:508–526.
- Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range-wide patterns of greater sage-grouse persistence. *Diversity and Distributions* 14:983–994.
- Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for Gunnison sage-grouse: a spatially explicit hierarchical approach. *Journal of Wildlife Management* 76:391–406.
- Anderson, G.S., and B. J. Danielson. 1997. The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. *Landscape Ecology* 12:261–271.
- Armentrout, D. J., and F. Hall. 2005. Conservation strategy for sage-grouse (*Centrocercus urophasianus*) and sagebrush ecosystems within the Buffalo-Skedaddle population management unit. Bureau of Land Management, Eagle Lake Field Office, Susanville, California, USA.
- Atamian, M. T., J. S. Sedinger, J. S. Heaton, E. J. Blomberg. 2010. Landscape-level assessment of brood-rearing habitat for greater sage-grouse in Nevada. *Journal of Wildlife Management* 74:1533–1543.

- Bech, N., J. Boissier, S. Drovetski, and C. Novoa. 2009. Population genetic structure of rock ptarmigan in the 'sky islands' of French Pyrenees: implications for conservation. *Animal Conservation* 12:138-145.
- Beck, J. L., K. P. Reese, J. W. Connelly, and M. B. Lucia. 2006. Movements and survival of juvenile greater sage-grouse in southeastern Idaho. *Wildlife Society Bulletin* 34:107-1078.
- Beier, P., D. R. Majka, and W. D. Spencer. 2008. Forks in the road: choices in procedures for designing wildland linkages. *Conservation Biology* 22:836-851.
- Blickley, J. L., D. Blackwood, and G. L. Patricelli. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse leks. *Conservation Biology* 26:461-471.
- Bohonak, A. J. 1999. Dispersal, gene flow, and population structure. *Quarterly Review of Biology* 74:21-45.
- Bouzat, J. L., H. H. Cheng, H. A. Lewin, R. I. Westemeier, J. D. Brawn, and K. N. Paige. 1998a. Genetic evaluation of a demographic bottleneck in the greater prairie-chicken. *Conservation Biology* 12:836-849.
- Bouzat, J. L., H. A. Lewin, and K. N. Paige. 1998b. The ghost of genetic diversity past: historical DNA analysis of the greater prairie-chicken. *American Naturalist* 152:1-6.
- Braun, C. E. 1986. Changes in sage grouse lek counts with advent of surface coal mining. *Proceedings of Issues and Techniques in the Management of Impacted Western Wildlife* 2:227-231.
- Braun, C. E. 1998. Sage grouse declines in western North America: what are the problems? *Proceedings of the Western Association State Fish and Game Wildlife Agencies* 78:139-156.
- Braunisch, V., G. Segelbacher, and A. H. Hirzel. 2010. Modelling functional landscape connectivity from genetic population structure: a new spatially explicit approach. *Molecular Ecology* 19:3664-3678.
- Bush, K. L. 2009. Genetic diversity and paternity analysis of endangered Canadian greater sage-grouse (*Centrocercus urophasianus*). Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Bush, K. L., C. K. Dyte, B. J. Moynahan, C. L. Aldridge, H. S. Sauls, A. M. Battazzo, B. L. Walker, K. E. Doherty, J. Tack, J. Carlson, D. Eslinger, J. Nicholson, M. S. Boyce, D. E. Naugle, C. A. Paszkowski, and D. W. Coltman. 2011. Population structure and

