LEK ECOLOGY OF MALE GREATER SAGE-GROUSE

IN CARBON COUNTY, WYOMING

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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

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and hereby certify that, in their opinion, it is worthy of acceptance.

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ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*, hereafter "sage-grouse") have experienced range-wide population declines for several decades, and as a result they were considered warranted for listing under the Endangered Species Act in 2010. Therefore, wildlife managers need to understand how sage-grouse breeding behavior influences long-term reproductive success, and should be able to accurately relate sage-grouse lek count data to population sizes. Behavior during the breeding season, such as how frequently males visit their leks or move among leks, could relate to a male sage-grouse's ability to establish dominance at his lek and mate, so it is important to understand how these behaviors may change with environmental conditions. Additionally, some males are not seen by observers performing lek counts, and it is necessary to understand why the individual may not have been seen and counted so managers can improve lek count protocols to maximize detection and relate lek count data to population abundance estimates. We investigated factors influencing the probability of attending a lek (Chapter 1), daily probabilities of moving among leks (i.e. "interlek movements", Chapter 2), and detection probabilities for males during lek counts (Chapter 3).

We monitored GPS-PTT radio-equipped male sage-grouse (2011 n = 22, 2012 n = 36, 2013 n = 59, 2014 n = 55) throughout the spring breeding season to assess attendance and interlek movements, and included additional males equipped with VHF transmitters (n = 188) for assessing detectability. We performed lek counts on 57 leks in Carbon County, Wyoming and mapped the boundaries of all active leks (n = 20 – 33 per year). We examined attendance in three ways: at the hourly scale by 1) individual male lek attendance and daily by 2) daily probabilities of lek attendance and 3) visitation rates per

lek. We used logistic regression to evaluate whether or not a male attended a lek (i.e. had a GPS-PTT transmitter location within lek boundaries) during an hour or day, and negative binomial regression to determine the number of locations a male had within lek boundaries during a day. We examined interlek movements by modeling transitions among leks as a function of their covariates using a multi-state mark-recapture model, assuming constant survival. We considered 3 states, including Lek, Lek', and Dead, which allowed us to estimate survival and movements from an initial lek to any other lek. Finally, we estimated male detectability during lek counts using sightability surveys, in which two observers, one with access to telemetry equipment, located marked males during lek counts. We then compared males that were seen by both observers to males that were only seen by the observer with telemetry equipment. We used logistic regression to identify factors influencing detection, and applied lek specific detection rates to lek counts to estimate the number of males per lek, including males unseen by the observer.

Average daily attendance rates per lek ranged from 16.1% in 2011 to 82.0% in 2014, with high annual variability. This challenges use of lek counts as an index to population size because a good index is temporally consistent, but we observed substantial changes from year to year in probabilities males that are not detected on leks because they are not attending leks. Males were 2-3 times less likely to attend a lek on days with 0.5 – 0.75 cm precipitation in all years and all metrics of attendance, and about 2 times less likely to attend a lek on days following 0.5 cm precipitation. Date also predicted attendance, with peak dates of attendance ranging from April 7 in 2012 to May 13 in 2011. Broad time-scale precipitation and weather patterns likely shifted the peak date of attendance, with males attending earlier in the season when conditions were dry and warm in 2012, and later in the season when conditions were wet with high snowpack in 2011. Attendance also generally decreased with higher wind speeds, but the effects were not as strong as for precipitation or date. Lek counts should be avoided during precipitation and the day following precipitation due to lower lek attendance.

Males had a 1.04% - 2.22% daily probability of moving to a new lek on any given day, demonstrating high daily lek fidelity as expected for a lek-breeding bird. However, the yearly probability of moving to a new lek ranged from 38.6% - 69.9% per year, suggesting many males may make at least one interlek movement at some point during the breeding season. Males that attended a lek every morning were 28 times less likely to move than males that rarely attended leks, and males with greater mass were also 15 times less likely to move than males with less mass. Dominant males with high attendance and mass were less likely to move to a new lek possibly because they established themselves at their preferred lek and therefore would be more likely to mate. Males were 5 times less likely to move during a day with 0.5 cm precipitation than with no precipitation, but 2 times more likely to move on the day following precipitation. Males were 4-12 times more likely to move at the beginning of the lek season, and 12 times more likely to move to a high elevation lek than a low elevation lek. Males may display at low elevation leks and move to higher elevations in the beginning of the season as precipitation declines and snowpack melts at the higher elevation leks. Additionally, males may move down in elevation following precipitation at high elevation leks, which can potentially bias lek counts on the day following precipitation.

