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SAGE-GROUSE AND THE HUMAN FOOTPRINT: IMPLICATIONS FOR CONSERVATION OF SMALL AND DECLINING POPULATIONS

By

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Thesis

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Sage-grouse and the human footprint: implications for conservation of small and declining populations.

Chairperson: Dr. David E. Naugle

Implementing conservation in the face of unprecedented landscape change requires an understanding of processes and scales that limit wildlife populations. We assessed landscape-level processes influencing sage-grouse (*Centrocercus urophasianus*), to a migratory population in the Milk River Basin (MRB), northeast Montana, USA, and south-central Saskatchewan, Canada. A regional analysis of leks (e.g., communal breeding sites) documented that populations are impacted by the increasing extent of agricultural tillage, roads, and energy development out to spatial scales larger than previously known. Using bird abundance as a novel way to evaluate human impacts revealed relationships that would have been missed had we not incorporated lek size into analyses. For example, large leks are 4.5 times less likely to occur than small leks when agricultural tillage fragments 21% of land within 1.0km of breeding sites. Sage-grouse in the MRB met or exceeded demographic rates of stable or increasing populations, and thus, are not likely the cause for annual declines. Spring and summer survival of radio-marked females was higher in 2008 (0.91), than in 2007 (0.55), the year we documented an outbreak of West Nile virus. Nest sites in the MRB had lower shrub cover (15%) than range-wide estimates (15-56%), and overall shrub cover instead of sagebrush cover, was a better predictor of nest-site selection. Plains silver sagebrush (*Artemesia cana cana*) made up half of total shrub cover (7.1%) at nest sites, suggesting that other shrubs compensate for lower sagebrush densities in the MRB. We discovered the longest migratory event observed for sage-grouse, with females travelling 40-120km from breeding to wintering areas in Wyoming big sagebrush (*A. tridentata wyomingensis*) habitats in Montana. Habitat may be sufficient to maintain a small population in the MRB, but its ability to persist through time and to buffer against stochastic events is depressed now that this once-large population has become small and isolated. For example, impacts of disease are compounded when acting on fewer individuals and working synergistically with fluctuations in growth rates. Consequently, conservation of sage-grouse in the MRB will depend on maintaining the current habitat base, and on restoring sagebrush-dominated grasslands currently occupied by agricultural tillage.

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CHAPTER 1: INTRODUCTION

European settlement in western North America has forever changed the ecology of sagebrush-dominated grasslands. Arable lands, once rich in biodiversity, have been converted for agricultural production, and livestock have replaced native ungulates, further degrading rangelands and altering fire regimes (Noss et al. 1995). An expanding human population continues to sprawl beyond existing urban areas (Theobald et al. 2005). The increased human footprint of energy development has emerged as a major threat to biodiversity in sagebrush landscapes as coal-bed natural gas (Copeland et al. 2009), biofuels (Fargione et al. 2009), and wind power are harvested at accelerated rates (Pruett et al. 2009). Sagebrush habitats are now the most imperiled biome in North America (Knick et al. 2003).

The sagebrush ecosystem is representative of the struggle to maintain biodiversity in a landscape that bears the debt of our ever-increasing demands for natural resources. One species, the greater sage-grouse, is a native galliform of semiarid sagebrush landscapes (Schroeder et al. 1999). Previously wide spread, sage-grouse have been extirpated from half of their historic range, and populations continue to decline by 2% annually (Connelly et al. 2004). Ecologists now consider sage-grouse a ‘landscape’ species that view their environment at spatial scales that encompass whole landscapes. As a result, sage-grouse are often used an indicator of the overall health of the sagebrush ecosystem (Hanser and Knick 2009). The Committee on the Status of Endangered Wildlife in Canada listed sage-grouse as threatened in 1997 and endangered in 1998 under the federal Species at Risk Act. Sage-grouse in the US have been petitioned for listing range-wide under the federal Endangered Species Act three times, but in 2005 the US Fish and Wildlife Service determined that listing was not warranted. This decision was litigated in 2007 and is again under review. Petitions to list the species in the US and other political wrangling will continue until society commits to long-term habitat conservation.

Past research provides invaluable insights into local-scale habitat features that influence vital rates of individuals, but we largely lack an understanding of landscape features that drive the ecology of populations. New research integrates the importance of large-scale ecology with local-scale vegetation. Findings represent a paradigm shift that replaces single-scale studies focused largely on productivity, with multi-scale questions that explore habitat relationships across life-stages. Landscape context must be considered along with local-scale habitat features to provide managers a hierarchy in which to view and manage habitats (Aldridge and Boyce 2007, Doherty 2008).

We split this thesis into three main themes: relationships between landscape features and populations, local vegetation and demography, and migration. In total these themes integrate across scales our understanding of factors that influence sage-grouse populations. We hypothesized that the persistence and size of populations is tied to large spatial scales, and will set the biological sideboards for conservation of sage-grouse range wide.

In Chapter 2, we evaluate the influence of anthropogenic stressors and biogeography on populations by conducting a regional lek analysis for sage-grouse across their northeastern range. Our analyses are novel in that we are the first to use lek size to predict the probability of lek occurrence in response to human impacts. We documented negative impacts of agricultural tillage, roads, and energy development on occurrence and abundance, out to 1300ha around leks, relationships which would have been underestimated or completely missed had we focused solely on lek occurrence. Areas with the largest sage-grouse leks will likely play the greatest role in conserving sage-grouse populations range wide, and the spatial scales at which we discovered impacts highlight the need to manage all stressors across large landscapes.

In Chapter 3 we examine local habitat selection and demography of a small population on the fringe of its range in the Milk River Basin (MRB), northeast Montana, USA, and south-central Saskatchewan, Canada. This population met or exceeded demographic rates of stable or increasing populations, and thus, local habitat is not likely the cause for annual declines. Our findings suggest that habitat may be sufficient for populations to respond to favorable conditions, but that large-scale ecological processes may ultimately dictate the fate of this population of sage-grouse (Lacy 2000). We believe stochastic population events, such as an outbreak of West Nile virus we documented in 2007, may be acting synergistically with other factors causing declines in this small and isolated population (Gilpin and Soulé 1986). The ability of the sage-grouse in the MRB to persist through time and to buffer against periodic declines is greatly depressed now that a once-large population has become small (Aldridge 2000) and isolated (Bush 2009).

Lastly, Chapter 4 describes our discovery of the longest migratory event ever observed in sage-grouse. We documented sage-grouse from Saskatchewan travelling up to 120km from breeding to wintering areas in Wyoming big sagebrush (*A. tridentata wyomingensis*) in northeast Montana. Movements suggest that habitat management in the US will in part dictate the conservation of this endangered population of Canadian sage-grouse. Long distance movements in the MRB are not unique to sage-grouse. Multiple species in short-grass prairie including swift fox (*Vulpes velox*; Ausband and Moehrenschlager 2009), prairie rattlesnakes (*Crotalus viridis viridis*; Jorgensen et al. 2009), and pronghorn (*Antilocapra americana*; Andrew Jakes, University of Calgary, Personal Communication) make uncharacteristically large movements for dispersal and migration. Convergence of emerging research viewed in total highlights the scale and nature of collaborative partnerships necessary to conserve biodiversity in short-grass prairie ecosystems.

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CHAPTER 2: INCORPORATING ABUNDANCE INTO OCCURRENCE MODELS REVEALS DIFFRENTIAL HABITAT REQUIREMENTS FOR LARGE POPULATIONS.

Introduction

Conservation plans are increasingly dependent on the ability of researchers to accurately predict where species occur and where they are likely to persist (Araújo and Williams 2000). Those interested in guiding conservation at scales relevant to policy are fortunate to have a wealth of tools that can be used to build predictive models of occurrence, rigorously test them, and apply results to landscapes (Millspaugh 2008). Resulting maps provide conservation practitioners and policy makers with the information necessary to make decisions on where land mitigation, easements, and acquisition will be most effective. However, developing models using only species occurrence may produce misleading results. Generating models from population-level occurrence data give equal weight to small, declining populations that may have an increased probability of extirpation as a result of stochastic events (van Teeffelen et al. 2006). In turn, this may obscure the importance of habitat requirements for larger populations that may contribute more to the species persistence. Maintaining large populations should be a primary conservation goal because thousands of individuals are typically required to buffer against extinction threats and to maintain evolutionary processes (Traill et al. 2009).

Incorporating abundance thresholds into occurrence models may be a more robust method for identifying the populations most likely to persist through time. Size of local populations is assumed to have a positive relationship with habitat quality, but with several notable caveats. Factors that may decouple relationships between population size and habitat quality include movements between seasonal ranges, social dominance such as despotism, and habitat opportunism (Van Horne 1983). Using abundance to identify areas most likely to persist could be a false indicator of habitat quality when populations exhibit high variability in reproductive rates that reflect short-term phenomena rather than long-term population processes (Joseph et al. 2006). We hypothesized that incorporating abundance into habitat-based occurrence models would provide a better estimate of overall habitat quality by allowing larger populations to be treated independently in occurrence analyses. Understanding how habitat requirements change with population size will be valuable to conservation practitioners with limited resources, who attempt to maximize species persistence.

Greater sage-grouse (*Centrocercus urophasianus*; hereafter ‘‘sage-grouse’’) are an exemplary species for exploring the union of occurrence and abundance data. A gallinaceous species native only to western semiarid sagebrush habitats, sage-grouse were previously widespread, but loss and degradation of sagebrush habitat has resulted in extirpation of the species from almost half of its original range (Schroeder et al. 1999, 2004). Previous studies on sage-grouse have successfully evaluated landscape-level occurrence (Aldridge and Boyce 2007, Doherty et al. 2008, Yost et al. 2008), abundance (Doherty et al. 2010), and lek persistence (Walker et al. 2007, Aldridge et al. 2008, Wisdom et al. 2010). These models have been effective at describing the relationship between occupied landscapes and recently or historically extirpated areas based on the presence of sage-grouse. However, these studies did not account for abundance within occurrence models. Because of this, their estimates for factors contributing to extirpation may be conservative, with equal weight given to small declining populations.

We used sage-grouse leks in their northeast range to predict the probability of occurrence of active leks using data from emerging anthropogenic stressors known to impact sage-grouse populations. We asked the question: *Does incorporting abundance thresholds into occupancy models change biological interpretations, and if so, how do resulting outcomes change conservation recommendations?* We built similar habitat models, but with lek abundance incorporated into analyses, to examine if there are different requirements for large leks that are less susceptible to stochastic population processes. We tested this hypothesis by comparing probabilities of occurrence between small and large leks. We predicted that larger leks would be more sensitive than smaller leks to increasing human impacts.

Study Area

We analyzed data from sage-grouse leks within a 148,000-km^2 area including portions of Montana and western North and South Dakota, USA, and southeast Alberta and southwest Saskatchewan, Canada (Figure 1). Natural vegetation consists of sagebrush-dominated grasslands and short-grass prairie interspersed with limited stands of conifers. Sagebrush grasslands south of the Milk River (Figure 1) in Montana are dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with an understory of native and nonnative grasses and forbs. North of the Milk River in Montana and in North and South Dakota plains silver sagebrush (*A. cana cana*) replaces Wyoming big sagebrush. Silver sagebrush is resilient to fire and typically exhibits lower canopy coverage than the more dense but fire-intolerant Wyoming big sagebrush (Jones et al. 2005). Land tenure is a diverse mixture of public and private lands, with the former being largely administered by provincial or federal governance, while state-side public lands are managed predominately by the Bureau of Land Management. The extant range of sage-grouse is shrinking into itself as changes in land use that result in local extirpations move towards the interior of formally secure sagebrush habitats (Figure 2 and Aldridge et al. 2008).

Land use in this region is a diverse mixture of cattle grazing and tillage agriculture interspersed with concentrated areas of oil and gas development (Figure 2). Agricultural tillage that replaces sagebrush habitats with row crop and small grain production results in a direct loss of habitat. Removing sagebrush habitat can adversely impact sage-grouse and has been attributed to initiating declines in populations (e.g. Klebenow 1970, Connelly et al. 2000 *a*, *b*, Leonard et al. 2000, Smith et al. 2005, Walker et al. 2007, Beck et al. 2009). To date, the footprint from oil and gas extraction occupies a ~ 5% of Montana, North and South Dakota, Alberta, and Saskatchewan, an area much smaller than that in nearby Wyoming where the geologic potential for extraction exceeds that of our study area (Copeland et al. 2009). Primary and secondary roads are largely clustered in and around human developments where they enhance access to oil and gas or agricultural fields and connect rural population centers.

Methods

Sage-grouse lek database:

Lek Status and Count Data – We obtained sage-grouse lek (e.g., communal breeding sites) location and count data from state and provincial agencies responsible for maintaining these datasets (Table 1). Leks are widely used by state and federal agencies to monitor population trends and are considered a reasonable index to relative abundance (Walsh et al. 2004, Reese and Bowyer 2007). Each spring, sage-grouse are counted at leks by state, federal, provincial and contract employees across our study area, where surveyors record number of displaying males. Ideally, leks are visually surveyed ≥ 3 times each spring from the ground or during aerial surveys. However, remote access, inclement weather and permission to access leks on privately-owned lands prohibit all leks from being consistently surveyed within the study area. We verified records of lek data with the appropriate agency personnel to resolve potential discrepancies in lek location or count information.

Definition and status of a lek —We defined a lek as a site where multiple males were documented displaying on multiple visits within one or more years (Walker et al. 2007). We defined a lek complex as multiple leks located < 2.5km from the largest and most regularly attended lek in the complex (Connelly et al. 2004). We defined an initial set of lek complexes based on those known since the beginning of surveys through 2008 (Table 1). We determined the final status of leks by examining count data. We used lek complexes from 1999 to 2008 as the sample unit in analyses, and defined a lek as active if ≥ 2 males were recorded during the most recent count. For complexes formed entirely of inactive leks, we selected the lek with the highest average historical count for use in analyses. Satellite leks are leks within 2.5km of the complex center (Connelly et al. 2004). We removed satellite leks from analyses because they are irregularly attended, and we did not add counts to lek complexes because they are inconsistently monitored. We censored leks from analyses that were not surveyed or were inadequately surveyed from 1999 to 2008. Final screening provided 802 active lek complexes (hereafter “leks”), and 297 inactive leks for analyses.

Incorporating abundance into occupancy models — We used the maximum count from the last year of observation to estimate male abundance at leks. We used the distribution of male counts on leks to define what we considered a large lek that would be less susceptible to stochastic population processes (Figure 3). We defined large leks as those with >25 males for later abundance analyses because this was the break point for the upper quartile of lek abundance (Figure 3). Large leks in our study accounted for 53% of the total males counted in the study area. We used this definition of a large lek to compare relative affects of landcover and anthropogenic features to occurrence estimates between active and inactive leks, small and large leks to inactive leks, and large to small leks.

Scale and Descriptions of Explanatory Variables:

Scale — We selected spatial scales that represented the behavior of breeding sage-grouse populations or that reflected the scale at which current management actions are implemented. We calculated relevant variables at five radii around leks: 1.0km (314ha; 1.2mi^2 in English units), 3.2km (3,215ha), 5.3km (8,820ha), 6.8km (14,519ha), and 12.3km (47,505ha; 183mi^2; 5 cadastral townships). Female sage-grouse spatially distribute their nests in relation to lek location (Holloran and Anderson 2005), so we selected scales to represent the lek-to-nest distances that encompassed 50, 75, and 95% of radio-marked female sage-grouse in our study area (5.3km, 6.8km, and 12.3km respectively; Figure 4 in Chapter 3). We selected the 1.0-km scale to represent processes that impact breeding birds at or near leks, while avoiding problems with spatial error in lek locations (Walker et al. 2007). The 3.2-km scale is that at which agencies apply mitigation for oil and gas impacts (e.g., timing restrictions for drilling) on state and federal lands.

Variables for Landcover — We chose seven variables to explain occurrence and abundance of sage-grouse leks (Table 2), based on disturbances known to impact sage-grouse populations, and habitat features we hypothesized were conducive to the persistence of sage-grouse. We hypothesized that agricultural tillage would result in higher rates of inactivity or lower overall abundance due to habitat loss. In turn, we expected lower overall rates of lek occurrence and decreased abundance as agricultural tillage is increased. Sage-grouse are sagebrush obligates, reliant on sagebrush habitats for each stage of their life-history (Connelly et al. 2004). Sagebrush layers have been used to accurately predict nesting habitat (Doherty 2008), brood-rearing habitat (Aldridge and Boyce 2007), winter occurrence (Homer et al. 1993, Doherty et al. 2008), and large scale persistence (Aldridge et al. 2008), and would ideally be used for estimating lek occurrence and abundance. However there is no conterminous layer of sagebrush that includes coverage for both silver and big sagebrush (Aldridge et al. 2008). Therefore, we chose to move forward without a sagebrush predictor variable to maintain the full dataset.

Variables for oil and gas development and roads—We hypothesized that human infrastructure in the forms of oil and gas development and roads can affect lek occurrence and male abundance at leks and included appropriate covariates to examine each covariate. Energy development and roads may affect lek occurrence in proportion to their extent. Alternately, male abundance may be a better predictor of vulnerability to disturbance if large leks decline rapidly at the onset of development despite the persistence of small remaining leks. Cumulative impacts that result from oil and gas development also may depend on how long the lek has been subjected to disturbance. High site fidelity but low survival of adult sage-grouse combined with lek avoidance by younger birds resulted in a time lag of 3-4 years between the onset of deep gas drilling and lek loss in southwest Wyoming (Holloran et al. 2010). The time lag observed in Wyoming matched that for leks that became inactive 3-4 years following shallow coal-bed natural gas development in eastern Wyoming and Montana (Walker et al. 2007). If this is the case, then male attendance may not decrease immediately following disturbance or leks may persist for some time before becoming inactive.

Lek distribution and lek density covariates—We hypothesized that leks within the core of the species range would have a higher probability of remaining active (Brown 1984), and a greater abundance of males than leks near the edge of their range. Predicted patterns, if apparent, would help quantify variables that best explain the continued contraction of the species range. We also hypothesized that leks within Wyoming big sagebrush communities would have a higher probability of occurrence and a greater abundance of males on leks than leks within silver sagebrush communities. Silver sagebrush is more sparsely distributed on a landscape than big sagebrush (Aldridge and Brigham 2002), providing less overall nesting cover for sage-grouse. If so, then the increased vulnerability of leks in silver sagebrush communities may further elevate concern for declining populations in North and South Dakota and in Canada. Lastly, we hypothesized that the best available habitats would have higher lek densities than marginal habitat. This hypothesis suggests that the probability of occurrence and abundance of males will be higher at an individual lek with more active leks in the immediate vicinity.