- genetic diversity of greater sage-grouse (*Centrocercus urophasianus*) in fragmented landscapes at the northern edge of their range. *Conservation Genetics* 12:527-542.
- Caizergues, A., A. Bernard-Laurent, J. F. Brenot, L. Ellison, and J. -Y. Rasplus. 2003a. Population genetic structure of rock ptarmigan *Lagopus mutus* in northern and western Europe. *Molecular Ecology* 12:2267-2274.
- Caizergues, A., O. Rätti, P. Helle, L. Rotelli, L. Ellison, and J.-Y. Rasplus. 2003b. Population genetic structure of male black grouse (*Tetrao tetrix* L.) in fragmented vs. continuous landscapes. *Molecular Ecology* 12:2297-2305.
- Carpenter, J. E., C. L. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. *Journal of Wildlife Management* 74:1806-1814.
- Chetkiewicz, C-L. B., and M. S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. *Journal of Applied Ecology* 46:1036-1047.
- Chetkiewicz, C-L. B., C. C. St. Clair, and M. S. Boyce. 2006. Corridors for conservation: integrating pattern and process. *Annual Reviews of Ecology and Evolutionary Systems* 37:317-342.
- Connelly, J. W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. *Wildlife Biology* 6:227-232.
- Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Unpublished report. Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.
- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2008. Greater sage-grouse winter habitat selection and energy development. *Journal of Wildlife Management* 72:187-195.
- Doherty, K. E., D. E. Naugle, and B. L. Walker. 2010. Greater sage-grouse nesting habitat: the importance of managing at multiple scales. *Journal of Wildlife Management* 74:1544-1553.
- Dunn, P. O., and C. E. Braun. 1985. Natal dispersal and lek fidelity of sage grouse. *Auk* 102:621-627.
- Elith, J. 2002. Quantitative methods for modeling species habitat: comparative performance and application to Australian plants. Pages 39-58 in S. Ferson and M. Burgman, editors. *Quantitative methods for conservation biology*, Springer-Verlag, New York, USA.

- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151.
- Elith, J., M. Kearney, and S. J. Phillips. 2010. The art of modeling range-shifting species. *Methods in Ecology and Evolution* 1:330–342.
- Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17:43–57.
- Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torre, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. *Journal of Applied Ecology* 44:714–724.
- Evans, J. 2002. Compound topographic index, AML script. ESRI Support Center Downloads. ESRI, Redlands, California, USA.  
<<http://arcscripts.esri.com/details.asp?dbid=11863>>.
- Fahrig, L. 2007. Non-optimal animal movement in human altered landscapes. *Functional Ecology* 21:1003–1015.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* 8:50–59.
- Flake, L. D., J. W. Connelly, T. R. Kirschenmann, and A. J. Lindbloom. 2010. Grouse of plains and mountains: the South Dakota story. South Dakota Department of Game, Fish, and Parks, Pierre, South Dakota, USA.
- Frair, J. L., E. H. Merrill, H. L. Beyer, and J. M. Morales. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. *Journal of Applied Ecology* 45:1504–1513.
- Gallant, A. L. 2009. What you should know about land-cover data. *Journal of Wildlife Management* 73:796–805.
- Gessler, P. E., I. D. Moore, N. J. McKenzie, and P. J. Ryan. 1995. Soil-landscape modeling and spatial prediction of soil attributes. *International Journal of GIS* 9:421–432.
- Goodwin, B. J. 2003. Is landscape connectivity a dependent or independent variable? *Landscape Ecology* 18:687–699.
- Hagen, C. A. 2003. A demographic analysis of lesser prairie-chicken populations in