Male sage-grouse were most likely to be detected on leks with shorter sagebrush and higher snow cover. The average detection rate across all leks was 87%, and there was little variation from lek to lek in their lek-specific detection rates (77 – 93%), suggesting the lek count is an appropriate index to population size from lek to lek because it is spatially consistent. Lek count protocols already in place are sufficient, and cannot be improved to maximize detection. When accurate population abundance estimates are necessary, sightability methods can be used to determine detection rates at leks.

Throughout all chapters, lek ecology was strongly influenced by weather, and understanding factors affecting attendance, interlek movements, and detection allows managers to estimate abundance from lek count data. Attendance was lower with precipitation, and interlek movements and detection of males on leks also changed at multiple time scales with precipitation and snow. Daily attendance and interlek movement rates can be used to predict when males are most likely to be present and available for detection on a lek during a count, which could be combined with sightability detection probabilities for accurate abundance estimates incorporating availability for detection and detection during counts.

CHAPTER 1: MALE GREATER SAGE-GROUSE ATTENDANCE RATES AT LEKS IN CARBON COUNTY, WYOMING

ABSTRACT

Daily lek attendance of male greater sage-grouse (*Centrocercus urophasianus*) is important because it may reflect breeding effort, it might complicate the use of lek counts as a population index, and could indicate a change in breeding behavior after a disturbance. The role that bird age and mass, weather, and lek characteristics may play in daily lek attendance have not been explored despite their potential influence. We assessed the probability of an individual male's lek attendance and daily probability of attendance per lek, and the daily number of visits to a lek. We fit 145 males with Solar Argos Global Positioning Systems Platform Transmitter Terminals over 4 years in Carbon County, Wyoming. We evaluated the importance of bird characteristics, lek characteristics, date, and weather at multiple time scales. The daily probability of attendance per lek ranged considerably, from 0.161 ± 0.118 (mean ± standard error) in 2011 to 0.820 ± 0.045 in 2014 with peak attendance dates ranging from 7 April in 2012 to 13 May in 2011, and attendance was highest at the beginning of the day. Date and time of day were the most influential factors predicting attendance. Additionally, in most years, attendance decreased with increasing precipitation on the observation day and in 2011 attendance decreased with precipitation the preceding day. Wind did not impact attendance rates as strongly as precipitation. Lek or bird characteristics were not correlated with attendance. Lek counts do not accurately reflect the breeding population on days with or following precipitation, and should be avoided on those days.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) have experienced extensive population declines in the last 50 years, with population abundance declines averaging 2% per year since 1965 (Connelly et al. 2004). Sage-grouse were historically widespread in sagebrush (*Artemisia spp.*) steppe habitats, but their current range is restricted to <60% of their pre-settlement distribution (Schroeder et al. 2004). Sage-grouse are considered “warranted but precluded” for protection under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service [USFWS] 2010). Therefore, it is important to understand male lek ecology and factors that may impact long-term reproductive rates and success on leks, as well as accurately monitor population sizes.

Male sage-grouse do not attend leks every day throughout the breeding season, and females attend even less frequently, so the entire population is not counted during lek counts. Counting a male during a lek count depends on if the male is available for detection because they are attending the lek during the count, as well as the observer’s ability to detect the male when present on the lek (Alldredge et al. 2007, Schmidt et al. 2013, Chapter 3). However, little is known about what factors influence lek attendance, and therefore a male’s availability for detection during lek counts (Dalke et al. 1963, Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh et al. 2004). Lek attendance is the rate at which sage-grouse attend a lek, historically expressed as the proportion of days a male was present on a lek throughout the season (Emmons and Braun 1984, Dunn and Braun 1985). Estimating daily attendance therefore represents the probability that a male will attend a lek on a given day and can be used to evaluate the correlation between count data and population size as count data fluctuates throughout the season (Walsh et al. 2004, Dahlgren 2010, Baumgardt 2011).