Statistical Analyses:

We used logistic regression to assess the influence of variables on lek activity by comparing the distribution of variables between active (1) and inactive (0) leks, which we will refer to as occurrence only (Hosmer and Lemeshow 2000). We then used multinomial logistic regression to assess the influence of covariates on three dependent outcomes: inactive leks (0), leks ≤ 25 males (1), and leks > 25 males (2) (Hosmer and Lemeshow 2000). We used multinomial logistic regressions between inactive (0) and small leks (1), and inactive (0) and large leks (2) to assess the influence of lek size on occurrence, compared to occurrence only models, which we refer to as abundance-based occurrence. Multinomial logit models estimated between small (1) and large (2) leks were used to compare the influence of variables on abundance on active leks, because some stressors may not cause a lek to go inactive, but will impact male abundance (Doherty 2008). We refer to the multinomial logit models between active leks as abundance only models. Because estimates for multinomial logistic regressions are consistent with those of separate binomial logistic regression models, we fit all variables to a global multiple logistic regression model using a binomial logistic regression approach (Begg and Gray 1984). We selected multinomial rather than ordinal logistic regression because we suspected that the log odds of covariates were not linear in relation to ordered dependent variables (Hosmer and Lemeshow 2000).

We used an information-theoretic approach (Burnham and Anderson 2000) to select the most parsimonious model from a set of plausible candidate models. We first allowed each univariate at each scale to compete and used the scale for each covariate that best predicted lek status and male abundance at leks to construct the final set of candidate models. We did not allow correlated covariates ($r \geq |0.7|$) in the same model. If covariates were correlated, we chose the covariate we felt had the greatest biological meaning according to our hypotheses. When variables were moderately correlated (i.e., $|0.3| \leq r < |0.7|$), we checked for stability and consistency of regression coefficients as we added covariates to models. If a regression coefficient switched signs or standard errors increased substantially when correlated variables were in the same model, we removed one of the variables from analyses. We also checked multicollinearity of multivariate models using variance inflation factors (VIF), and considered multicollinearity problematic if the mean VIF score was > 1 (Chatterjee et al. 2000). We judged occurrence only models based on Akaike's Information Criterion (AIC) and examined beta coefficients and associated standard errors in all models to determine the direction and magnitude of effects. We used the full multinomial model for all significant variables because it allowed for comparisons among all significant logits, while holding insignificant values at 0 (Hosmer and Lemeshow 2000).

We used Wald's test statistic to evaluate if all models had an overall good fit (Hosmer and Lemeshow 2000). We used Receiving Operating Characteristic (ROC) to evaluate the predictive ability of our best approximating occurrence only model (Pearce and Ferrier 2000). We evaluated models by classifying observations of active and inactive leks for a continuous range of cutoff points between zero and one. We used area under the ROC Curve (AUC) as an index to the ability of our model to discriminate between active and inactive leks. We interpreted the predictive power of the occurrence only logistic model with the associated AUC score as poor (< 0.7), moderate (0.7 to 0.9) and excellent (>0.9; Swets 1988).

We used bootstrap analyses to quantify the relative influence of individual model variables on lek occurrence and abundance of males at leks while holding constant the effects of all other covariates at their mean values. We used beta coefficients from covariates in our best approximating binomial and multinomial models (see Results; Burnham and Anderson 2002), and conducted 5,000 iterations to predict the probabilities across the observed range of values for each covariate of interest. We held variables at 0 if their logit estimate was non-significant in the multinomial model (Hosmer and Lemeshow 2000). We then ordered these probabilities and used a rankit adjustment (Chambers et al. 1983) to compute 2.5% and 97.5% percentiles for the upper and lower 95% confidence intervals.

Results

Occurrence only models produced at least one significant estimate for each variable at least at one scale (Table 3). The effect of lek density on occurrence was best explained by the largest scale evaluated (12.3km), while proportion of agricultural tillage and road lengths had the greatest support at 1.0km and 3.2km, respectively (Table 3). Well density with and without a time lag were both best explained at 12.3km, yet these two variables are inherently correlated. We chose to only include well density with a simulated time lag, because it had better overall fit

(Table 4). Screening for variables between inactive and large leks, and small to medium and large leks produced the same best fit scales for each variable, with the exception of road lengths. Road lengths within 1.0km radius around leks was the best fit scale explaining abundance, but roads within 3.2km had a ΔAIC value < 2 when comparing scales, so we chose to continue with the 3.2km radius for continuity between analyses, and consistency with management policies.

We used the best scale as estimated by AIC for each uncorrelated variable in the global binomial logistic regression model between active and inactive leks. Lek density was the only non-significant variable in the global model examining persistence, and was subsequently removed. The global model was also the best approximating model (Table 4), and predicted occurrence of active leks based on lower proportions of agricultural tillage ($\beta_{till} = -1.346$; 0.502) and fewer roads ($\beta_{road} = -0.0216$; 0.005), insular leks ($\beta_{Distrange} = 0.0293$; 0.0004) in big sagebrush habitat ($\beta_{sagespp} = 1.109$; 0.202), and higher well density ($\beta_{welllag} = 1.503$; 0.480). The occurrence only model had good fit (Wald's $\chi^2 = 116.40$, $p < 0.001$), and was able to adequately discriminate (ROC= 0.71) between active and inactive leks. We subsequently built a global multinomial model containing the same variables as the occurrence-only model, with the inclusion of lek density because coefficients were significant for several pair-wise comparisons.

The global multinomial logistic regression model estimated the same direction of variables for comparing inactive to small and large leks with the exception of well density, which was negative ($\beta_{lag}=-0.057$; 0.786) but non-significant ($p=0.941$) for the large lek classification (Table 5). Lek density was non-significant between inactive and small leks. Remaining significant coefficient estimates between inactive and large leks were greater than those estimated from inactive to small leks. Agricultural tillage had the greatest change between occurrences of different sized leks, with an estimated coefficient 4 times larger for the occurrence of large leks (Table 5). Coefficients for distance to range (Figure 5), roads (Figure 6), and sagebrush species increased 1.2 to 1.8 times larger in large lek occurrence compared to small leks (Table 4).

Regressions between small and large leks produced significant estimates for well and lek density, and agricultural tillage (Table 6). Estimates predicted larger leks had less agricultural tillage (β_{till}=-2.83; 1.108) and higher lek density (β_{leks}= 17.61; 5.619). Leks were more likely to be small with increased well density (β_{lag}=-1.702; 0.655) (Figure 9). Overall, the full multinomial model had good fit (Wald's χ^2=185.92, p <0.0001).

Discussion

Multi-scale assessments of resources have been widely used in studies to estimate species occurrence (Wiens 1989), and this study highlights the value of selecting scales in the response variable such as population size, that are appropriate for management and conservation. Our results indicate that failing to account for abundance underemphasizes the importance of landscape-level disturbances causing declines in sage-grouse populations. By incorporating lek size as a response to human impacts, we documented relationships between agricultural tillage, energy development, and roads that would have been largely underestimated or completely missed if we had looked solely at occurrence. Our results demonstrate that conserving the largest sage-grouse leks will be even more difficult as the human footprint increases in sagebrush landscapes.

Agricultural tillage is a range-wide stressor to sage-grouse populations (Connelly et al. 2004) that is most pronounced at northern latitudes (Figure 2). Recent changes to the US Food

Security Act coupled with increased commodity prices of grains to meet the demand for biofuels threatens remaining arable lands as tillage becomes more profitable than ranching (Fargione et al. 2009). Agricultural tillage was a significant stressor to lek occurrence that was exacerbated in large leks. We estimated that 65ha (160ac) of agricultural tillage within 1.0km of a lek would result in a 4% (0 to 16%) decline in occurrence of small leks, while the occurrence of large leks would decrease by 18% (8 to 35%) (Figure 4). This suggests land easements should be focused around large leks situated in or adjacent to private lands. In Montana alone, 430 (58%) active leks are located on private land, compared to 223 (30%) active leks on public lands managed by the Bureau of Land Management. Larger spatial scales should also be considered when planning for easements around leks, as we identified negative impacts of agricultural tillage on occurrence and abundance of males on leks out to 5.3km (Table 3).

Our models suggest that maintaining large leks at the edge of their range will require greater efforts than conservation of insular leks, particularly in silver sagebrush habitats. Lek occurrence for medium and large leks declines precipitously both near the edge of their range (Figure 5) and in isolation from other leks (Figure 7). Populations in silver sagebrush habitats are disproportionately impacted by stressors such as agricultural tillage (Figure 8). While sage-grouse can fulfill their life history needs within silver sagebrush habitats (Aldridge and Brigham 2002), occurrence may be limited within this ecologically marginal habitat. Consequently, these populations will be more sensitive to loss of sagebrush, and increases in human disturbance.

Road networks will likely increase as the human population increases, and as infrastructure expands to accommodate energy development. Sage-grouse can suffer direct mortality from traffic, or avoid roads altogether (Holloran 2005, Aldridge and Boyce 2007) as linear features functionally decrease and degrade the amount of available habitat. We found negative relationships with more roads around leks at all levels of lek occurrence, but impacts were greatest for the largest leks (Figure 6). Intensity of road use may be a better predictor of sage-grouse occurrence and abundance, than road density. For example, roads used to access well pads will have higher rates of traffic and involve larger vehicles than roads used primarily in ranching operations (Holloran 2005). However no existing data quantifies the use of current road networks. Understanding how different road types and uses impact sage-grouse populations will be an important future relationship to understand in impacted areas, but our results highlight the value of roadless areas in sagebrush habitats, regardless of use.

Estimates showed oil and gas development decreases lek size, but has yet to result in lek extirpation (Figure 9). We suspect four non-independent reasons that leks impacted by energy development do not have higher rates of inactivity in our study area: 1) the onset of development is too recent to manifest into lek extirpation, 2) energy-impacted areas are in otherwise good habitat and negative effects of agricultural tillage are inflating overall rates of lek inactivity, 3) clustered and linear development may provide refuge outside impacted areas for sage-grouse to persist, and 4) the sample of leks impacted by energy is too small to detect potential differences. Post-hoc analysis showed that agricultural tillage and oil and gas development rarely overlapped within our study area (Figure 10). Only 27 of 1,099 leks have sufficient development known to increase inactivity rates ($\geq$ 13 wells within 3.2km; Holloran 2005, Walker et al. 2007, Doherty 2008), of which one was inactive as of 2008.

Poor monitoring of leks in some areas may have underestimated the extent to which energy development has impacted sage-grouse populations in our study area. Most active oil and gas fields in our study area do not have known lek locations within their boundaries, except for the Cedar Creek Antacline (CCA),a shallow gas field near the junction of Montana, and North and South Dakota, which held the majority of impacted leks in our analysis (21 of 27) (Figure 11). Between 2008 and 2009 lek abundance decreased by 52% at 16 leks in the CCA with current well densities $\geq$ 40 wells in 3.2km, and no males were counted at four leks that had multiple displaying males during counts in 2008. A recent study showed that time lags between the onset of development and manifestation in lek loss may take 2 to 10 years (Harju et al. *in press*). In our study area > 37% of the wells were drilled within the past four years (Figure 12), therefore decreased rates of lek activity may not yet be fully realized. Estimates show that intensity of development could increase dramatically in the next 20 years (International Energy Agency 2007).

Areas with the largest sage-grouse leks will likely play the greatest role in conserving sage-grouse populations range-wide. Because populations are highly clustered, prioritizing landscapes for conservation should focus on areas with the highest male counts (e.g., Doherty et al. 2010). We documented impacts of agricultural tillage, roads, and energy development on occurrence and abundance, out to 1300ha around leks (5 cadastral townships). The scales at which these processes act upon populations highlight the need to manage all stressors across large landscapes. Our results also underscore relationships between undisturbed habitat and the maintenance of large leks at scales larger than disturbances are currently mitigated. Identifying priority conservation areas, or core areas, is a documented strategy to conserve wide-ranging species that face threats through a significant portion of their range (Groves et al. 2002). Several western agencies have delineated core areas based on lek density and male abundance, which, along with expert opinion are being used to prioritize implementation of conservation actions to benefit populations (Doherty et al. 2010). Our findings validate the use of core areas as a way to maintain the largest concentrations of sage-grouse in the smallest habitat area. In Montana, >55% of leks occur on privately owned land, with the balance of remaining leks in lands owned and managed by the Bureau of Land Management. Maintaining large landscapes with minimum disturbance is paramount to sage-grouse conservation and will require collaborative efforts from a diverse group of stakeholders.

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Table 1. Sources for lek location and male count data for Montana and North and South Dakota, USA, and Alberta and Saskatchewan, Canada.

State / Province	Data Sources:	First Year Data Collected	Number of Leks	Number of Records
Montana	Montana Fish, Wildlife, and Parks	1952	1,713	14,672
North Dakota	North Dakota Game and Fish Deparment	1952	52	1,821
South Dakota	South Dakota Game, Fish, and Parks	1971	60	503
Saskatchewan	Parks Canada; Environment Saskatchewan	2000	18	123
Alberta	Alberta Fish and Wildlife	1968	36	374

Table 2. Descriptions and sources of variables used to construct occurrence and abundance models, and associated scales at which variables were evaluated.

Variable	Description	Buffers Used	Data Source
Tillage	Proportion of agricultural tillage lands within fixed buffers around leks.	1.0 km, 3.2 km, 5.3 km, 6.8 km, and 12.3 km	USDA Forest Service 2006 Landfire® coverage in US states (Zhu et al. 2006), and Agricultural Finacial Services Corporation 2004 Agricultural Lands Classification in Canada (Finnigan et al. 2008). Conterminous layer created at minimum mapping unit of 56m.
Wells	Producing oil and gas well density calculated in well per section for respective buffers	1.0 km, 3.2 km, 5.3 km, 6.8 km, and 12.3 km	MT: MT Oil and Gas Board; AB: AB Energy Utility Board; SK: Govt. of SK Energy and Resources; ND: ND Oil and Gas ; Commission; SD: SD Department of Environment & Natural Resources: Minerals and Mining Program; WY: WY Oil and Gas Conservation Commission.
Lag	Same as well density, but with simulated four year time-lag by reclassifying well densities to 4 years prior to year of last count or activity.	1.0 km, 3.2 km, 5.3 km, 6.8 km, and 12.3 km	Same as *WellDens* variable.
Road	Summed road lenghts within fixed buffers.	1.0 km, 3.2 km, 5.3 km, 6.8 km, and 12.3 km	TIGER® Line Data from 2000 for US states, and 2005 National Road Network data for Canadian provinces.
Distrange	Distance (km) to the edge of the current range of greater sage-grouse	None	Schroeder et al. (2004) delination of greater and gunnison sage-grouse current and historic distribution.
Sage	Categorical classification for big sagebrush (*Artemesia tridentata*) and silver sagebrush (*A. cana*)	None	Leks dominated by silver sagebrush were delineated in areas north of the Milk River and in North and South Dakota. Remaining leks were classified as dominated by big sagebrush.
Leks	The density (leks per section) of active lek complexes within buffers greater than 2.5km.	3.2 km, 5.3 km, 6.8 km, and 12.3 km	Table 1.

Table 3. Best fit scales for relevant variables, and other significant estimates within scales. *ns* denotes non-significant estimates for all scales evaluated.

	Variable	Best Fit Scale	AIC weight of best scale	Other Signficant Scales ($p < 0.05$) in order of nest lowest Log-Likelihood. * Denotes DeltaAIC < 2
Inactive to Active	*Tillage*	1.0km	0.99	3.2km
	Road Lengths	3.2km	0.33	5.3km*, 6.8km*, 1.0km*, 12.3km*
	Lag	12.3km	0.67	6.8km, 5.3km
	Leks / Section	12.3km	0.99	6.8km, 5.3km
Inactive to Leks with ≤ 25 Males	*Tillage*	1.0km	1	NA
	Road Lengths	1.0km	0.72	3.2km*, 5.3km*, 6.8km*, 12.3km*
	Lag	12.3km	0.75	6.8km, 5.3km, 3.2km
	Leks / Section	12.3km	0.84	6.8km, 5.3km, 3.2km
Inactive to Leks with > 25 Males	*Tillage*	1.0km	0.97	3.2km, 5.3km, 6.8km
	Road Lengths	3.2km	0.57	5.3km, 6.8km, 12.3km, 1.0km
	Lag	*ns*	NA	NA
	Leks	12.3km	0.99	6.8km, 5.3km, 3.2km
Small to Large Leks	*Tillage*	1.0km	0.64	3.2km*, 5.3km
	Road Lengths	*ns*	NA	5.3km, 6.8km, 12.3km, 1.0km
	Lag	12.3km	0.88	6.8km, 5.3km, 3.2km
	Leks	12.3km	0.99	6.8km, 5.3km, 3.2km

Table 4. AIC Model selection of occurrence models between all active and inactive sage-grouse leks.