- southwestern Kansas: survival, population viability, and habitat use. Dissertation. Kansas State University, Manhattan, Kansas, USA.
- Hagen, C. A., J. C. Pitman, T. M. Loughin, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2011. Impacts of anthropogenic features on habitat use by Lesser Prairie-Chickens. Pages 63-76 in B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. Studies In Avian Biology (no. 39), University of California Press, Berkeley, California, USA.
- Hanley, J. A., and B. J. McNeil. 1982. The meaning and use of the area under a Receiver Operating Characteristic (ROC) curve. *Radiology* 143:29-36.
- Hanser, S. E., and S. T. Knick. 2011. Greater sage-grouse as an umbrella species for shrubland passerine birds : a multi-scale assessment. Pages 475-487 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Hanski, I., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California, USA.
- Hirzel A. H., G. Le Lay, and V. Helfer. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199:142–152.
- Holloran, M. J., R. C. Kaiser, and W. A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. *Journal of Wildlife Management* 74:65-72.
- Höglund, J., J. K. Larsson, H. A. H. Jansman, and G. Segelbacher. 2007. Genetic variability in European black grouse (*Tetrao tetrix*). *Conservation Genetics* 8:239-243.
- Johnson, D. H., M. J. Holloran, J. W. Connelly, S. E. Hanser, C. L. Amundson, and S. T. Knick. 2011. Influences of environmental and anthropogenic features on greater sage-grouse populations, 1997-2007. Pages 407-450 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Johnson, J. A., M. R. Bellinger, J. E. Toepfer, and P. Dunn 2004. Temporal changes in allele frequencies and low effective population size in greater prairie-chickens. *Molecular Ecology* 13:2617-2630.
- Knick, S. T., and S. E. Hanser. 2011. Connecting patterns and process in greater sage-grouse populations and sagebrush landscapes. Pages 383-406 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape

- species and its habitats. *Studies in Avian Biology* (vol. 38), University of California Press, Berkeley, California, USA.
- LANDFIRE. 2006. National existing vegetation type layer. USDI Geological Survey. <<http://gisdata.usgs.net/website/landfire/>>. Accessed 12 October 2011.
- Larsson, L. C., C. L. Pruett, D. H. Wolfe, and M. A. Patten. *In press*. Fine-scale habitat selection by the lesser prairie-chicken. *Southwestern Naturalist*.
- Leonard, K. M., K. P. Reese, and J. W. Connelly. 2000. Distribution, movements and habitats of sage grouse *Centrocercus urophasianus* on the Upper Snake River Plan of Idaho: changes from the 1950s to the 1990s. *Wildlife Biology* 6:265-270.
- Lillesand, T. M., and R. W. Kiefer. 2000. Remote sensing and image interpretation. John Wiley and Sons, New York, New York, USA.
- Lyon, A. G., and S. H. Anderson. 2003. Potential gas development impacts on sage grouse nest initiation and movement. *Wildlife Society Bulletin* 31:486-491.
- Malczewski, J. 2000. On the use of weighted linear combination method in GIS: common and best practice approaches. *Transactions in GIS* 4:5-22.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. Erikson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition, Kluwer Press, New York.
- McRae, B. H., and D. M. Kavanagh. 2011. Linkage Mapper Connectivity Analysis Software. The Nature Conservancy, Seattle, Washington, USA. Available at: <http://www.circuitscape.org/linkagemapper>.
- Merrill, M. D., K. A. Chapman, K. A. Poiani, and B. Winter. 1999. Land-use patterns surrounding greater prairie-chicken leks in northwestern Minnesota. *Journal of Wildlife Management* 63:189-198.
- Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145-184 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. *Studies in Avian Biology Series* (vol. 38), University of California Press, Berkeley, California, USA.
- Moore, I. D., R. B. Grayson, and A. R. Ladson. 1991. Digital terrain modeling: a review off hydrological, geomorphological, and biological applications. *Hydrological Process* 5:3-30.