Daily lek attendance is also important because it reflects breeding effort, which may vary by bird age or body condition. Larger, older males have higher lek attendance (Gibson and Bradbury 1985) and attend leks earlier in the season than juveniles which allows them to achieve a dominant position with more frequent mating opportunities, which could have broader implications because few males on the lek mate (Jenni and Hartzler 1978, Emmons and Braun 1984, Gibson and Bradbury 1985). Throughout the season, adult males may attend the lek 42 - 58% of the days, yearlings may attend 19 - 30% of the days, and female lek attendance may be as low as 3.8% (Walsh et al. 2004, Dahlgren 2010), but the factors influencing these rates are unknown. Body condition might also influence attendance, with heavier males attending more frequently (Beck and Braun 1978, Vehrencamp et al. 1989). Many factors could further influence when males attend leks and which leks they favor, and these factors could ultimately influence reproduction on different leks or for different males.

Spring weather in sagebrush habitats can be highly variable and unpredictable, and sage-grouse may be less likely to attend leks during poor weather. Precipitation and high winds on the count day resulted in reduced male attendance, whereas temperature had no effect on counts (Bradbury et al. 1989b, Boyko et al. 2004). Precipitation and wind can decrease attendance on the observed day and subsequent days (Bradbury et al. 1989b), potentially creating a lag effect on attendance. As a result, managers may lose the ability to collect accurate data for several days after precipitation during a typical lek counting season. The timing of the lek season, and peak attendance, is largely based on elevation and snow cover (Morton 1978, Schroeder et al. 1999, Connelly et al. 2004, Green 2006), so weather may also influence lek season dynamics at smaller scales as well. We estimated attendance rates of male sage-grouse by individual male and by lek and the factors affecting daily attendance in Carbon County, Wyoming in 2011 – 2014. This information provides an understanding of the influence of weather on daily male lek attendance so managers can better interpret fluctuations in their count data.

STUDY AREA

This research was part of a long-term study with a Before-After Control-Impact design to assess the response of male sage-grouse to a wind energy development. The wind energy development was proposed on The Overland Trail Ranch (OTR), a 320,000 acre (1,295 km^2) checkerboard of public (BLM and Wyoming Game and Fish Department [WGFD]) and private land ownership south of Rawlins, WY. Throughout the study area, there were 57 leks (Fig. 1). Each year throughout the study period, there were about 20-33 active leks. The OTR lies within a sagebrush steppe basin with rocky ridges to the north and northeast and foothills to the south and southwest, with elevations from 1,890 m to 2,590 m above sea level. The study area was in the intermountain semidesert province (Bailey 1995).

The climate was semiarid, with cold winters and short, hot summers (Bailey 1995). Highest temperatures averaged a maximum of 31 °C in July and lowest temperatures averaged a maximum of -1°C in December and January (Western Regional Climate Center [WRCC] 2008). Most precipitation fell between April and October, with an annual precipitation of 19-26 cm in the basin (WRCC 2008). Higher elevations received more snowfall and precipitation. In our study area, 2011 was a wet winter and spring compared to average precipitation, 2012 was a drought and received about half of the average precipitation, and 2013 and 2014 fell within the historic range with respect to precipitation (National Climatic Data Center 2014).

Vegetation consisted largely of sagebrush (*Artemisia spp*.) with some shadscale (*Atriplex confertifolia*) and short grasses (Bailey 1995). Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*) dominated higher elevations, with black sagebrush (*A. nova*) in rocky, exposed soils, silver sagebrush (*A. cana*) in lowlands, and greasewood (*Sarcobatus vermiculatus*) in moist alkaline flats, and willows (*Salix spp*.) and sedges (*Carex spp.*) in stream and valley bottoms (Bailey 1995, Connelly et al. 2004, Welch 2005).

METHODS

Trapping and marking

We trapped birds near all active leks. Dominant males captured near leks in spring may have high site fidelity and could artificially increase lek attendance (Walsh et al. 2004), so we attempted to capture birds in late fall, and in spring. We captured male sage-grouse using two-person teams that searched sage-grouse roosting sites at night using spotlighting and hoop-netting techniques (Giesen et al. 1982, Wakkinen et al. 1992) facilitated by All-Terrain Vehicles (ATV). Once we located a bird, one person approached on the ATV while shining a light in the bird's eyes. The second person walked behind the ATV, carrying a 75 cm diameter hoop net with 1.75 cm nylon mesh netting, captured the grouse, and restrained it to reduce injuries. We weighed and classified captured males as yearlings (<1 year old) or adults (≥ 2 years old) based upon primary wing feather characteristics (Eng 1955, Crunden 1963). Trapping and handling procedures were approved through the University of Missouri Institutional Animal Care and Use Committee (Protocol #6750).