Model Description	K	Log Likelihood	ΔAICc	AIC weights
Lag 12.3km + Tillage 1.0 km + Road 3.2km + Sage + Distrange	6	-583.071	0	0.689
Wells 12.3km + Tillage 1.0 km + Road 3.2km + Sage + Distrange	6	-584.220	2.299	0.218
Distrange + Sage + Road 3.2km + Lag 12.3km	5	-586.606	5.049	0.055
Distrange + Sage + Road 3.2km + Wells 12.3km	5	-587.751	7.339	0.018
Wells 12.3km + Distrange + Sage + Road 3.2km	5	-587.751	7.339	0.018
Distrange + Sage + Tillage 1.0km + Lag 12.3km	5	-590.464	12.765	0.001
Distrange + Sage + Tillage 1.0km + Road 3.2km	5	-591.069	13.974	0.001
Distrange + Sage + Tillage 1.0km + Wells 12.3km	5	-591.639	15.114	0.000
Wells 12.3km + Distrange + Sage + Tillage 1.0km	5	-591.639	15.114	0.000
Lag 12.3km + Distrange + Sage	4	-594.431	18.680	0.000
Lag 12.3km + Distrange + Sage + Road 3.2km	5	-593.642	19.120	0.000
Lag 12.3km + Distrange + Sage + Tillage 1.0km	5	-594.598	21.031	0.000
Wells 12.3km + Distrange + Sage	4	-595.618	21.054	0.000
Distrange + Tillage 1.0km + Sage	4	-596.597	23.013	0.000
Distrange + Tillage 1.0km + Road 3.2km + Lag 12.3km	5	-597.864	27.564	0.000
Sage + Leks 12.3km + Distrange	4	-599.031	27.880	0.000
Distrange + Tillage 1.0km + Road 3.2km + Wells 12.3km	5	-598.414	28.664	0.000
Sage + Distrange	3	-600.898	29.600	0.000
Distrange + Leks 12.3km	3	-605.398	38.600	0.000
Lag 12.3km + Distrange	3	-606.653	41.110	0.000
Wells 12.3km + Distrange	3	-607.265	42.333	0.000
Sage + Tillage 1.0km + Road 3.2km + Lag 12.3km	5	-606.919	45.674	0.000
Sage + Tillage 1.0km + Road 3.2km + Wells 12.3km	5	-607.943	47.723	0.000
Leks 12.3 + Tillage 1.0km + Lag 12.3km	4	-620.199	70.216	0.000
Leks 12.3 + Tillage 1.0km + Wells 12.3km	4	-620.756	71.331	0.000
Tillage 1.0km + Lag 12.3km + Road 3.2km	4	-623.290	76.398	0.000
Tillage 1.0km + Wells 12.3km + Road 3.2km	4	-623.714	77.247	0.000
Sage + Leks 12.3km	3	-625.405	78.614	0.000
Tillage 1.0km + Road 3.2km	3	-628.722	85.248	0.000
Lag 12.3km + Road 3.2km	3	-628.904	85.611	0.000
Tillage 1.0km + Lag 12.3km	2	-630.166	86.125	0.000
Wells 12.3km + Road 3.2km	3	-629.268	86.340	0.000
Leks 12.3km	2	-630.935	87.662	0.000
Sage	2	-631.291	88.374	0.000
Distrange	2	-631.291	88.374	0.000
Tillage 1.0km + Wells 12.3km	3	-630.648	89.099	0.000
Tillage 1.0km	2	-634.515	94.822	0.000
Road 3.2km	2	-634.831	95.455	0.000
Lag 12.3km	2	-636.537	98.866	0.000
Wells 12.3km	2	-636.973	99.739	0.000

Table 5. Estimates of β-coefficients for small lek occurrence (inactive to small leks), and large lek occurrence (inactive to large leks) from full multinomial logistic regression model.

	Covariate	β_i	SE	p	Proportion Change from different lek size
Inactive to Leks ≤ 25 Males	*Tillage 1.0km*	-0.939	0.511	0.066	0.25
	Leks 12.3km	2.720	5.615	0.628	*ns*
	Sage	0.894	0.218	<0.001	0.57
	Distrange	0.026	0.004	<0.001	0.84
	Lag 12.3km	1.644	0.485	0.001	*ns*
	Road 3.2km	-0.018	0.005	0.001	0.65
Inactive to Leks > 25 Males	*Tillage 1.0km*	-3.771	1.132	0.001	4.02
	Leks 12.3km	20.332	6.795	0.003	*ns*
	Sage	1.581	0.391	< 0.001	1.77
	Distrange	0.031	0.005	< 0.001	1.19
	Lag 12.3km	-0.057	0.786	0.941	*ns*
	Road 3.2km	-0.028	0.007	< 0.001	1.54

Table 6. Estimated β-coefficients from abundance only logits (small to large leks) from full multinomial model.

	Variable	β_i	SE	p
Abundance Only: Small Leks to Large Leks	*Tillage 1.0km*	-2.832	1.108	0.011
	Leks 12.3km	17.612	5.615	0.002
	Sage	0.688	0.380	0.071
	Distrange	0.004	0.000	0.369
	Lag 12.3km	-1.702	0.655	0.009
	Road 3.2km	-0.009	0.006	0.202

Figure 1. Current (green) and historic (tan) occupied range of greater sage-grouse (Schroeder et al. 2004). Habitat north of the Milk River and in North and South Dakota is dominanted by plains silver sagebrush while the remaining range is predominately Wyoming big sagebrush.

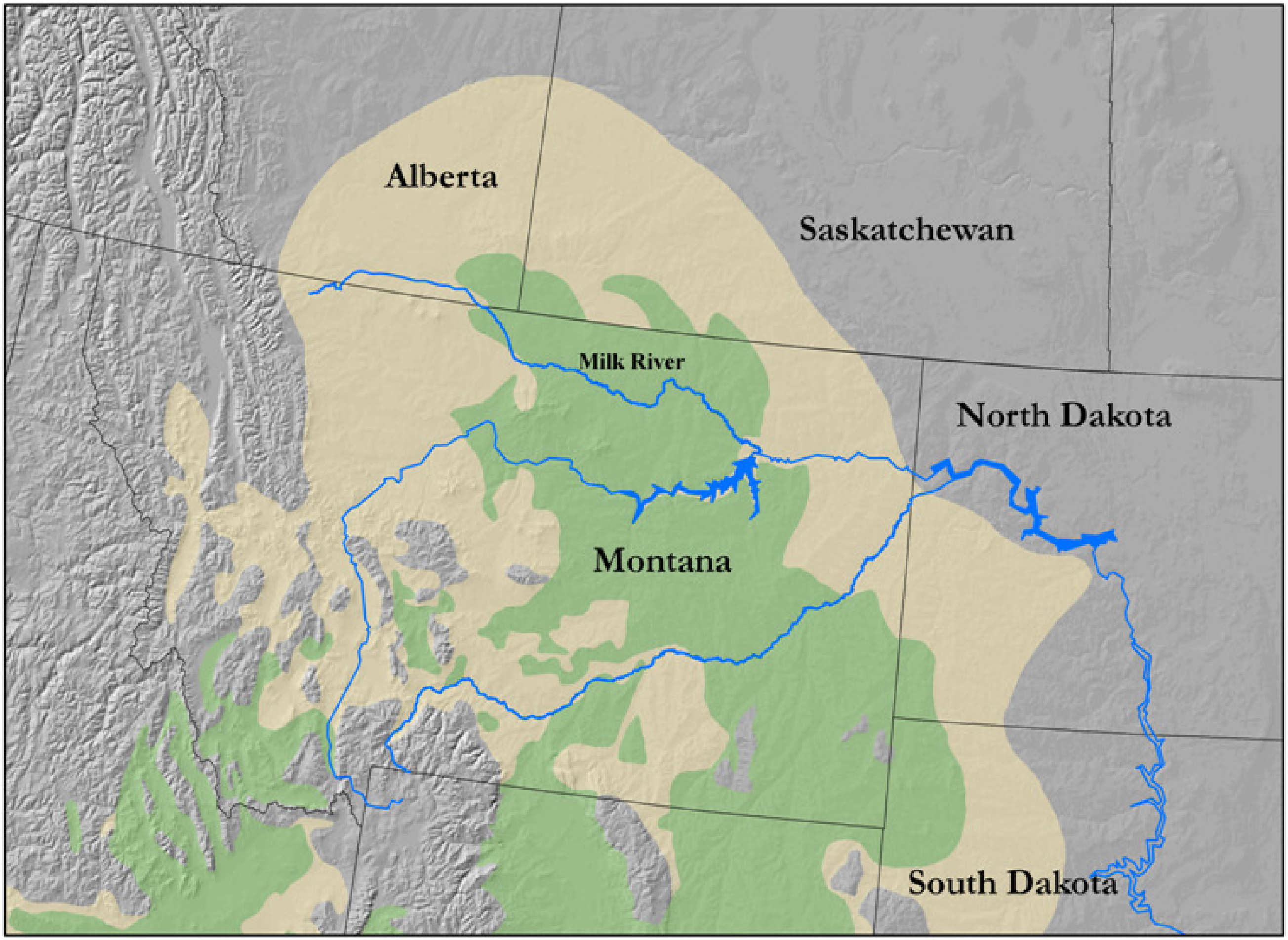
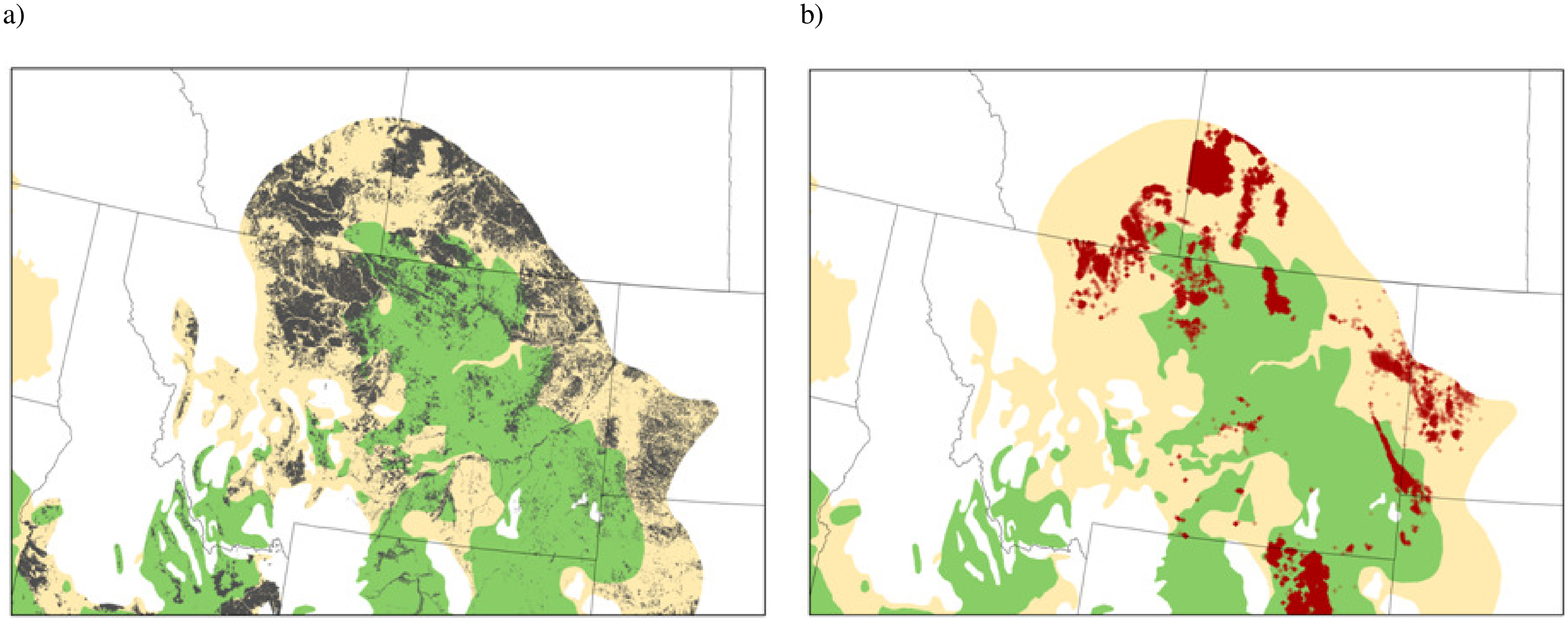


Figure 2. Agricultural tillage (a), and producing oil and gas wells (b) in the historic (tan) and occupied (green) range of sage-grouse within our study area.


a)

b)

Figure 3. Frequency of male counts at leks within the study area. Shaded bars represent upper quartile of leks, containing > 25 males.

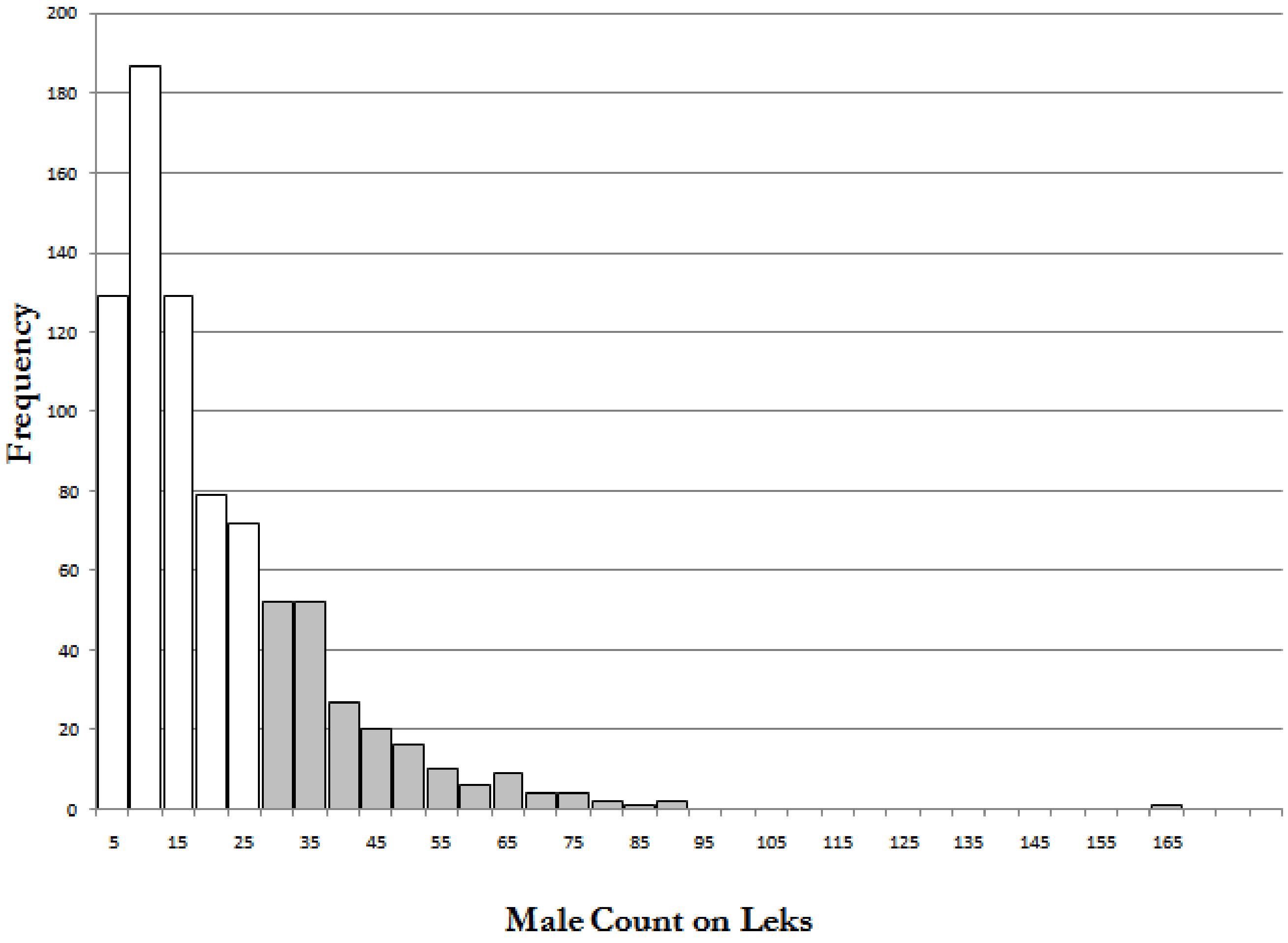


Figure 4. Probability of active lek occurrence of leks with ≤ 25 males (open circles), and leks >25 males (closed circles) and agricultural tillage within 1.0km of a lek, values predicted for leks in big sagebrush habitat.

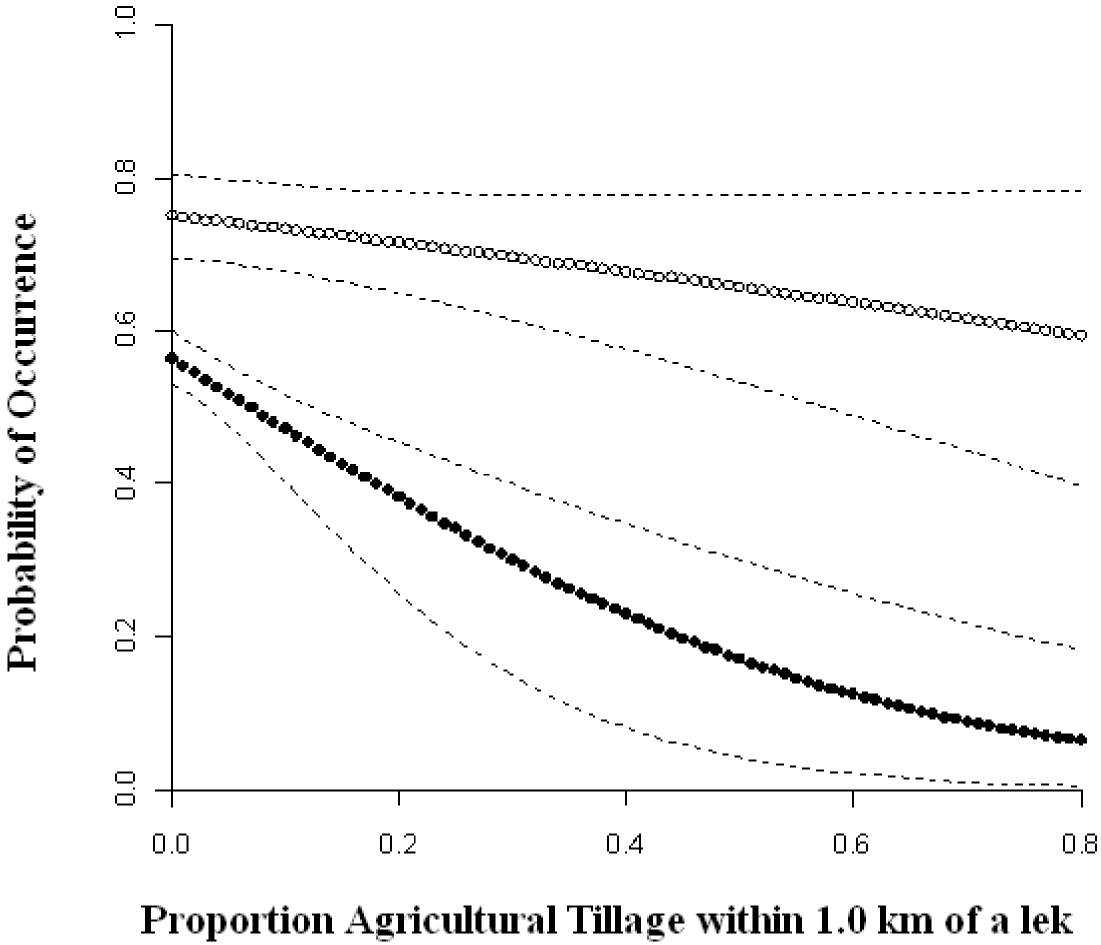


Figure 5. Probability of active lek occurrence of leks with ≤ 25 males (open circles), and leks >25 males (closed circles) and leks are located in from the edge of the historic range, values predicted for leks in big sagebrush habitat.