- Newbold, T. 2010. Applications and limitations of museum data for conservation ecology, with particular attention to species distribution models. *Progress in Physical Geography* 34:3-22.
- Niemuth, N. D. 2000. Land use and vegetation associated with greater prairie-chicken in an agricultural landscape. *Journal of Wildlife Management* 64:278-286.
- Noss, R. F., and K. M. Daly. 2006. Incorporating connectivity into broad-scale conservation planning. Pages 587-619 *in* K. R. Crooks and M. Sanjayan, editors. *Connectivity conservation*. Cambridge University Press, Cambridge.
- Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* 10:949-963.
- Oyler-McCance, S. J., N. W. Kahn, K. P. Burnam, C. E. Braun, and T. W. Quinn. 1999. A population genetic comparison of large- and small-bodied sage grouse in Colorado using microsatellite and mitochondrial DNA markers. *Molecular Ecology* 8:1457-1465.
- Oyler-McCance, S. J., S. E. Taylor, and T. W. Quinn. 2005. A multilocus population genetic survey of the greater sage-grouse across their range. *Molecular Ecology* 14:1293-1310.
- Paradis, E. 1998. Interactions between spatial and temporal scales in the evolution of dispersal rate. *Evolutionary Ecology* 12:235-244.
- Patten, M. A., D. H. Wolfe, E. Schochat, and S. K. Sherrod. 2005. Habitat fragmentation, rapid evolution and population persistence. *Evolutionary Ecology Research* 7:235-249.
- Pearce, J. and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling* 133:225-245.
- Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161-175.
- Phillips, S. J., M. K. Dudík, and R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. Pages 655-662 *in* Proceedings of the twenty-first international conference on machine learning. ACM. Banff, Alberta, Canada.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231-259.

- Pitman, J. C., C. A. Hagen, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2005. Location and success of lesser prairie-chicken nests in relation to vegetation and human disturbance. *Journal of Wildlife Management* 69:1259-1269.
- Popham, G. P. 2000. Sage grouse nesting habitat in northeastern California. Thesis. Humboldt State University, Humboldt, California, USA.
- Pruett, C. L., M. A. Patten, and D. H. Wolfe. 2009. Avoidance behavior of prairie grouse: implications for wind and energy development. *Conservation Biology* 23:1253-1259.
- Pulido, F. 2007. The genetics and evolution of avian migration. *Bioscience* 57:165–174.
- Remeš, V. 2000. How can maladaptive habitat choice generate source-sink population dynamics. *Oikos* 91:579–581.
- Richard, Y., and D. P. Armstrong. 2010. Cost distance modeling of landscape connectivity and gap-crossing ability using radio-tracking data. *Journal of Applied Ecology* 47:603-610.
- Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences* 5:1-4.
- Robel, R. J., J. A. Harrington Jr., C. A. Hagen, J. C. Pitman, and R. R. Reker. 2004. Effect of energy development and human activity on the use of sand sagebrush habitat by lesser prairie-chickens in southwestern Kansas. *Transactions of the North American Wildlife and Natural Resources Conference* 69:251-266.
- Roloff, G. J., and J. B. Haufler. 1997. Establishing population viability planning objectives based on habitat potentials. *Wildlife Society Bulletin* 25:895-904.
- Rowland, M. M., M. J. Wisdom, L. H. Suring, and C. W. Meinke. 2006. Greater sage-grouse as an umbrella species for sagebrush-associated vertebrates. *Biological Conservation* 129:323–335.
- Schroeder, M. A., and L. A. Robb. 2003. Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape. *Wildlife Biology* 9:369-377.
- Scott, J. W. 1942. Mating behavior of the sage grouse. *Auk* 59:477-498.
- Segelbacher, G., J. Höglund, and I. Storch. 2003. From connectivity to isolation: genetic consequences of population fragmentation in capercaillie across Europe. *Molecular Ecology* 12:1773-1780.