We began trapping in May 2011 and increased our sample size of marked males each year. We deployed transmitters on 20 males in 2011, an additional 20 in 2012, and 10 more in 2013 with 30 g solar powered platform transmitter terminal (PTT-100) Global Positioning System (GPS) transmitters (accuracy ± 18 m, Microwave Telemetry, Inc., Columbia, MD). We attached GPS-PTT transmitters using the Rappole and Tipton (1991) method, and each bird also received a uniquely identifiable colored and aluminum leg band combination. We attempted to achieve a balance of adult and juvenile males marked with GPS-PTT transmitters. From March 1 to June 14, GPS-PTT transmitters recorded locations every hour from 0400 to 0900, and collected 3 additional locations at staggered times throughout the day on 5 schedules to ensure locations were during different periods in the 24-hour cycle.

Lek attendance estimates

We attempted to locate unknown leks in the study area if a male's GPS-PTT locations indicated visitation to a lek previously unknown to state or federal agencies, to avoid negative bias when calculating lek attendance. Attendance was only assessed when the male was in the study area and we did not exclude data after the male was captured because many males began to attend leks within 1-2 mornings after being captured. We considered the lek season to start with the first GPS-PTT marked bird's arrival on a lek, and end as the last day any GPS-PTT marked bird was on a lek. We grouped leks into the control and treatment areas to assess the season's start and end date, but data were combined across the study area for the remainder of analysis.

To determine a GPS-PTT tagged male bird's location in relation to the lek, we mapped perimeters of all known leks. Because lek perimeters may shift over time (Bergerud and Gratson 1988), we mapped lek perimeters for each year separately except for 2011 where we used 2012 boundaries. We mapped lek perimeters after observing the lek multiple times each year during lek counts following Connelly et al.'s (2003) protocols, to incorporate temporal variation in lek shape and size within the year. During each lek count, observers used a compass and rangefinder to estimate locations of several grouse on the lek edges to help delineate the boundary. We mapped the boundary keeping observed bird locations (average 9 – 13 locations per lek per year) and concentrations of cecal tar, droppings, and feathers on or inside the boundary. We added a 40 m buffer in a Geographic Information System (GIS; Environmental Systems Research Institute, Redlands, California, USA) because there were concentrations of GPS-PTT locations on the boundary periphery that were likely attending the lek. We used 6 lek boundaries mapped in 2013 for analysis in 2011 and 2012 because they more accurately represented the lek boundaries and we wanted to avoid negatively biasing results by failing to include male locations that likely should have been visible and counted by an observer.

We identified whether each GPS-PTT location in spring was within or outside the lek boundary to assess if a bird was attending a lek, and considered a male to be attending the lek when his GPS-PTT location was within the mapped lek boundary. We summarized lek attendance three ways: 1) an individual male's hourly attendance at a lek (individual male lek attendance), 2) at the lek level both as the number of lek visits per day (visitation rates per lek) and 3) whether the bird attended the lek at any time during the day (daily attendance per lek). To assess individual male lek attendance, we used the individual grouse as the sample unit, and summarized attendance as attending or not attending a lek for all locations recorded throughout the day. At the lek level, we summarized visitation rates per lek as the number of GPS-PTT locations per day within a lek's boundaries for all males that attended the lek on the observed day. Additionally at the lek level, we summarized daily attendance per lek as a binary response in which a male was considered attending the lek if he had any locations within the lek boundary on the observed day, or he was considered not attending the lek if the male did not have any locations within lek boundaries on the observed day.

Covariates for lek attendance models

To assess the correlation of landscape features with attendance primarily at the lek level, we calculated several covariates using a GIS. For individual male lek attendance, we estimated elevation for all bird locations using a 10 x 10 m digital elevation model (DEM). For visitation rates per lek and daily attendance per lek, we used the DEM to calculate the average slope, aspect, and elevation for each lek in the Geospatial Modelling Environment (Beyer 2012). For aspect, we first converted DEM aspect cells to radians, took the sine and cosine of each cell, and then averaged the values of the sine and cosine cells within the lek perimeter. We converted back to degrees using the arctan transformation. Additionally, we used a 30 m resolution land cover layer (Wyoming Geographic Information Science Center [WyGISC] 2004) reclassified as sage or other to determine the proportion of sage within 603 m of the lek; 603 m represents the median distance from the lek boundary for all male locations in spring 2011 – 2013 in our study site. For all three analyses, we recorded precipitation and average wind speed at sunrise daily from the National Oceanic and Atmospheric Administration (NOAA) weather station in Rawlins, WY for the study area. We calculated the average wind speed and average precipitation the previous 1, 4, 6, 8, 10, and 12 days to assess a lag effect of weather at longer time scales (Bradbury et al. 1989b).