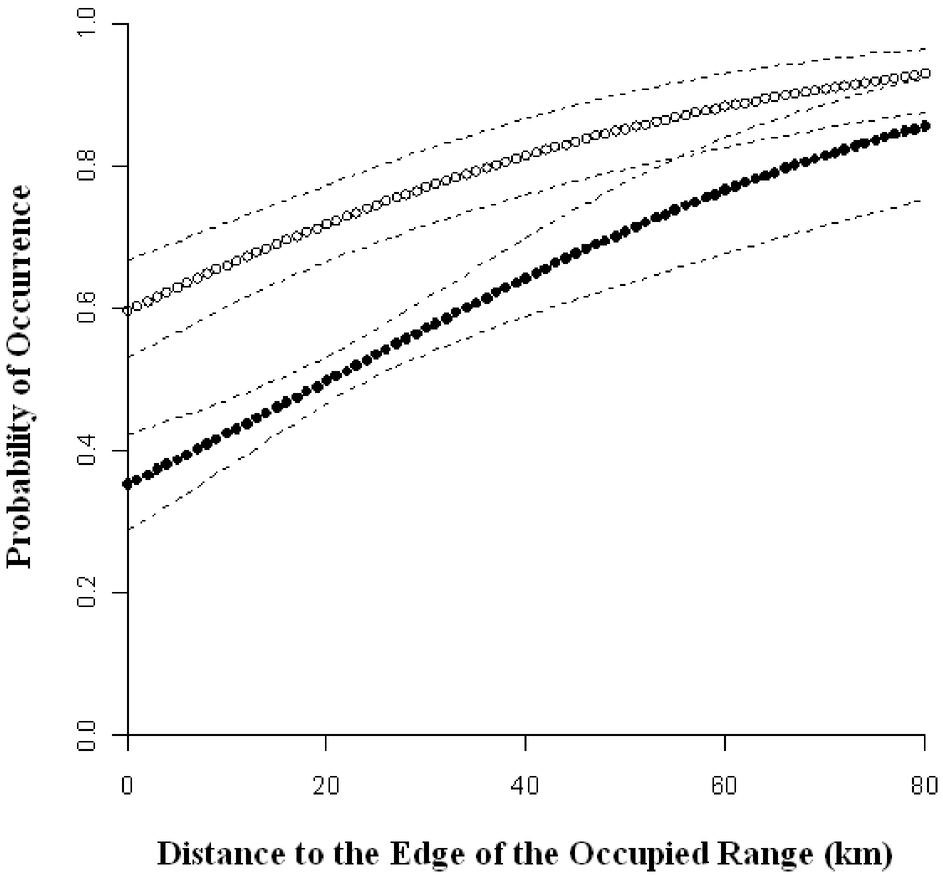


Figure 6. Probability of active lek occurrence with < 25 males (open circles), and leks >25 males (closed circles) with increasing roads within 3.2km of a lek, values predicted for leks in big sagebrush habitat.

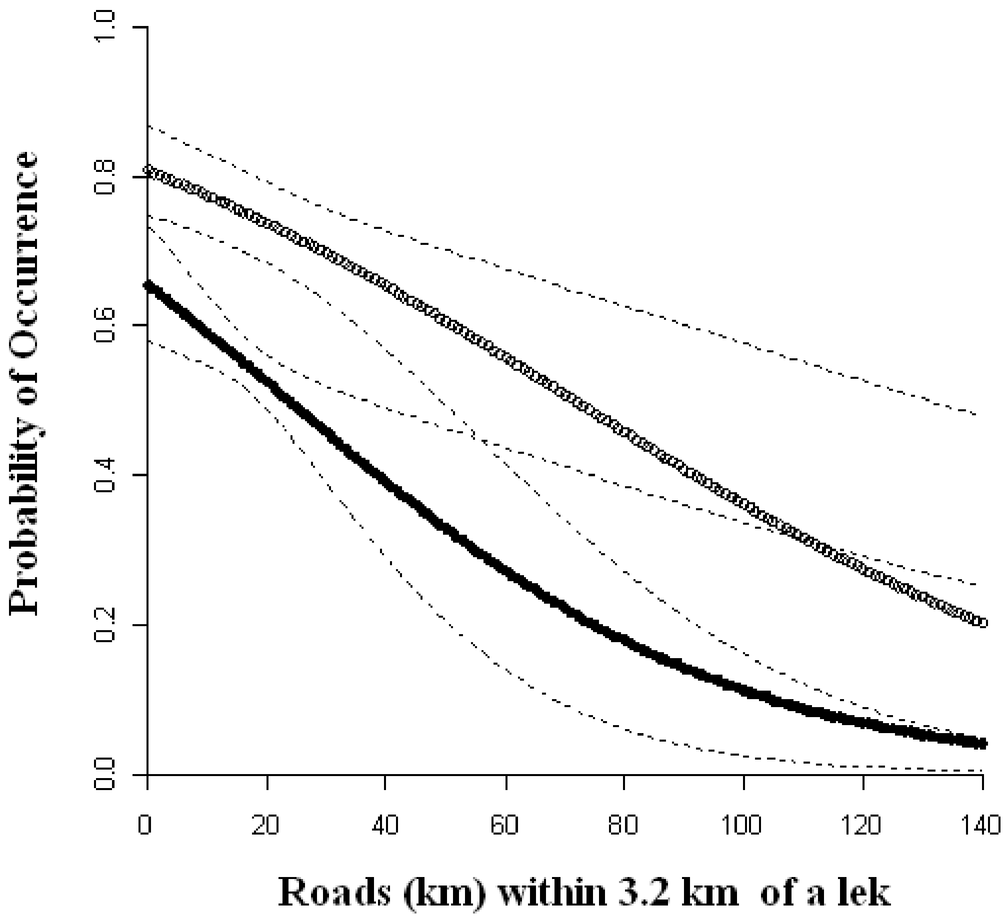


Figure 7. Probability of active lek occurrence with > 25 males with the number of active leks within 12.3km, predicted for leks in big sagebrush habitat.

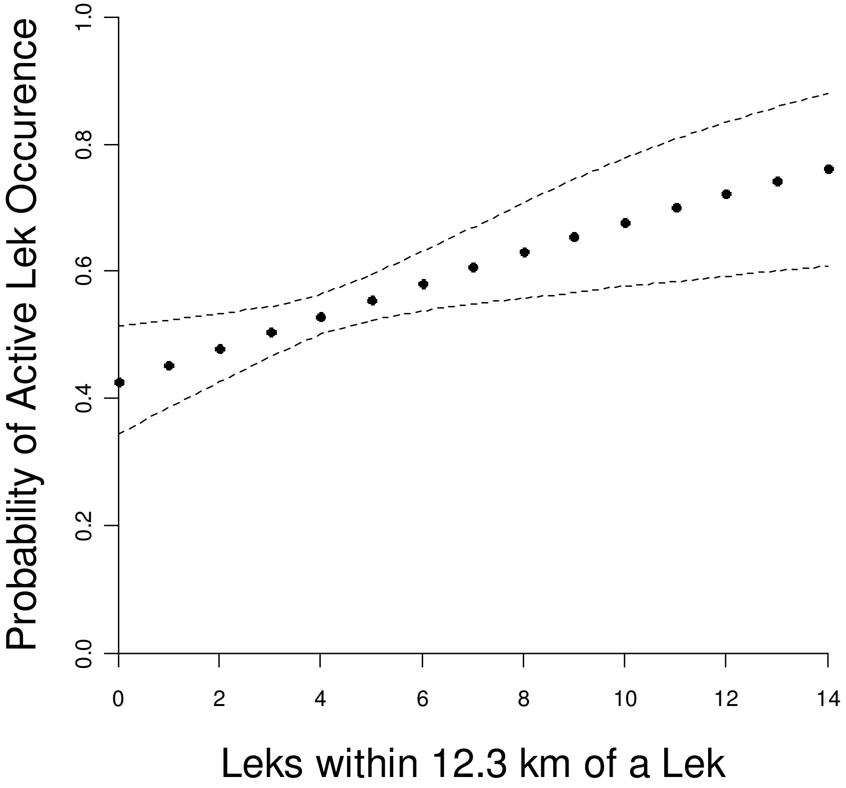


Figure 8. Probability of a lek being large (> 25 males) and agricultural tillage. Closed circles represent leks in big sagebrush habitats and open circles are estimates for leks in silver sagebrush.

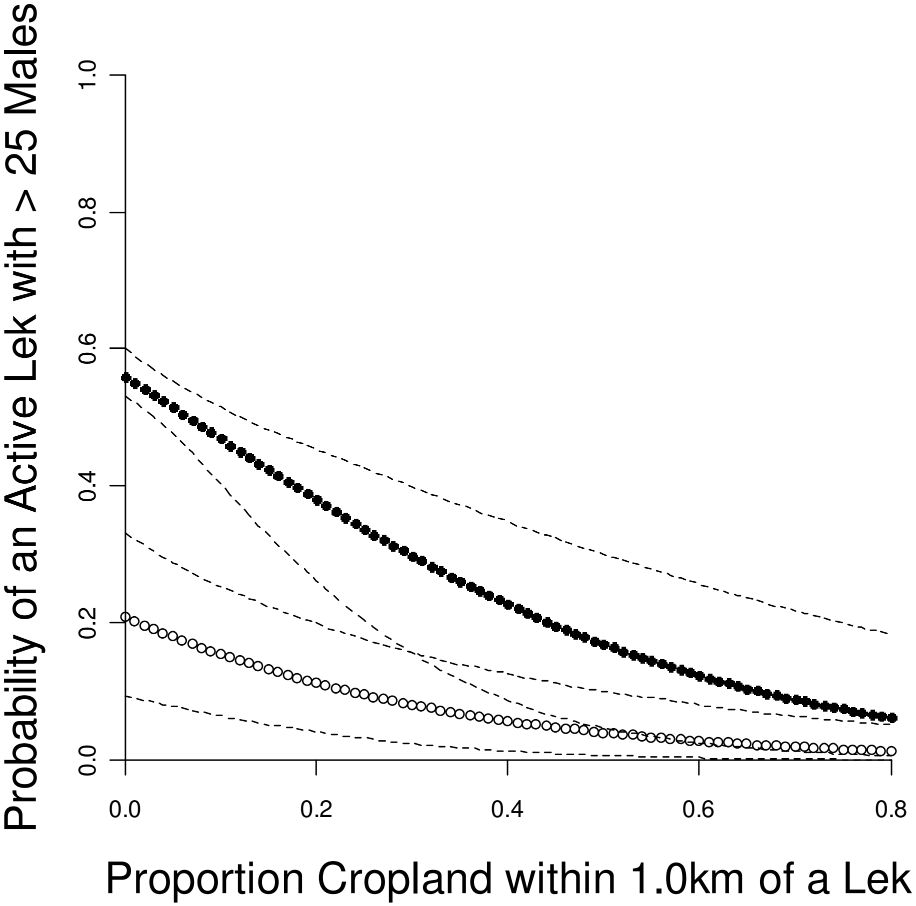


Figure 9. Probability of a lek being large (> 25 males) with increasing well density. Well densities have a simulated 4 year time lag, which represents wells 4 years prior to current counts, or the year a lek went inactive.

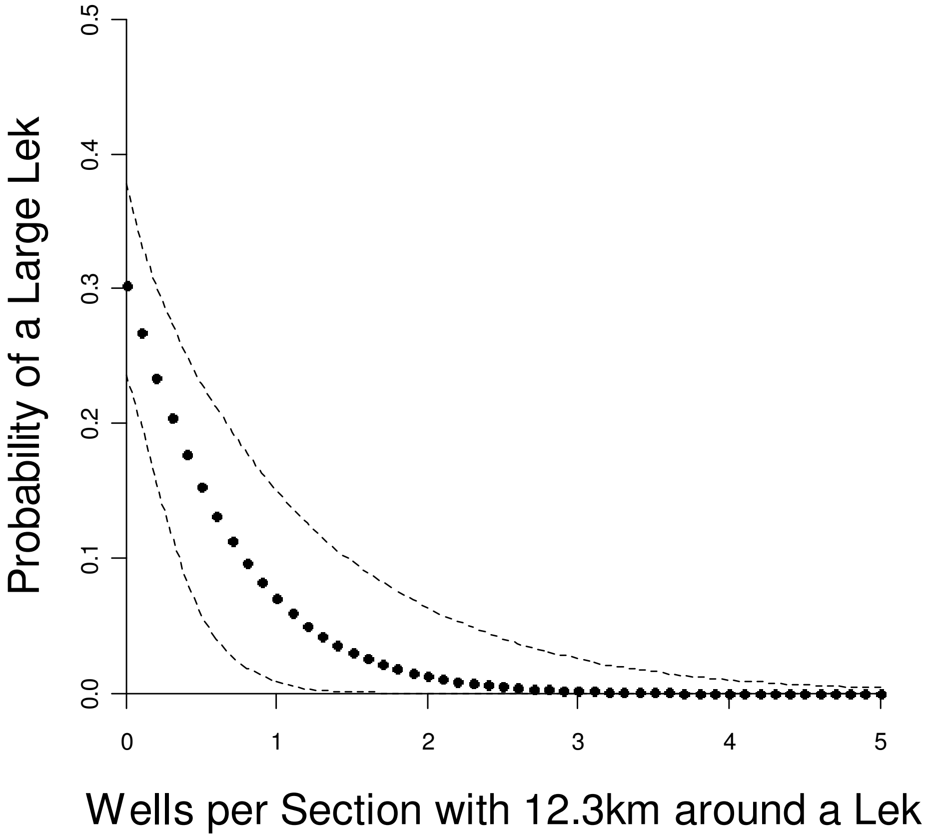


Figure 10. Well density within 12.3km, and agriculture within 1.0km at active leks (x) and inactive leks (o).

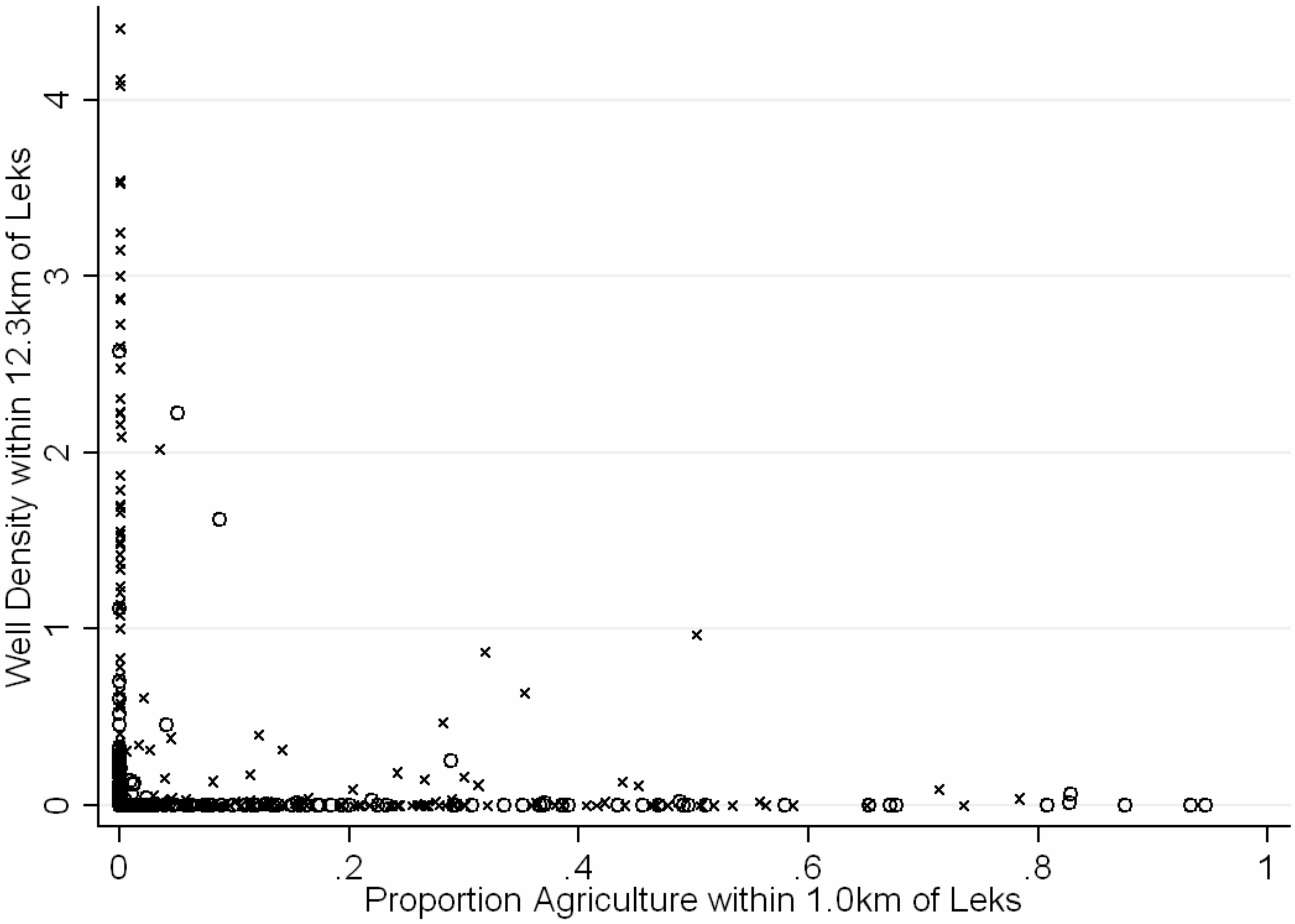


Figure 11. Well pad locations within greater sage-grouse habitat in the Cedar Creek Anticline. Open circles are 3.2km radii around active leks; hatched circles denote inactive leks in 2008.