- Segelbacher, G., S. Manel, and J. Tomiuk. 2008. Temporal and spatial analyses disclose consequences of habitat fragmentation on the genetic diversity in capercaillie (*Tetrao urogallus*). *Molecular Ecology* 17:2356-2367.
- Segelbacher, G., and I. Storch. 2002. Capercaillie in the Alps: the genetic evidence of metapopulation structure and population decline. *Molecular Ecology* 11:1669-1677.
- Segurado, P., M. B. Araujo, and W. E. Kunin. 2006. Consequences of spatial autocorrelation for niche-based models. *Journal of Applied Ecology* 43:433-444.
- Shepherd, J. F., K. P. Reese, and J. W. Connelly. 2011. Landscape fragmentation and non-breeding greater sage-grouse. Pages 77-88 in B. K. Sandercock, K. Martin, and G. Segelbacher, editors. *Ecology, conservation, and management of grouse. Studies in Avian Biology* (no. 39), University of California Press, Berkeley, California, USA.
- Stevens, B. S., J. W. Connelly, and K. P. Reese. 2012. Multi-scale assessment of greater sage-grouse fence collision as a function of site and broad scale factors. *Journal of Wildlife Management* 76:1370-1380.
- Storfer A., M. A. Murphy, J. S. Evans, C. S. Goldberg, S. Robinson, S. F. Spear, R. Dezzani, E. Delmelle, L. Vierling, and L. P. Waits. 2007. Putting the 'landscape' in landscape genetics. *Heredity* 98:128-142.
- Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240:1285-1293.
- Taylor P. D., L. Fahrig, K. Henein, and M. Gray. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68:571-573.
- Taylor, P. D., L. Fahrig, and K. A. With. 2006. Landscape connectivity: a return to the basics. Pages 29-43 in K. R. Crooks and M. Sanjayan, editors. *Connectivity conservation*. Cambridge University Press, Cambridge.
- Thomas, C.D. 2000. Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London B* 267:139-145.
- Thompson, T. R. 2012. Dispersal ecology of greater sage-grouse in northwestern Colorado: evidence from demographic and genetic methods. Dissertation. University of Idaho, Moscow, Idaho, USA.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18-30.
- United States Department of the Interior (USDI). 2001. SAGEMAP: a GIS database for sage grouse and shrub steppe management in the Intermountain West. USDI Geological Survey. <<http://sagemap.wr.usgs.gov>>. Accessed 29 September 2011.

- USDI. 2010. Endangered and threatened wildlife and plants; 12-month findings for petitions to list the greater sage-grouse (*Centrocercus urophasianus*) as threatened or endangered. Federal Register 75:13910-14014 (23 March 2010).
- Venier, L. A., and L. Fahrig. 1996. Habitat availability causes the species-abundance distribution. *Oikos* 76:564-570.
- Walker, B. L., and D. E. Naugle. 2011. West Nile virus ecology in sagebrush habitat and impacts on greater sage-grouse populations. Pages 127-142 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitat. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Walker, B. L., D. E. Naugle, and K. E. Doherty. 2007. Greater sage-grouse population response to energy development and habitat loss. *Journal of Wildlife Management* 71:2644-2654.
- Washington Wildlife Habitat Connectivity Working Group (WHCWG). 2012. Washington connected landscapes project: analysis of the Columbia Plateau ecoregion. Washington's Department of Fish and Wildlife, and Department of Transportation, Olympia, Washington USA.
- Wiens, J. A., L. Schooley, and R. D. Weeks. 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos* 78:257-264.
- Wisdom, M. J., C. W. Meinke, S. T. Knick, and M. A. Schroeder. 2011. Factors associated with extirpation of sage-grouse. Pages 451-472 in S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Series (vol. 38), University of California Press, Berkeley, California, USA.
- Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, A. Guisan, and N. P. S. Distribut. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions* 14:763-773.
- Wolfe, D. H., M. A. Patten, E. Shochat, C. L. Pruett, and S. K. Sherrod. 2007. Causes and patterns of mortality in lesser prairie-chickens *Tympanuchus pallidicinctus* and implications for management. *Wildlife Biology* 13:95-104.
- Woodward, A. J. W., S. D. Fuhlendorf, D. M. Leslie Jr., and J. Shackford. 2001. Influences of landscape composition and change on lesser prairie-chicken populations. *American Midland Naturalist* 145:261-274.