Model building and selection process

We constructed *a priori* models for individual male lek attendance, visitation rates per lek, and daily attendance per lek. For individual male lek attendance, we considered the influence of weather, time, and bird characteristics and we included day of year in all *a priori* models because we expected it to be the most important factor affecting lek attendance based on previous literature (Jenni and Hartzler 1978, Walsh et al. 2004). We also created a post-hoc model set for individual male lek attendance using the same models as in the *a priori* model set (Appendix A), but we added time of day in all models. For visitation rates per lek and daily attendance per lek, we considered the influence of weather, time, and lek characteristics (Appendix B). We created models using biologically reasonable combinations of these variables.

Prior to fitting models, we assessed the best structural form of variables by evaluating data across all years (Franklin et al. 2000, Washburn et al. 2004) and eliminated several weather timescales from analysis to test a smaller model set. We used Akaike Information Criteria adjusted for small sample sizes (Akaike Information Criterion [AIC_C], Burnham and Anderson 2002) to rank linear, quadratic, and pseudothreshold structures for each variable. Quadratic terms were centered on their means to avoid multicollinearity between the linear effect and the quadratic term in the polynomial equation (Bonnot et al. 2011). If the linear structural form was within 2 AIC_C points of the highest ranked nonlinear structural form, we selected it for simplicity. Also, if one structural form was strongly supported in one year (>8 AIC_C points from the next best model), and was <2 AIC_C points of the top form in another year, we chose that form for both years. Variables we used in the models included linear, quadratic, and pseudo-threshold structural representations (Table 1), with some consistency across years and analyses. Additionally, we evaluated whether data could be combined across years by comparing AIC_C scores for models including year as a covariate and the same models without year as an additive covariate. Model convergence was poor with data pooled and using year as an additive effect, and we wanted to avoid interactions but still incorporate annual variability. Year was an important factor for individual male lek attendance, visitation rate per lek, and daily attendance per lek. Therefore, we analyzed data by year for all three analyses. Finally, we also tested a subset of the average weather conditions over the previous 4, 6, 8, 10, and 12 days to assess the long-term effects of weather on attendance. For each year we tested all long-term weather time scales using the appropriate structural form, in models including date and time to determine the most influential weather time scales. We included only the 3 timescales that were most influential across all years to keep our model set smaller.

Overdispersion was present in the data in 2013 and 2014 for all analyses, so we selected the covariance matrix structure in SAS (SAS Institute Inc., Cary, North Carolina) that best reduced the Pearson χ^2/DF for the global model and used $QAIC_C$ for model selection. Covariance matrices tested included the default (variance component), compound symmetry, unstructured, and first-order autoregressive matrices using date and time. Additionally, we tested alternative covariance matrix structures if the default structure produced models that failed to converge or if it failed to produce standard error estimates for parameters. As a result, we used an unstructured covariance matrix in 2011 and 2012 for daily attendance per lek, a first-order autoregressive structure with 2013 individual male lek attendance, and a compound symmetry structure in the 2014 individual male lek attendance analysis.

We used logistic regression (PROC GLIMMIX in SAS 9.3) with bird identity as a random effect to assess how bird characteristics, weather, and day of year and time of day were correlated with individual male attendance. We used a logistic regression in PROC GLIMMIX with random effects for both lek and grouse identity to assess how lek characteristics, day of year, and weather affect daily attendance per lek. Finally, to assess how lek characteristics, weather, and day of year influence visitation rates per lek, we used negative binomial regression in a mixed model with PROC GLIMMIX including lek and grouse identity as random effects.

Model fit and validation

We evaluated goodness-of-fit several ways. We examined the Pearson Chi-Square statistic divided by degrees of freedom (χ^2/DF). In addition, we calculated McFadden's pseudo- R^2 as

$$Pseudo\ R^2 = 1 - \frac{LL_1}{LL_0}$$

where LL_1 is the log likelihood of the top model in the model set, and LL_0 is the log likelihood of the null model (McFadden 1974).