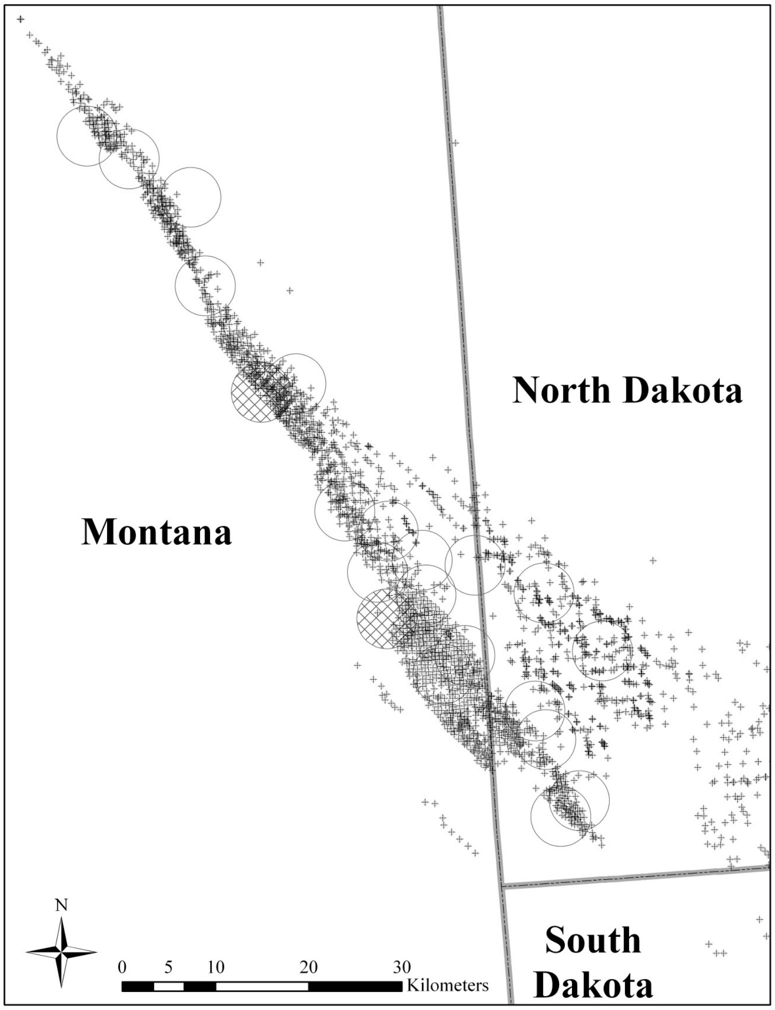
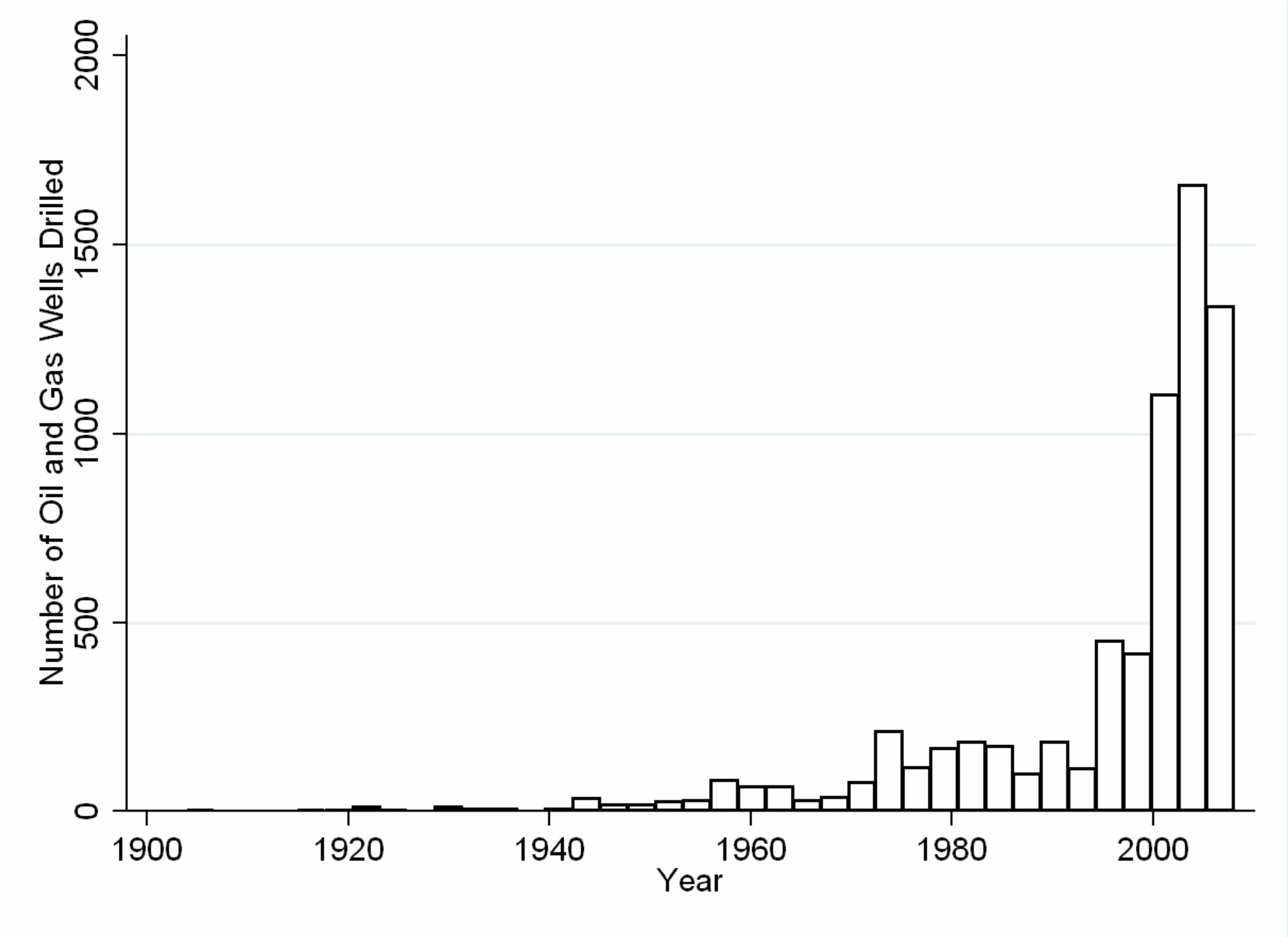


Figure 12. Number of producing oil and gas wells through time within study area.



CHAPTER 3: LOCAL HABITAT ECOLOGY AND DEMOGRAPHICS OF GREATER SAGE-GROUSE IN THE MILK RIVER BASIN OF NORTHEAST, MONTANA, USA AND SOUTH-CENTRAL SASKATCHEWAN, CANADA.

Introduction

Greater sage-grouse (*Centrocercus urophasianus*) historically occupied sagebrush habitats throughout western North America, occupying 16 US states and three Canadian provinces (Schroeder et al. 2004, Figure 1). Sage-grouse are inextricably linked to sagebrush for each stage in their life history. Conservation of sage-grouse populations is difficult in part because the sagebrush ecosystem is the most imperiled biome in North America (Noss and Peters 1995, Mac et al. 1998). Impacts to biodiversity are primarily attributed to human activities that have resulted in the direct loss and degradation of sagebrush (Knick et al. 2003). Major stressors include conversion of native rangeland to agricultural tillage (Connelly et al. 2004), invasion by exotic plant species (Knick et al. 2003), energy development (Naugle et al. 2010), and over-grazing (Hayes and Holl 2003, Crawford et al. 2004). Increasing energy demand (Copeland et al. 2009), subdivision (Theobald 2005), and the potential impacts of climate change (Thomas et al. 2004) further threaten the conservation of the sagebrush ecosystem. Half of the historic range of sage-grouse is no longer occupied (Schroeder et al. 2004), and remaining populations are decreasing by 2% annually (Connelly et al. 2004). Conservation of local populations on the edge of the species range is especially difficult (Chapter 2; Brown 1984), where isolated populations occupy marginal habitats (Chapter 2; Knick and Hanser 2010).

Local population declines of sage-grouse have previously been attributed to decreased productivity such as low chick survival (Aldridge and Boyce 2007), nest success (Schroeder et al. 1999), and female survival (Moynahan et al. 2006). Nest success and chick survival are linked to vegetative characteristics including shrub canopy cover and herbaceous understory (Aldridge and Brigham 2002, Holloran et al. 2005, Aldridge and Boyce 2008). Consequently, low productivity could reflect poor habitat conditions due to over-grazing or drought (Connelly et al. 2000), while stochastic events such as disease (Naugle et al. 2004) and severe weather (Moynahan et al. 2006) can greatly impact female survival. Identifying limiting factors is critical to ensure that conservation actions influence vital rates that drive population growth. Because negative growth rates exacerbate extinction risk for small populations, it becomes even more important to correctly identify factors.

In the US, distinct subspecies and regional populations of sage-grouse have been petitioned six times since 2001 for potential listing as a threatened or endangered species under the federal Endangered Species Act. The USDI Fish and Wildlife Service (FWS) has deemed each petition as not warranted, or warranted, but precluded for threatened or endangered status. The FWS recently began yet another range-wide status review of greater sage-grouse, and a listing decision will be issued in February 2010. Sage-grouse are still a harvestable game species in most states including Montana, where ~3,000 individuals were harvested in 2007. In Canada, sage-grouse occupy less than 10% of their historic habitat (Schroeder et al. 2004), and populations are declining annually at far greater rates than range-wide (Figure 2, Alberta Fish and Wildlife, and Grasslands National Park of Canada, unpublished data). The Committee on the Status of Endangered Wildlife in Canada listed sage-grouse as threatened in 1997 and endangered in 1998 under the federal Species at Risk Act. Provincially, Saskatchewan listed sage-grouse as threatened in 1987 and endangered in 1996. Sage-grouse have not been hunted in the province since 1938 (Kerwin 1971).

In this chapter, we estimate vital rates including nest, chick, and adult survival, and compare results to estimates from previous studies from declining, and stable to increasing populations. We also estimate nest-site selection in relation to vegetative characteristics to identify if habitat is limiting the ability of this population to respond well to habitat conditions. We hypothesized that one or more vital rates would be significantly lower than range wide estimates from stable and increasing populations, explaining continued population declines. One vital rate that may be disproportionately low is nest success. We hypothesized that overall shrub cover and density would be lower than range wide estimates around nest sites because of the less dense silver sagebrush, which may explain possible decreased nest success.

Study Area

We studied a population of sage-grouse in the East Block of Grasslands National Park (GNP), Saskatchewan, Canada and northern Valley County, Montana comprising the eastern portion of the Milk River Basin (MRB) (Figure 3). The MRB is a semi-arid landscape at 800m elevation, receiving 299mm of annual precipitation (181mm to 465mm annually). Average temperatures range from -18.0 to -6.3°C in January to 9.85 to 27.16°C in August (Opheim 12 SSE weather station, unpublished data). Short-grass prairie upland dominates the landscape with a predominantly native understory of western and northern wheatgrass (*Agropyron smithii, A. dasytachyum*), needle and thread grass (*Stipa comata*), and blue grama (*Bouteloua gracilis*). Sparse patches of shrubs are interspersed in prairie uplands, the most common being plains silver sagebrush (*Artemesia cana cana*), with lesser amounts of black greasewood (*Sarcobatus vermiculatus*), silver buffaloberry (*Shepherdia argenea*), gray horsebrush (*Tetradymia canescens*) and yellow rabbitbrush (*Chrysothamnus viscidiflorus*). Uplands are disrupted by drainages with perennial to semi-perennial water flows, which are surrounded by large overflow areas with dense shrubs, predominantly silver sagebrush. Sage-grouse typically occur in Wyoming big sagebrush (*A. tridentata wyomingensis*) habitats, which is replaced by silver sagebrush north of the Milk River in Montana. Silver sagebrush is a structurally less dense shrub providing less cover than big sagebrush, and silver sagebrush occurs in much lower densities across the range (Aldridge and Brigham 2001). Land is owned primarily by the Bureau of Land Management (BLM) in Montana, and is leased for grazing by domestic livestock. In recent years, most of the East Block of GNP has not been grazed by domestic livestock. Small portions of the East Block are grazed by cattle, including a 1,800ha parcel of land that is part of a grazing biodiversity experiment within park boundaries (Parks Canada 2006).

Methods

Capture and Handling— We captured sage-grouse during the breeding seasons of 2007 - 2008 on four leks in north Valley County, Montana, USA and on one of six remaining leks in Saskatchewan, Canada in GNP. Sage-grouse were captured using rocket nets and spotlighting with hoop-nets (Wakkinen et al. 1992), and modified walk-in traps (Schroeder and Braun 1991). All female sage-grouse were fitted with A4060 22 gram VHF radio-collars that have an expected battery life of 434 days (Advanced Telemetry Systems; Isanti, MN, USA). We measured cranial and tarsus lengths, and massed each female. We then determined if the female was hatched from the previous nesting season, or was a second-year adult based on primary feather development (Eng 1963). We collected 2 mL of blood from each female for genetic sampling. All animal handling was approved by the Institutional Animal Care and Use Committee, permit number 035-05DNCFC-020106.

<u>Nest and Brood Monitoring</u>— We monitored females every two to four days to document nest initiation. We monitored from a distance of > 30m so as not to flush females, which could result in nest abandonment (Walker 2008). If females were in different locations on consecutive visits, we checked each previous location to identify if females had constructed a nest. We assumed females had begun to incubate a nest if they were in the same location for two consecutive visits (Schroeder et al. 1999). We defined the nest initiation date as the midpoint between the last date the female was located and the first known date of incubation. Once a nest was located, we monitored fate of the nest every two to five days until it hatched or failed. If a nest failed, we estimated clutch size by counting the number of eggs present and recorded whether the nest was depredated (eggs destroyed) or abandoned (eggs in tact). We defined a nest as hatched if ≥ 1 egg had a detached membrane (Klebenow 1969).

When a nest hatched, we attempted to determine whether or not the female had a brood by approaching the hen, searching for chicks, and observing hen behavior. We classified a female as having a brood if chicks were observed or heard near the hen, if the hen gave a wing-dragging or flutter-hopping display, walked or ran away from the observer while vocalizing rather than flying, or aggressively approached the observer. If chicks were present, we monitored each female and her brood every three to five days. At 35 days, and at 50 days post hatch we flushed females to determine if there were broods and if so, to count chicks.

Sage-grouse exhibit a social brood-rearing strategy in which chicks may amalgamate with other broods. This behavior could bias low estimates of brood success if chicks from one female were successfully raised by another female or high if a radio-marked female adopted and raised chicks from a different brood. Thus, we only compare our estimates of brood survival to those from other studies with similar methodologies to reduce bias in our interpretations. Evidence suggests that a brood may be comprised of chicks hatched by $\geq$ 1 female, and that females without broods may still have chicks survive to independence. A study in Colorado found that domestic sage-grouse chicks are adopted >90% of the time when released near a wild-born brood (T. Apa, Colorado Division of Wildlife, unpublished data). We observed several broods with different sized chicks suggesting younger or older chicks were adopted, and in 2008 we observed a sage-grouse adopt a chick from a brood of sharp-tailed grouse (*Tympanuchus phasianellus*).

West Nile virus Monitoring— We continued to track females every two to five days through September to document mortalities due to West Nile virus (WNV). We collected all remains of birds that died throughout the summer and froze samples as soon as possible. We sent carcasses to the Wyoming State Veterinary Laboratory in Laramie, Wyoming to be tested for neutralizing WNV antibodies using a micro plaque reduction neutralization test (Weingartl et al. 2003).

Winter Monitoring— We conducted 6 flights each winter between November and March in 2008 and 2009 to relocate radio-marked females and determine if they were still alive. If we received a mortality signal, a technician on the ground relocated the radio-collar to ensure that the individual was dead, and that the signal was not due to collar loss or failure.

Vegetation Sampling— We estimated fourth order (Johnson 1980) nest-site selection by measuring shrub and grass characteristics at nests and at an equal number of paired random sites. Random sites were assigned by pairing the distance each respective female nested from the capture lek to a random decimal degree direction. We sampled the shrub nearest to the random location because sage-grouse center nests under shrubs. We measured vegetation characteristics known from other studies to influence nest-site selection, so we could make direct comparisons to guidelines used for managing sage-grouse habitat (Connelly et al. 2000). We estimated shrub canopy cover, along two 30m line transects aligned north to south and east to west, centered at the used or randomly selected nest shrub (Wambolt et al. 2006). We measured shrub height, and the tallest and average grass heights in $1m^2$ quadrats along 3m intervals along each transect line. We counted shrubs > 15cm within 1m of transect lines, and divided the total by $120m^2$ to estimate shrub density. To estimate visual obstruction around the nest, we took measurements from a Robel pole at the nest site in each cardinal direction, as well as from 1-, 3-, and 5m intervals from the nest (Robel et al. 1970). At each quadrat we measured the coverage of herbaceous material, native and exotic grasses, and forb cover in ranked percentages (Daubenmeyer 1959). Because dense sagebrush limits understory growth, and may inhibit ability to detect predators, we also calculated a quadratic term for shrub canopy cover (Aldridge and Boyce 2007).

Demographic Analyses— We estimated female survival from March – September in 2007 and 2008 using the Kaplan-Meier product limit estimator (Kaplan and Meier 1958) with staggered entry design (Pollock et al. 1989, Winterstein et al. 2001). We right-censored females with collars that malfunctioned, and those that could not be relocated. We excluded estimates of cause-specific mortality because it is difficult to assess whether or not the carcass had been scavenged (Thirgood et al. 1998). We tested for differences in survival between years and age classes using a log rank test modified for staggered entry and observations censored according to Pollock et al. (1989).

We defined nesting effort as the proportion of females that attempted to initiate a nest. We estimated fledgling success as the proportion of females that raised $\geq$ 1 chick to 50 days (Schroeder 1997). We estimated chick survival by counting the number of chicks present at 35 and 50 days post hatch. We compared the number of chicks to the number of eggs hatched by females, using the maximum estimate from flush counts.

We defined apparent nest success as the proportion of nests that hatched $\geq$ 1 egg. Estimates for apparent nest success may be biased high because early nest failures may not be detected. We accounted for this potential bias by calculating a maximum likelihood estimate of daily survival rates of nests using program MARK (Rotella et al. 2004). Program MARK requires information on 1) the day incubation began, 2) the last day the nest was known to be alive, 3) the last day the nest was checked and 4) the fate of the nest. We estimated the incubation date for successful nests by backdating 28 days from the estimated or known hatch date. For unsuccessful nests, we estimated the start date for incubation as the midpoint between the first day the female was on the nest and the date of the previous location (Walker 2008).

Lastly, we estimated apparent survival of sage-grouse in winter. We hypothesized that during average winter conditions, we would observe a high rate of survival (>75%) if females occupied suitable winter habitat (Connelly et al. 2000). We calculated apparent survival as the proportion of radio-marked females alive at the start of winter relocations divided by the proportion that survived until the last flight in March.