Yost, A. C., S. L. Peterson, M. Gregg, and R. Miller. 2008. Predictive modeling and mapping sage grouse (*Centrocercus urophasianus*) nesting habitat using maximum entropy and a long-term dataset from Southern Oregon. *Ecological Informatics* 3:375-386.

Table 1. Environmental variables used to model the geographic distribution of greater sage-grouse habitat in Lassen County, California.

Environmental variable	Variable description	Data source
TOWERS	Communication towers	SAGEMAP
POWER	Transmission lines	SAGEMAP
ROADS	Primary interstate highways and secondary roads (paved and unpaved)	TIGER
FIRE	Historical fire record (1907-2007) of wildfire and prescribed burns within study area	SAGEMAP
LAND	Landcover reclassified into 8 landcover classes: sagebrush, agriculture (cultivated crops, pasture, and hayland), riparian, juniper, grassland, shrub and/or woodland types (other than sagebrush or juniper) open water, and developed (urban and suburban areas)	LANDFIRE
TRI	Topographic Ruggedness Index calculated from 30-m DEM to describe topographic complexity	Digital Elevation Model (DEM)
CTI	Compound Topographic Index calculated from DEM where high values indicate increased moisture	DEM

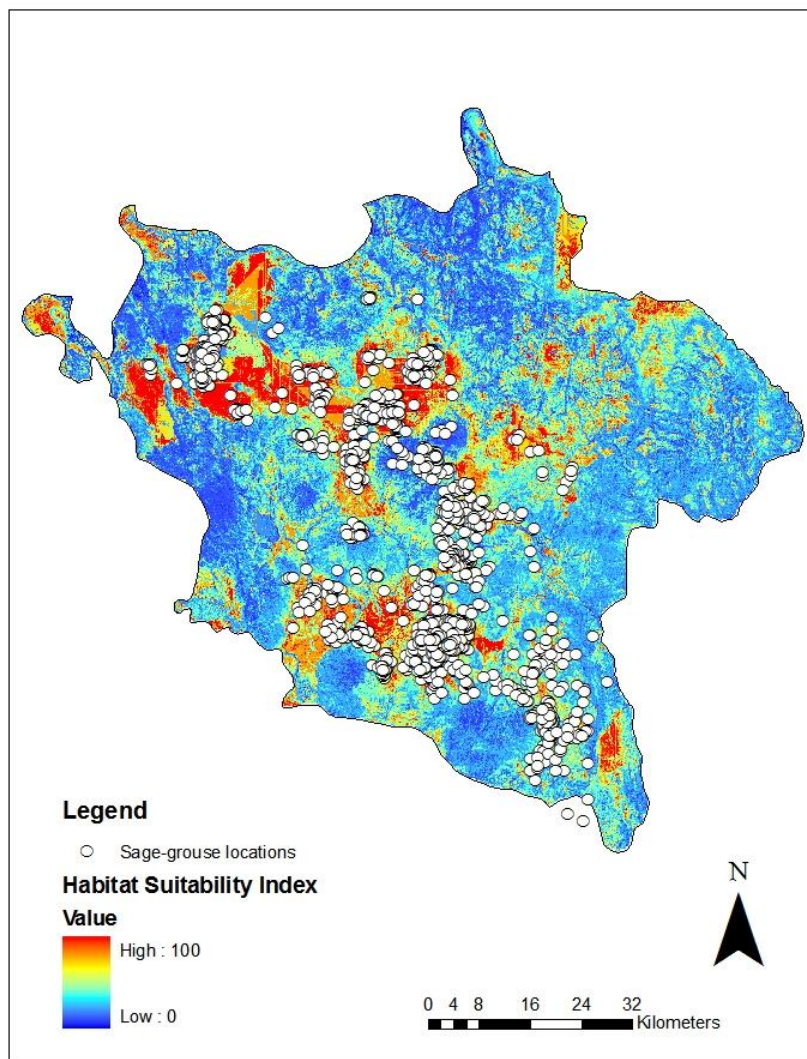


Figure 1. Habitat Suitability Index (HSI) map predicted by MaxEnt models based on presence-only data from greater sage-grouse locations (2007-2009) and Topographic Ruggedness Index (TRI), landcover type, Compound Topographic Index (CTI), and fire (both natural and wild) as environmental predictors. Warmer colors show areas with better predicted conditions to describe the geographic distribution of greater sage-grouse habitat in northeastern California.

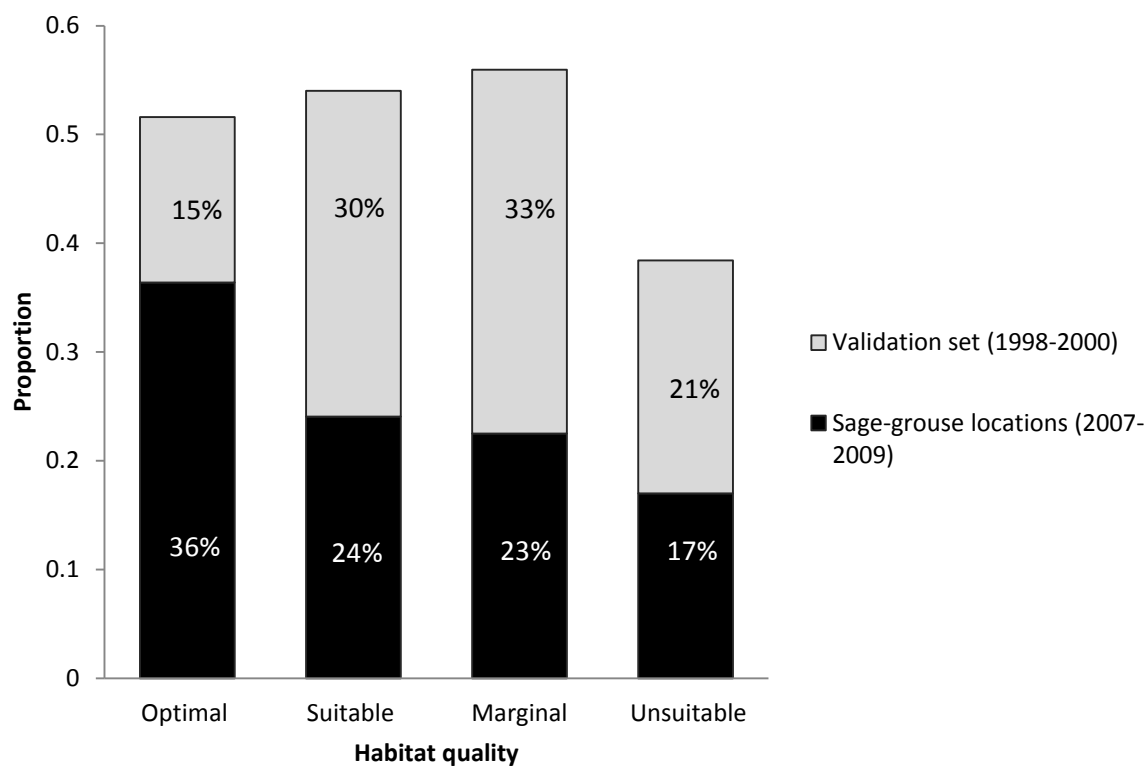


Figure 2. Comparison of habitat quality among an independent sample of greater sage-grouse locations ( $n = 1,426$ ) used for model validation and greater sage-grouse locations collected from 2007-2009 across the Lassen County study area for model development ( $n = 2,441$ ).