Habitat Analyses— We analyzed vegetative characteristics that best explained nest-site selection by comparing sage-grouse nest-sites to paired random locations with matched-case logistic regression (Hosmer and Lemeshow 2000). Matched-case logistic regression is superior to traditional multivariate analyses (e.g., discriminate function) because it does not assume identical covariance matrices between used and random locations, and allows for non-normal distributions among independent variables (North and Reynolds 1996). Matched-case control logistic regression inherently controls for local habitat availability (Compton et al. 2002).

We developed an *a priori* global model to explain habitat selection by nesting females (Table 1), followed by an exploratory analysis of correlated predictor variables (Chatfield 1995). We tested highly collinear variables ($r \geq |0.7|$) using univariate conditional logistic regression, and retained the predictor variable with the best model fit (highest log-likelihood value). Moderately correlated variables ($|0.3| < r < |0.7|$) were included in development of *a priori* candidate models, but were removed if the direction of the coefficient changed or if the standard errors increased dramatically. We then developed candidate models based on previous literature about sage-grouse habitat selection in silver sagebrush habitats, and biological knowledge of the study system. We tested candidate models using Akaike Information Criteria (AIC_c), corrected for small sample sizes (Burnam and Anderson 1998). To determine plausible models for nest-site selection, we used all models within 2 units of the minimum AIC_c value. We used a log-link survival analysis in program MARK using the same model building strategy for nest-selection models to estimate the influence of vegetation on daily survival rates (Rotella et al. 2004).

Results

Reproductive Effort and Success— Nesting effort was 90% in 2007 (n=30) and 95% in 2008 (n=41). Average clutch size differed between years or age class (6.6 ± 1.6; range 4-11 eggs). Females placed nests an average of 5,297m (± 3397m; range 609m-15,684m) from the lek of capture (Figure 4). In 2007, 13 females were unsuccessful in their first nesting attempt, and 3 females initiated a second nest (23%), and of 17 unsuccessful first nesting attempts in 2008, 7 females initiated a second nest (41%). Apparent nest success and maximum likelihood estimates were different for age classes and years, and varied in magnitude and direction (Table 2). Apparent nest success and maximum-likelihood estimates for all females was 57% and 62% in 2007, and 53% and 54% in 2008.

Fledging success was 37% (10/27) for all females that attempted to initiate a nest in 2007 was, and 59% (10/17) for females with successful nests. In 2008, fledgling success was 31% (12 of 39 females) for reproductively active females, and 60% (12/20) for successfully nesting females. Estimated chick survival was 33% in 2007 (34/102), and 38% in 2008 (42/110).

Survival— No individuals were censored from survival analyses in 2007. In 2008 we censored two individuals due to known collar failure (one collar emitting solid tone at low volume, one collar emitting weak and erratic tones), and two females were censored after we were unable to relocate them shortly after the radio was affixed. Estimated survival was 0.55 (± 0.09) from 19 March – 3 September 2007 and 0.91 (± 0.04) during 20 March – 2 September 2008 (Figure 5). Spring and summer survival differed between years ($\chi^2 = 14.16$, $p < 0.001$). In 2007 juvenile survival (86% ± 8.77%) was higher than adult survival (20% ± 10.33%; $\chi^2 = 12.90$, $p < 0.001$). In 2008, juvenile survival (1.0) was higher than adult survival (90% ± 4.68%) but not significantly so ($\chi^2 = 0.67$, $p < 0.25$). In 2007, there were 6 mortalities in July suspicious for WNV, and laboratory results confirmed two positive WNV carcasses. The remaining carcasses were too decomposed or degraded by predation or scavenging to determine the cause of death. Apparent survival in winter was 84% (16/19) in 2008 and 92% (24/26) in 2009.

Local Nest Vegetation— Vegetation measurements at nests differed between years, with more shrub cover and higher shrub density at nests compared to random sites (Table 3). Average and tallest grass heights were correlated (r > 0.7), and were not allowed to compete in the same models, nor were shrub cover variables with their respective quadratic equations. The most parsimonious model that differentiated between nests and random locations included shrub cover, robel measurements, and average grass height (Table 5). Models including silver sagebrush cover and shrub density were also considered plausible because the AIC_c value was $\leq$ 2 units away from the most parsimonious model (Table 6). Model estimates produced positive coefficients for overall shrub cover ($\beta_{\mathrm{Sh.Cov}}$= 21.69), average grass height ($\beta_{Gr.Avg}$= 0.14), and the plot averaged visual obstruction reading (β_{Robel}= 0.42), explaining sage-grouse nest occurrence. No variables were significant when evaluating the effect of vegetation on daily nest survival, likely due to a small sample size.

Discussion

Vegetative features and individual demographic vital rates do not appear to be limiting population growth of sage-grouse in the MRB. Declines in other populations near the edge of their range have been attributed to productivity, namely low chick survival (13%) in Alberta (Aldridge and Boyce 2007), and low nest survival in Washington (12%; Schroeder et al. 1999). In contrast, vital rates in the MRB are comparable to those of large and stable populations. Nest survival in the MRB (53-61%) was comparable to large, stable populations northern Wyoming (35-60% for Adults; Walker 2008), and in north-central (35-61%; Moynahan et al. 2007) and south-central Montana (40%; Sika 2006). Fledgling success in the MRB was 5-10% higher than for a neighboring population in Alberta (28%) where brood survival was impacted by energy development (Aldridge and Brigham 2001). Apparent chick survival in the MRB (33-38%) mirrored that of a stable Wyoming and Montana population (33-50%; Walker 2008), and survival was much higher than in Alberta (14-23%; Aldridge and Brigham 2001).

We found that sagebrush cover, grass height and visual obstruction best explain sage-grouse nest selection in the MRB (Table 4). As expected, nest sites in the MRB had lower shrub cover (15%), than what is typically found at nests range-wide (15-56%; Hagen et al. 2007). Results agree with a range-wide meta-analysis conducted by Hagen et al. (2007) with one notable exception. Overall shrub cover, instead of sagebrush cover in the MRB, was a better predictor of nest-site selection. Silver sagebrush around nest sites made up only about half of the total shrub cover estimates (7.1% of 14.6%), suggesting that other shrubs including greasewood and rabbitbrush compensate for lower sagebrush densities found in the MRB. At nest-sites sage-grouse selected shrubs other than sagebrush 26% of the time (19 of 72 nests), suggesting that the cover rather than species composition is more important in providing protection from predation. Small sample sizes of nests in the MRB preclude interpretation of the potential influence of herbaceous cover on nest survival. Lack of significance does not mean that herbaceous cover does not impact nest survival in the MRB. Several studies have shown that successful nests have more shrub cover, and higher grass height than unsuccessful nests (Gregg et al. 1994, Aldridge and Brigham 2002, Holloran et al. 2005).

Sage-grouse in the MRB experienced a 37% decline in female survival following an outbreak of WNV in 2007 (Figure 5). Outbreaks are known to result in local extirpations (Naugle et al. 2004), 90% population declines (A. Robinson, North Dakota Game and Fish, Personal Communication), and ultimately decrease population growth (Walker and Naugle 2009). West Nile virus further complicates conservation in the MRB because outbreaks in small and isolated populations are more likely to reduce population size below a threshold from which recovery is unlikely and the likelihood of demographic or genetic rescue by adjacent populations is low (Morris and Doak 2002). West Nile virus was first discovered in sage-grouse in Wyoming 2003 (Naugle et al. 2004), and since has spread throughout most of the species range (Walker and Naugle 2010). Laboratory experiments documented 100% mortality of sage-grouse within 6 to 8 days following experimental infections of WNV at all dosage levels (Clark et al. 2006). Sage-grouse resistance to WNV appears to be extremely low, and will likely not increase over the next 20 years (Walker et al. 2007).

Our results suggest that habitat may be sufficient for populations to respond to favorable conditions, but large scale ecological processes may ultimately dictate the fate of sage-grouse in the MRB (Lacy 2000). The ability of the sage-grouse in the MRB to persist through time and to buffer against periodic declines is greatly depressed now that a once-large population has become small (Aldridge 2000), and isolated (Bush 2009). This phenomenon, termed the "extinction vortex" inevitability leads to extirpation of small populations faced with repeated stochastic demographic events. For example, processes such as WNV that decrease population growth, are compounded when acting on fewer individuals, working synergistically with fluctuations in growth rates (Gilpin and Soule 1986). In all of Canada, one lek remains that consistently supports ≥ 20 displaying males. Consequently, conservation of sage-grouse in the

MRB will depend on maintaining the current habitat base (Chapter 2), and on restoring sagebrush-dominated grasslands currently occupied by agricultural tillage.

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Table 1. Predictor variables used to model sage-grouse nest site selection.

Variable	Description
Sh.Cov	Shrub cover at 30m plot (Wamboldt et al. 2006).
ARCA.Cov	Same as shrub cover with only *A. cana* counted in coverage.
Sh.Dens	Density of shrubs at transect (All shrubs within 1m of transect line / 120m^2).
ARCA.Dens	Same as shrub density, only sampling *A. cana.*
Sh.Quad	Shrub canopy cover = (shrub canopy cover * shrub canopy cover).
ARCA.Quad	*A.cana* canopy cover = (*A.cana* canopy cover * *A. cana* canopy cover).
Sh.Hght	Average shrub height from of shrubs occuring in quadrats.
Gr.Tlst	Average of the tallest grass "droop" height found in sampling quadrats.
Gr.Avg	Average of the grass height found nearest to the edge of the quadrat.
Robel.Nest	Robel measurements taken at each cardinal direction at the nest-site.
Robel.Plot	Robel measurements averaged across the plots.

Table 2. Apparent nest success and maximum likelihood estimates derived from daily survival rates (DSR ^ 28 incubation days) calculated in program MARK. All standard errors for maximum likelihood estimates are presented below nest survival estimates.

	Grouping	*n*	Apparent Nest Success	Maximum Likelihood Estimate	Difference
2007	Pooled	30	56.67%	61.64% 0.0049	4.97%
	Adults	21	52.38%	58.19% 0.0063	5.81%
	Juveniles	9	66.67%	78.66% 0.007	11.99%
	1st Attempts	27	59.26%	62.99% 0.0051	3.73%
	2nd Attempts	3	33.33%	17.72% 0.0412	-15.61%
2008	Pooled	45	53.33%	53.79% 0.0047	0.46%
	Adults	38	57.50%	60.46% 0.0046	2.96%
	Juveniles	7	14.28%	22.77% 0.0206	8.49%
	1st Attempts	37	50.00%	54.31% 0.0053	4.31%
	2nd Attempts	8	62.50%	55.68% 0.0118	-6.82%

Table 3. Estimates for vegetation characteristics measured at nests and paired random locations in 2007 and 2008. Cover and density estimates are presented as percentages; all standard errors are reported below estimates.

Habitat Variable	2007		2008		Combined	
	Nest	Random	Nest	Random	Nest	Random
Total Shrub Cover	10.39	5.67	17.13	3.28	14.6	4.21
	1.69	1.22	3.27	0.4	2.16	0.55
Artemesia cana Cover	5.37	2.40	8.26	3.25	7.18	2.91
	0.93	0.56	1.19	0.38	0.83	0.32
Total Shrub Density	12.93	7.82	36.04	16.17	27.37	12.89
	2.29	1.63	4.68	2.76	3.31	1.85
Artemesia cana Density	6.54	2.93	32.39	12.74	22.7	8.9
	1.14	0.60	4.32	1.76	3.1	1.23
Nesting Shrub Height	77.35	23.26	65.06	21.07	69.76	21.97
	9.63	2.89	4.07	1.79	4.48	1.58
Tallest Grass Height	27.45	18.9	27.57	23.72	27.53	21.83
	1.37	1.32	1.42	1.02	1.02	0.85
Nearest Grass Height	14.42	8.67	10.52	7.84	11.98	8.17
	1.08	0.88	0.65	0.38	0.61	0.41

Table 4. Estimates of silver sagebrush and shrub cover, and grass heights at successful and unsuccessful nests in 2007 and 2008.

	2007		2008		Combined	
Habitat Variable	Successful	Failed	Successful	Failed	Successful	Failed
Total Shrub Cover	11.51 2.74	8.97 1.73	14.13 4.32	20.54 4.96	13.12 2.84	16.34 3.34
Artemesia cana Cover	5.74 1.36	4.91 0.12	6.92 1.38	9.79 1.99	6.46 0.99	8.02 1.39
Tallest Grass Height	26.87 1.8	28.18 2.17	27.46 1.88	27.68 2.20	27.23 1.33	27.86 1.58
Nearest Grass Height	15.26 1.71	13.35 1.14	10.76 0.88	10.25 0.097	12.49 0.91	11.98 0.61

Table 5. β-coefficients and standard errors for predictor variables for top AIC model explaining nest-site by sage-grouse in the Milk River Basin.

Variable	Coefficient	SE	Lower 95% CI	Upper 95% CI
Sh.Cov	21.69	8.36	5.31	38.09
Gr .Avg	0.14	0.08	-0.03	0.29
Robel	0.42	0.16	0.01	0.72

Figure 1. Historic and current distribution of greater sage-grouse and Gunnison sage-grouse (*Centrocercus minimus*) in North America (Schoreder et al. 2004).

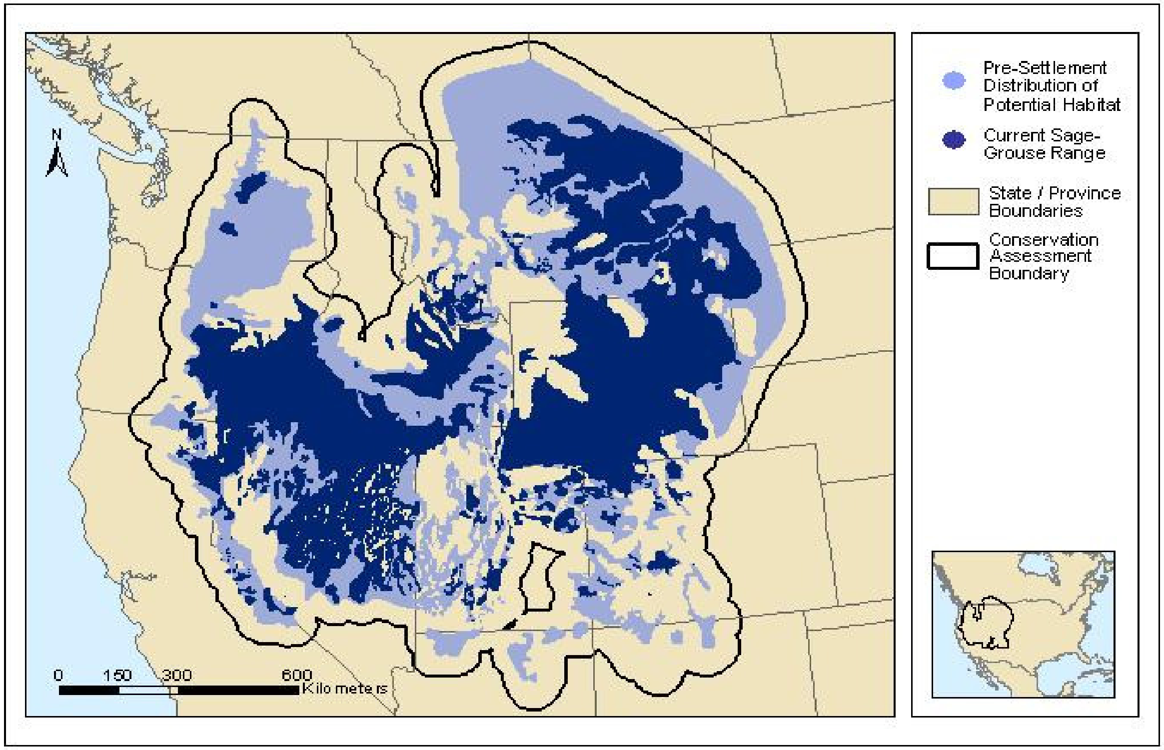


Figure 2. Change in male abundance of sage-grouse leks in Alberta and Saskatchewan 2000 - 2008.

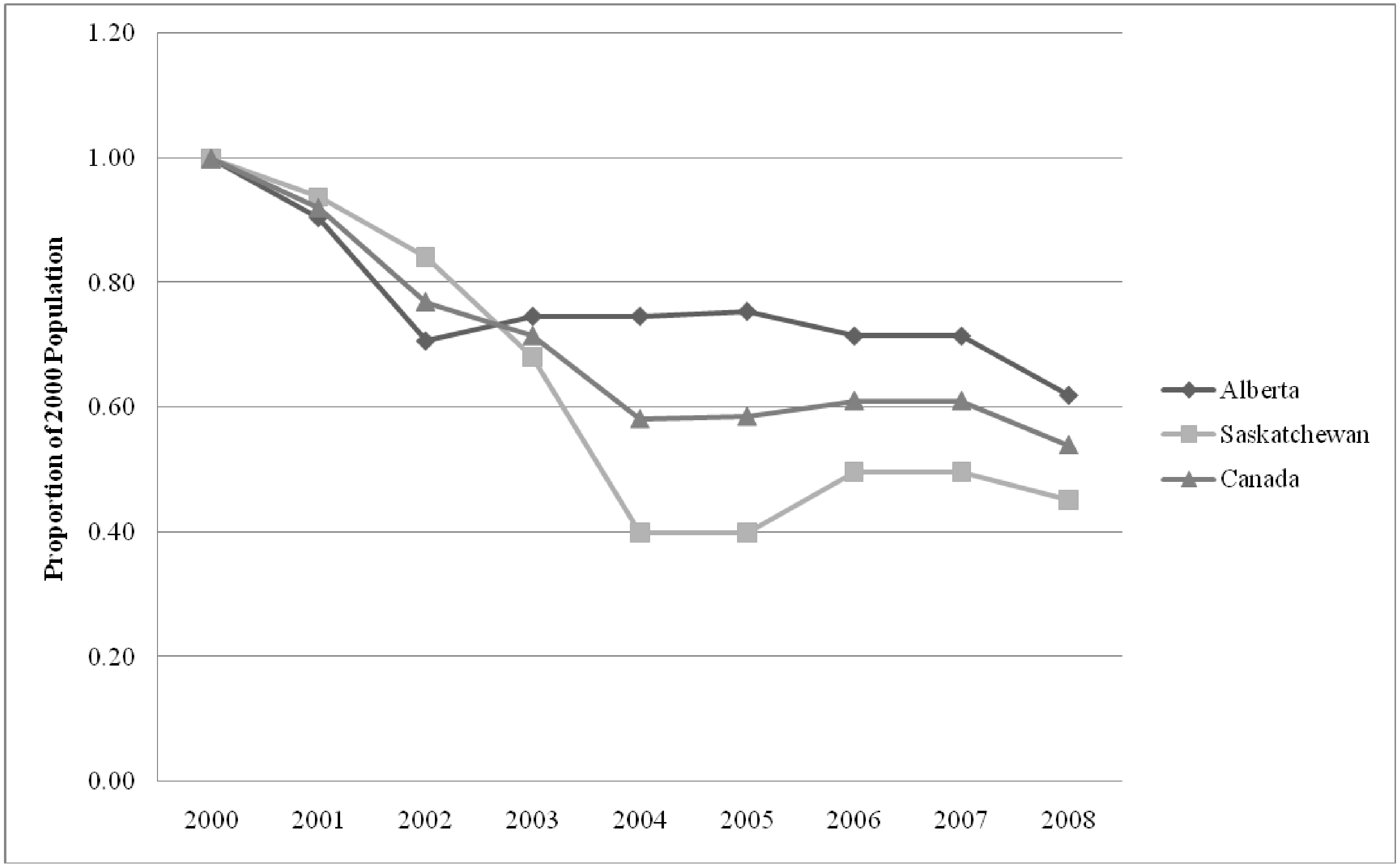


Figure 3. Location of sage-grouse leks in northeastern Montana, and southwest Saskatchewan. Plus signs represent 5 leks where females were captured in 2007 and 2008.

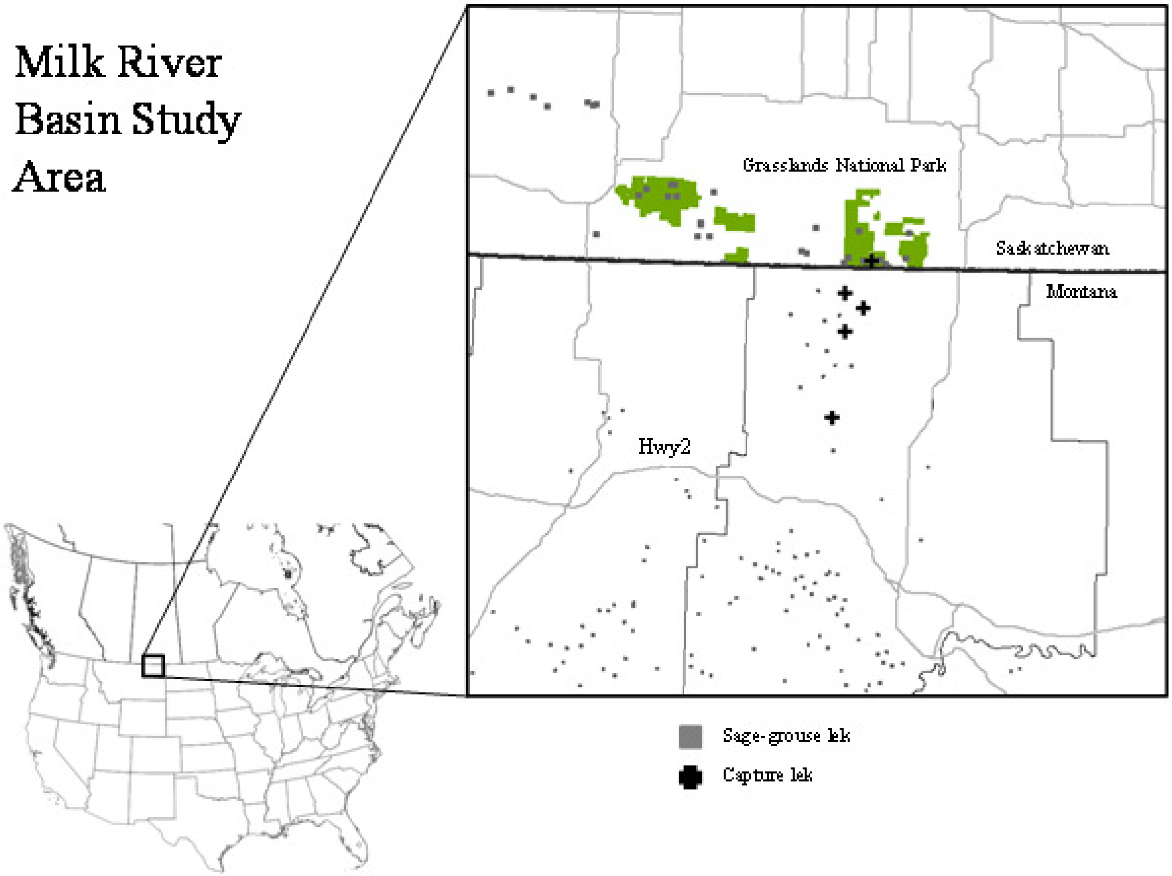


Figure 4. Distribution of greater sage-grouse nests (n=78) in relation to capture leks in north Valley County, Montana and the East Block of Grasslands National Park, Saskatchewan, 2007-2008.

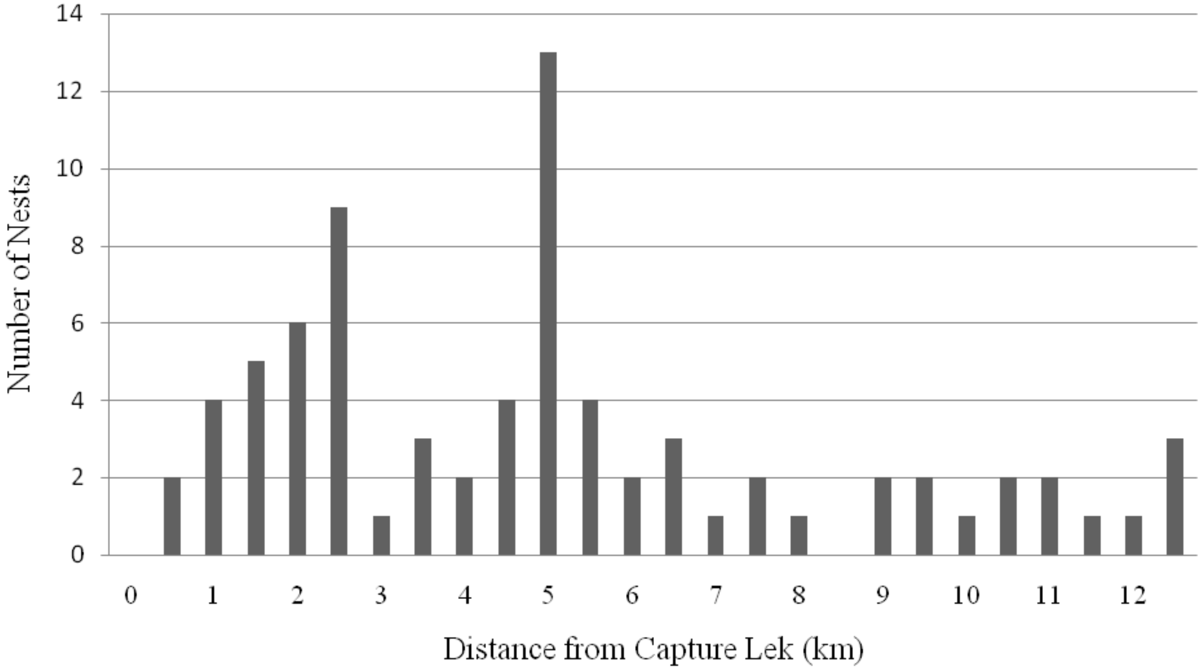
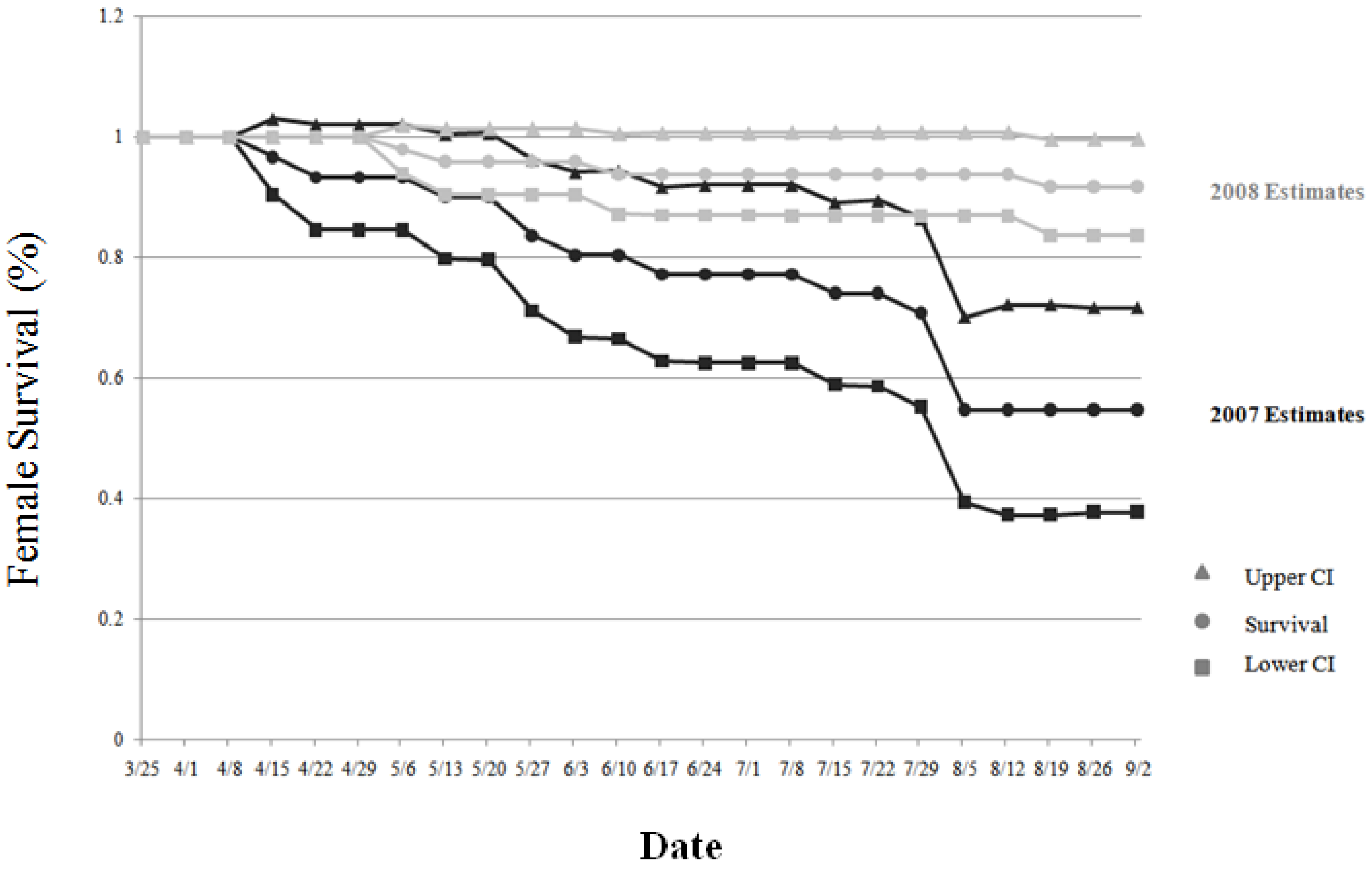


Figure 5. Kaplan-Meier product-limit estimates for survival of female sage-grouse, March through September, 2007 and 2008. West Nile virus (WNV) was confirmed in two sage-grouse carcasses in late July of 2007; no radio-marked females died of WNV in 2008.



CHAPTER 4: MIGRATION OF SAGE-GROUSE IN THEIR NORTHEASTERN RANGE: IMPLICATIONS FOR MANAGEMENT ACROSS AN INTERNATIONAL BORDER.

Introduction

As a sagebrush obligate species, sage-grouse are intricately linked to sagebrush habitats for each stage of their life-history. Following the spring breeding season, female-sage grouse seek out suitable amounts of canopy cover (15-25%) for nesting within sagebrush dominated grasslands (Hagen et al. 2007). Once eggs hatch, females move broods to more temperate areas to allow chicks to feed on ephemeral sources of forbs and insects (Aldridge and Boyce 2008, Gregg and Crawford 2009). The vegetative understory quickly desiccates in summer, forcing sage-grouse to congregate around limited remaining mesic areas (Connelly et al. 2000). In fall, sage-grouse begin to move to winter habitats (Connelly and Markham 1983, Connelly et al. 1989). Winter is when sage-grouse are most reliant on sagebrush for food and cover. Sage-grouse diets are comprised of >94% sagebrush during the winter (Remington and Braun 1985). Foraging habitat is typically found in the largest, densest stands of available sagebrush that remain above snow in winter (Homer et al. 1993, Doherty et al. 2008).

Sage-grouse have similar habitat requirements across their range, but the distances that different populations move to obtain resources are highly variable. Many non-migratory populations fulfill annual habitat requirements within overlapping seasonal ranges. Other populations are migratory, having distinct breeding, summer or winter ranges that are > 10km apart (Connelly et al. 2000). Distance between ranges is largely dependent on where suitable habitat is located within the landscape, and birds will make large movements when seasonal ranges are disparate. If suitable seasonal ranges are disparate from one another, sage-grouse will make large movements to use habitat. For example, a population in southeast Idaho travels up to 80km to use winter habitat, resulting in annual movements >150km (Dalke et al. 1963). The distance that some populations migrate highlights the need to document seasonal migration to ensure that conservation actions to benefit populations are delivered in the appropriate places.

Winter habitat is of particular interest in northern latitudes because large and dense tracts of silver sagebrush are limiting (Aldridge and Brigham 2002). Large, dense stands are limiting because land managers have used plowing, chaining, or prescribed burning to replace sagebrush with grass and forbs for livestock production (Knick et al. 2003). Sagebrush removal in selected areas may improve brood habitat by increasing forb production (Woodward 2006) but may also contribute to the loss of winter habitat. Sage-grouse habitat use in winter has received relatively little attention because survival is generally thought to be high. Yet following a severe winter in north central Montana, Moynahan et al. (2006) documented low overwinter survival associated with deep snow. Winter is also a time of year when a large portion of the population occupies a disproportionately small landscape. For example Beck (1977) found that 70% of a population in Colorado used only a ~7% portion of winter range. Sagebrush in winter represents a limited and at risk habitat that if not properly maintained could result in severe population-level impacts.

We radio-tracked a population of sage-grouse at the northeastern fringe of their range in Montana and Saskatchewan during the winters of 2008 and 2009. Breeding and summer ranges of this population encompassed silver sagebrush habitat, where habitat use in winter is poorly understood. Relocations throughout both winters enabled us to 1) assess the migratory status of a small population of conservation interest, and 2) determine the location and extent of their winter range to facilitate conservation actions to benefit this population.

Study Area

Our study area covered portions of Phillips and Valley Counties in Montana, USA and south central Saskatchewan, Canada. North of the Milk River is a short grass prairie ecosystem with a predominately native understory of western (*Agropyron smithii*) and northern wheatgrass (*A. dasytachyum*). Plains silver sagebrush (*Artemesia cana cana*) is found in dense patches along linear overflow areas in the banks of seasonal streams, and in sparse clumps in upland grasslands. A similar grassland understory is found south of the Milk river, but with a dominant shrub cover of Wyoming big sagebrush (*A. tridentata wyomingensis*). Big sagebrush is a denser, more ubiquitous shrub than silver sagebrush, with large tracts (>100ha) occurring in the uplands. These prairie habitats are synonymous with cold, windy winters. The average low temperature in January is -6.3°C, and an average snowfall of 400mm. The winter of 2007-2008 was the lowest snowfall recorded in 30 years in the area (194mm), with average low temperatures (-2°C January).

Methods

We captured female sage-grouse on leks in northern Valley County, Montana and in the East Block of Grasslands National Park, Saskatchewan during the spring breeding seasons of 2007 and 2008 (Figure 1 in Chapter 2). We aged sage-grouse as yearlings or adults based on primary feather development (Eng 1963) and fitted females with a 22 gram necklace-style radio collar with an 18h mortality switch (Advanced Telemetry Systems; Isanti, MN, USA). We conducted 6 flights each winter between November and March in 2008 and 2009 to relocate radio-marked females. We monitored the study area in a fixed-wing aircraft with strut-mounted telemetry antennas at 300m to 600m above ground level (AGL) until we located a radio-signal. We circled the individual at 30m to 100m AGL, until we reached maximum signal strength, and recorded the location with a global positioning system (GPS). To estimate location error we had an independent source place 10 collars within the study area near known winter locations in habitat similar in vegetation and ruggedness. We calculated the distance between recorded and known locations of the training collars and used the maximum value (105m) as our resolution to estimate locations.

This population used overlapping ranges during breeding and summer seasons. We considered individuals migratory if they made movements > 10km from their capture location on leks to winter locations. Because the distance to suitable winter habitat may be constrained by the lek location we stratified measurements by each lek where females were captured. To determine movements within winter habitat we measured the distance individuals moved between consecutive flights, and divided the measurement by the number of days between flights.

Juvenile sage-grouse may seasonally disperse farther than adults in some landscapes (Dunn and Braun 1985, Connelly et al. 1989, Beck et al. 2006). We could not test for differences in movements between juveniles and adults because females captured at leks had already survived ≥ 1 winter. However, younger birds may still be imprinting on winter ranges, and could make larger movements than adult birds if they are still seeking high quality habitat. To explore this hypothesis, we tested whether yearling and adults differed in average distances moved from summer to wintering range, and within their winter range.

Results

We collected 206 locations from 39 individuals on 12 flights between 26 January 2008 and 3 March 2009. Each radio-marked individual moved $\geq$ 21km from summer to winter ranges, and 122km was the longest documented movement (Table 1). All but five of these locations were south of the Milk River in big sagebrush habitat. Our last locations during the summer were September 9 and 15 in 2007 and 2008. All sage-grouse had migrated by our earliest winter flight on 17 November 2008, and were still on wintering ground on 16 March 2009. We documented females attending leks north of the Milk River as early as 22 March in 2008.

There were no differences in dispersal distance between yearlings and adults so we combined estimates by lek (Table 1). Distances by lek were different because some leks were further north from winter range. We also pooled individual movements between winter locations because yearling and adult movements were similar (p=0.31). We assumed no difference in movements between females from different leks once individuals had reached winter habitat.