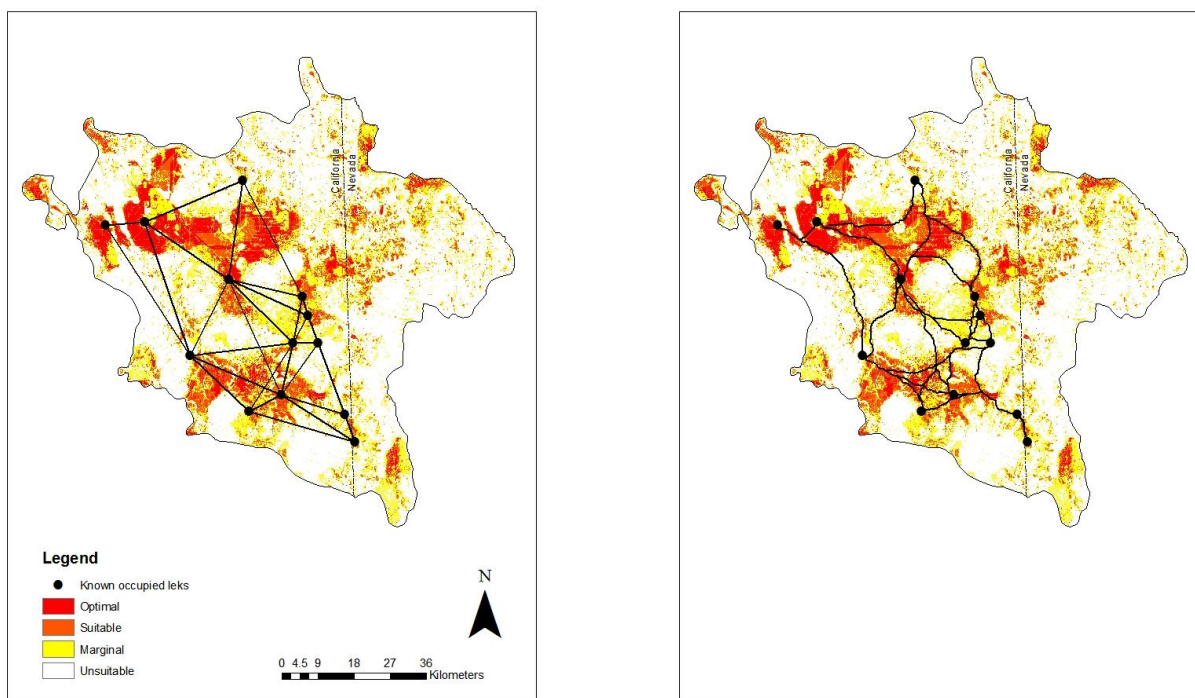


Figure 3. Stick map and least-cost path analysis for northeastern California. Each stick represents potential connections between adjacent sage-grouse lek sites (left) for which least-cost paths were calculated (right). Habitat quality is represented by 4 probability classes ranking from unsuitable to optimal habitat: Unsuitable (representing 60% of the total study area), Marginal (22%), Suitable (11%), and Optimal (7%).



Figure 4. Potential connections between adjacent lek sites for northeastern California, where each linkage represents non-weighted least-cost paths  $\leq 13$  km (left;  $n = 7$ ) and for which cost-weighted distances  $\leq 13$  km were calculated (right;  $n = 2$ ).

## Appendix. University of Idaho Animal Care and Use Committee Approval Verification.

**University of Idaho  
Animal Care and Use Committee**

**Date:** Wednesday, April 22, 2009  
**To:** Kerry Reese  
**From:** University of Idaho  
**Re:** Protocol 2007-33  
Population Dynamics, Habitat Use and Dispersal of Greater Sage-Grouse in California  
**Proposal(s):** 07656

Your requested renewal of the animal care and use protocol shown above was reviewed and approved by the University of Idaho on Wednesday, April 22, 2009.

This protocol was originally submitted for review on: Thursday, December 21, 2006  
The original approval date for this protocol is: Monday, February 26, 2007  
This approval will remain in effect until: Friday, February 26, 2010  
The protocol may be continued by annual updates until: Friday, February 26, 2010

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.



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IACUC Representative