On the wintering grounds, females moved an average of 250m per day, assuming straight-line uniform movements between flight intervals, with some movements estimated >2.5km per day (Table 2). We relocated eight females $\geq$ 2 times each winter. Three of the eight females overlapped a portion of areas used in both winters (Figure 2 f-h), and the remaining five females were located from 1-25km to the previous year's location (Figure 2, a-e). Females mixed freely with individuals from all capture leks (Figure 1). During flights we relocated several flocks that contained radio-marked females from multiple capture leks.

Discussion

We discovered the longest migratory event ever observed for sage-grouse. We believe this is an annual movement, not dependent on extreme winter weather events, because we recorded all individuals moving >20km in consecutive years including a winter with the lowest snowfall recorded in 30 years. Our results highlight the value of understanding movements associated with each life-history stage because sage-grouse research has largely focused on nesting and brood-rearing (Connelly et al. 2000). Migratory movements we observed were not a mechanism for dispersal because adult females returned to leks north of the Milk River in subsequent years. We cannot infer the same for males or for juveniles because females captured at leks had already survived ≥ 1 winter. We may be missing an age- or sex-specific trait of dispersal by examining only one sex and age class over two years. Genetic evidence suggests that populations north and south of the Milk River are distinct, yet a few individuals south of the Milk River assigned to leks in Alberta (Bush 2009).

Sage-grouse may have migrated because breeding areas lack sufficient sagebrush cover in winter. Females breeding in silver sagebrush habitats north of the Milk River used distinct areas throughout breeding and summer range (Figure 1). By early November sage-grouse migrated to a wintering range in big sagebrush habitat south of the Milk River. Sage-grouse captured from different leks mixed freely with each other on the wintering grounds (Figure1), a behavioral trait that may explain the disparate nature of suitable wintering habitat in silver sagebrush landscapes. Sage-grouse in nearby Alberta, Canada use silver sagebrush habitats in winter with high apparent survival (73-88%; J. Carpenter, Alberta Conservation Association, Personal Communication). Silver sagebrush in Alberta has large remaining tracts and high density of silver sagebrush in uplands which have been lost from Saskatchewan.

High misclassification rates for sagebrush maps (Fisher et al. 1998) precluded us from quantifying the influence of resource selection in winter (Doherty et al. 2008). All radio-marked females were located in sagebrush during aerial flights; however, available vegetation layers classified only 34% of our locations in sagebrush. A sagebrush layer that can accurately depict sagebrush and shrub canopy cover would greatly improve our ability to delineate high quality winter habitats across this landscape (Homer et al. 2008). The winter range we observed is likely used by a large population of sage-grouse south of the Milk River, an area with some of the highest sage-grouse densities in Montana (Doherty et al. 2010). Migratory movements documented here have obvious implications for international conservation. Correctly identifying winter habitat in this area could help guide management for not only an endangered population in Saskatchewan, but also one of the largest populations in Montana.

We are concerned that expanding human development could degrade otherwise suitable winter habitat. Expanding agricultural tillage results in the loss of sagebrush habitat and wintering sage-grouse avoid otherwise high quality winter habitat as well density from oil and gas development increases (Doherty et al. 2008). Agricultural tillage continues to encroach upon sagebrush habitat along the Milk River, and radio-marked females spent the winter in an undeveloped portion of the Vandalia gas field south of Hinsdale, Montana (Figure 3). Winter habitat will be reduced if agricultural tillage continues along the Milk River or if oil and gas development expands into authorized leases south of Highway 2 (Figure 3).

Understanding how and when sage-grouse migrate is pivotal in understanding mechanisms behind large movements and the role of transitional habitat in facilitating long and assumedly costly movements. Maintaining connectivity between seasonal ranges requires knowing if and how sage-grouse use transitional habitats. Habitat use along migratory pathways remains unknown because VHF technology cannot keep pace with the timing and distance of migratory movements. New GPS technology provides the ability to identify potential habitat pathways between seasonal ranges. Large deciduous trees line the banks of the Milk River and there is ~10km wide strip of agricultural tillage running the length of the Milk (Figure 3), both inhospitable habitats to the sagebrush-dependent sage-grouse (Doherty et al. 2008). If there are corridors that sage-grouse rely upon to connect summer and winter habitats, they may be at risk from conversion to agriculture or increased energy development (Figure 3). Identifying potential bottlenecks that restrict movement will be paramount to conserving this unique migratory event.

Conservation and management of habitat used by sage-grouse in Montana will largely determine the viability of sage-grouse populations in Saskatchewan. Migratory movements add urgency to maintaining populations that transcend international boundaries, because sage-grouse are an endangered species in Canada under the federal Species at Risk Act. Sage-grouse are not the only species known to make disproportionately large movements. Rather, we note an emerging pattern of long-distance movements across species. Juvenile swift fox (*Vulpes velox*) reintroduced into Canada and Montana made movements across Montana, Alberta and Saskatchewan that exceeded all known dispersal distances for kit (*V. macrotis*) or swift fox (Ausband and Moehrenschlager 2009). Prairie rattlesnakes (*Crotalus viridis viridis*) in south central Alberta migrate > 52km within 5 months, the longest documented movement for any terrestrial snake (Jorgensen et al. 2009). Similarly, pronghorn (*Antilocapra americana*) captured in northeast Montana moved >100km between into Saskatchewan (Andrew Jakes, University of Calgary, unpublished data). Convergence of this new knowledge viewed in total highlights the scale and collaborative nature of partnerships necessary to conserve biodiversity in short-grass prairie ecosystems.

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Table 1. Average and range of movement distances of radio-marked female sage-grouse from breeding leks to winter range, 2008 and 2009.

	Lek	Number of individuals	Number of locations	Average distance: lek to winter location (km)	Range (km)		
Yearlings	SG24-101	6	25	54274	38820	to	72315
	SG24-102	1	5	93893	77645	to	100109
	SG24-057	5	24	86447	77367	to	93761
	Fireguard	3	14	99129	81751	to	122138
Adults	SG24-101	10	52	58314	21560	to	98185
	SG24-102	7	34	77459	53986	to	93491
	SG24-057	4	21	78714	70613	to	89797
	Fireguard	8	31	97374	61042	to	119716
Combined	SG24-101	16	77	58314	21560	to	98185
	SG24-102	8	39	77459	53986	to	93491
	SG24-057	9	45	78714	70613	to	89797
	Fireguard	11	45	97374	61042	to	119716

Table 2. Average daily movements of radio-marked female sage-grouse on winter range in south Valley and Phillips County, Montana, USA.

	Number of Individuals	Number of Consecutive Locations	Mean Distance Between Consecutive Locations (km)	Mean Distance Range (km)	Distance per Flight Interval (km / day)	Distance per Interval Range (km)
Yearlings	15	53	4.3	1.0 to 43.3	0.2	0.0 to 2.5
Adults	26	107	5.5	1.3 to 46.1	0.3	0.0 to 2.2
Combined	36	160	5.1	1.0 to 46.1	0.3	1.0 to 2.5

Figure 1. Clustered locations north of US highway 2 are spring and summer female sage-grouse. Locations south of highway 2 are sage-grouse winter locations. Different colored symbols represent four different capture leks.

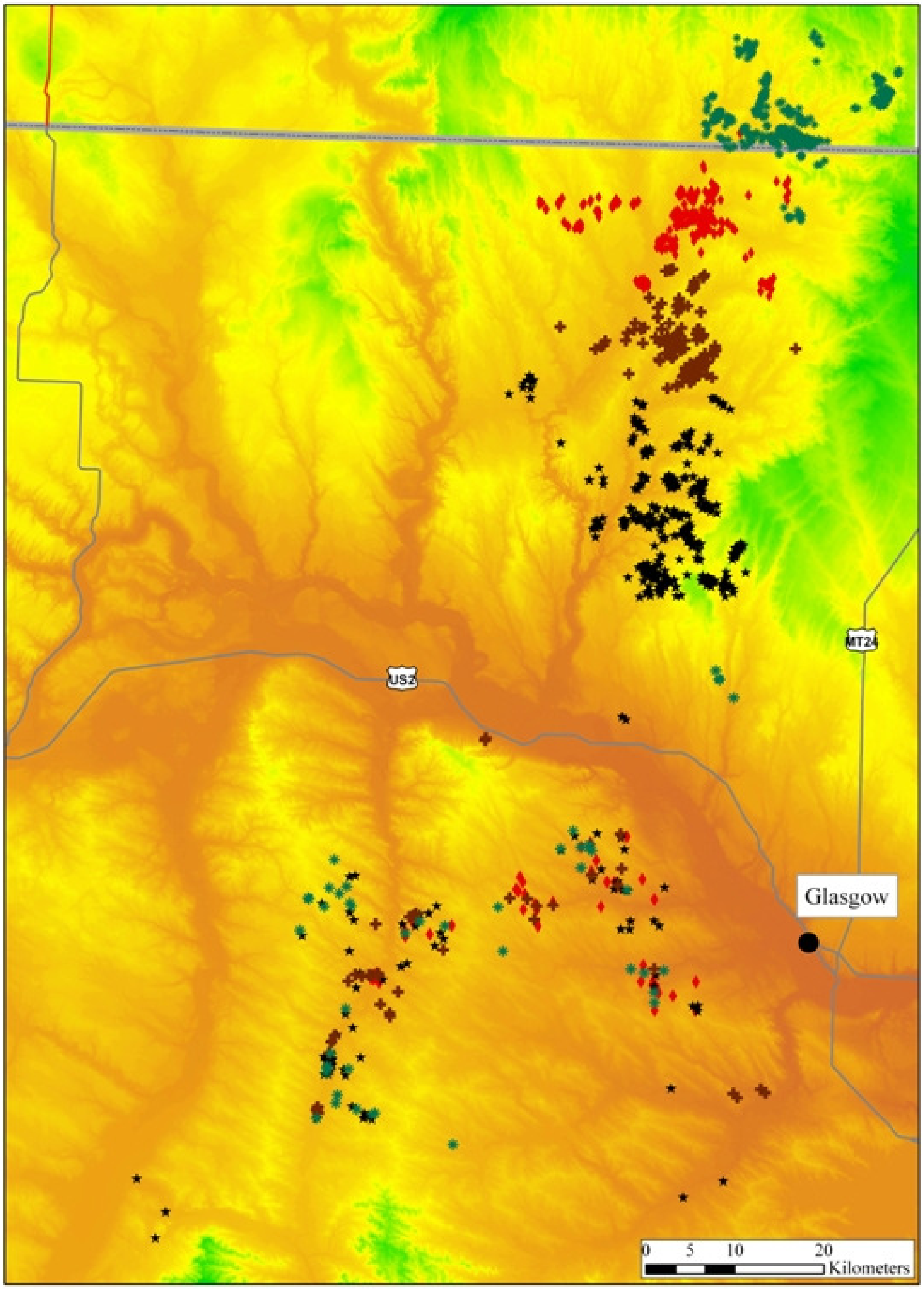
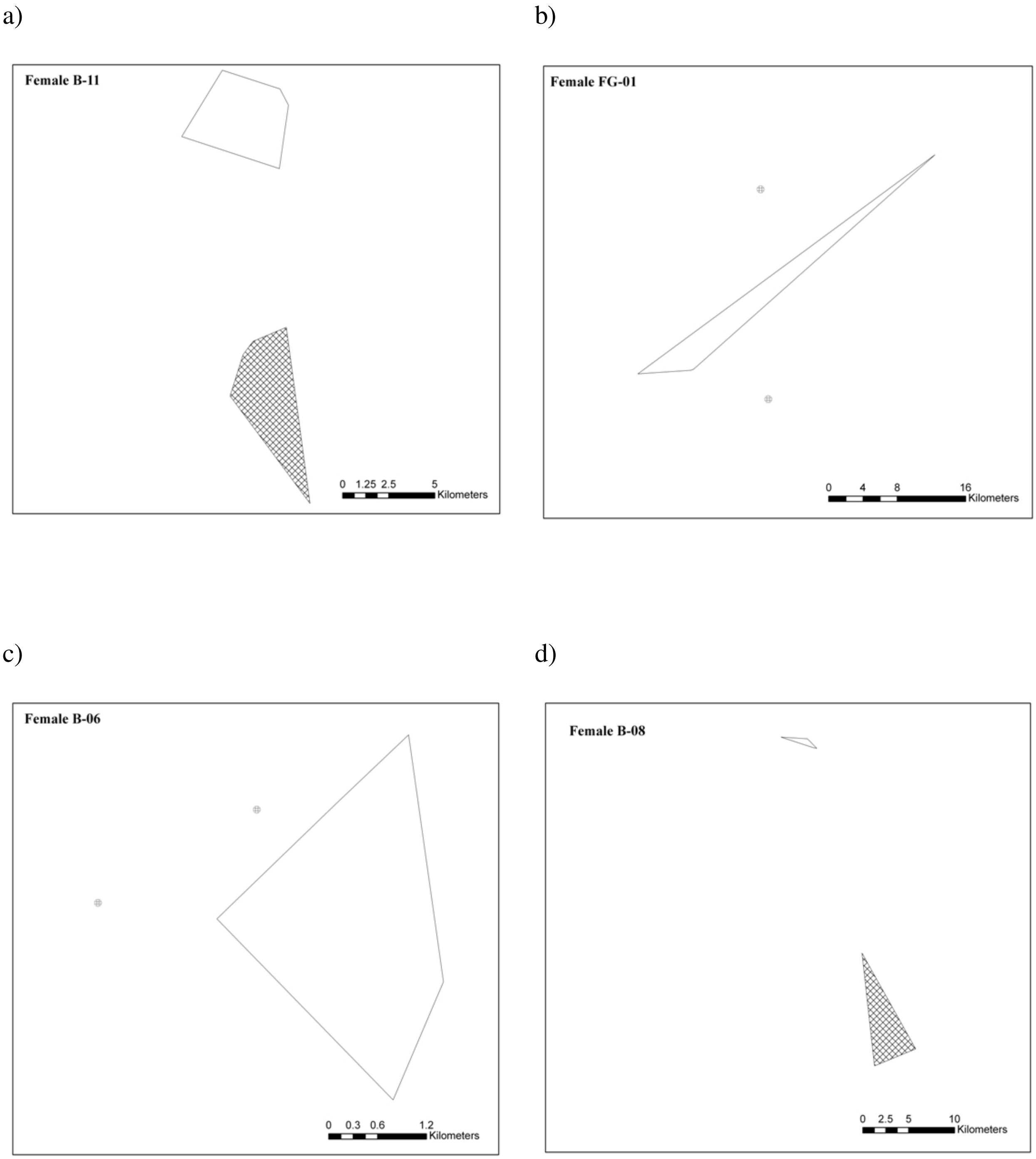
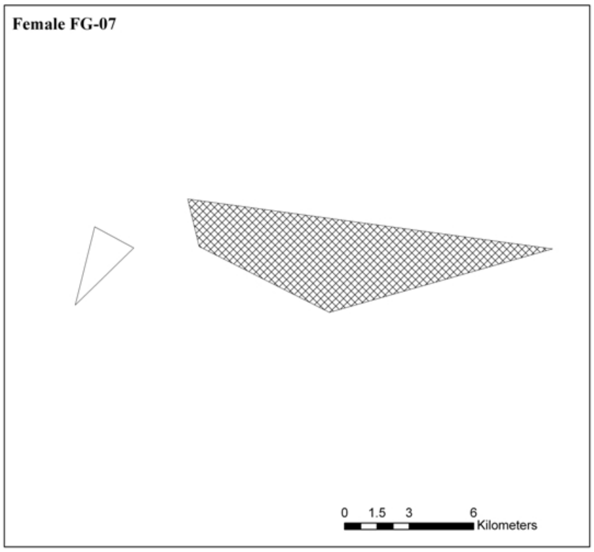


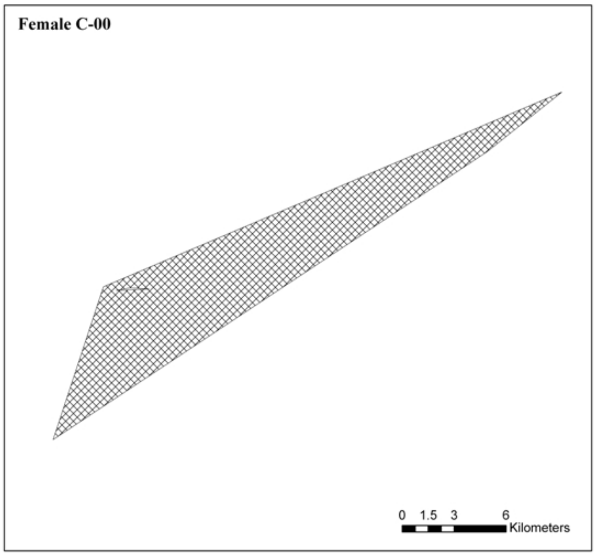
Figure 2. Minimum convex polygons, or points (females with 2 locations), for different winters used by female sage-grouse. Open polygons are during the 2007/2008 winter and hatched polygons or circles are from the 2008/2009 winter.



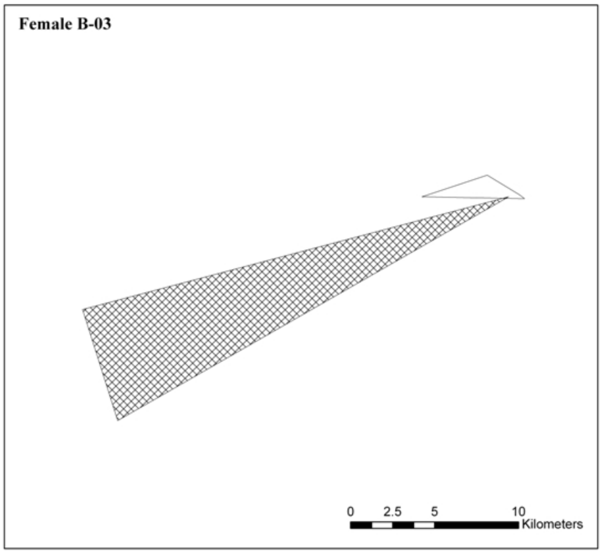
e)


Female FG-07
0 1.5 3 6
Kilometers

f)


Female C-00
0 1.5 3 6
Kilometers

g)


Female B-03
0 2.5 5 10
Kilometers

h)


Female B-10
0 0.5 1 2
Kilometers

Figure 3. Blue dots are female sage-grouse winter locations. Hatched areas are active gas fields, and maroon dots are producing oil and gas wells. Gray areas are lands occupied by agricultural tillage.