We used k-fold cross validation to evaluate the predictive ability of the most supported model (Boyce et al. 2002). We divided the data into 10 random subsets of approximately equal size. We removed one subset as the testing set, and fit the model set using the remaining 9 subsets as training data. We used model parameter estimates to calculate attendance probabilities for the corresponding testing set, and determined the average difference between observed attendance and the predicted probability of attendance. We then found the Spearman-rank correlation coefficient by dividing our observed attending locations into 10 bins based on their predicted probability of attendance, and using PROC CORR to find the Spearman-rank correlation between the predicted probability of attendance and the frequency of observed attendance in each bin. For the visitation rate per lek analysis, we evaluated predictive ability using a Pearson correlation between the observed frequency of attendance and the predicted frequency of attendance per day.

RESULTS

Trapping and marking

Each year we had 43 ± 9 birds that were active during spring (Table 2). The GPS-PTT transmitters recorded 16,774 ± 6,749 locations each spring and males could be assessed for attendance on 2,338 ± 976 days each spring. Lek sizes varied considerably (59806 ± 48729 m^2, range = 5915 m^2 – 268594 m^2).

Individual male daily lek attendance rates

The post-hoc analysis, in which time of day was also included in all models, fit the data better than the *a priori* models every year (Table 3). In post-hoc analysis, weather also contributed to model fit in most years, including precipitation on the observation day and previous day in 2011; elevation in 2012; precipitation on the observation day, wind the previous day, and average wind the previous 8 days in 2013; as well as precipitation on the observation day, wind the previous day, and average wind the previous 10 days in 2014. Many parameter estimate confidence intervals did not overlap zero (Table 4). The average hourly individual male probability of attendance was similar in 2011 and 2012 (0.062 ± 0.026 and 0.063 ± 0.023, respectively), but almost four times higher in 2013 (0.226 ± 0.025) and over six times higher in 2014 (0.387 ± 0.038). Peak individual male hourly lek attendance occurred on 7 April in 2012, over a month earlier than peak attendance in 2011 (13 May); 2013 attendance peaked 21 April and 2014 attendance peaked April 15 (Fig. 2). Time of day was also included in all post-hoc models, and males were at least 7 times less likely to attend as the day progressed across all 4 years (Fig. 3).

Precipitation generally decreased attendance, although differently each year. As precipitation on the observation day increased to 0.5 cm, the hourly probability of individual male lek attendance was about half to a third as likely as likely as with no precipitation (Fig. 4). Precipitation on the previous day also negatively affected individual male lek attendance in 2011, with the hourly probability of attendance with no precipitation being nearly twice as high as the probability with 0.5 cm of precipitation (Fig. 5).

Wind also decreased attendance (Fig. 6), although it was less important than precipitation and influenced attendance at larger timescales. Individual male hourly lek attendance generally declined with average wind the previous 8 days, with peak male hourly attendance at approximately 18 km/hr average wind the previous 10 days. Additionally, an individual male's hourly probability of attendance was almost two times higher on days with no wind the previous day than days with 60 km/hr wind the previous day.

The predictive ability of the models was marginal (Table 5), although some years did predict individual male lek attendance well.

Daily attendance per lek

There was low model uncertainty in 2011 and 2012; however, model selection uncertainty was higher in 2013 and 2014 (Table 6). Top models in all years included date and precipitation on the observation day, and additional weather variables. The probability of daily attendance per lek was more than twice as high in 2012 than 2011 (0.161 ± 0.118 in 2011, 0.412 ± 0.086 in 2012), and about twice as high in 2013 (0.760 ± 0.046) and 2014 (0.820 ± 0.045) than 2012. Similar to the individual male lek attendance predictions, day of year had the strongest effect on daily attendance per lek (Table 7, Fig. 7) and peaked over a month later in 2012 than in 2011 (12 May 2011, 9 April 2012), and the 2013 and 2014 peak attendance dates were between the two earlier years (20 April 2013 and 14 April 2014).

Precipitation on the observation day decreased the probability of a male attending a lek. Days with 0.5 cm of precipitation decreased attendance per lek by a factor of >2, and precipitation of approximately 0.7 cm decreased lek attendance by a factor of approximately 23 (Fig. 8). Precipitation the previous day decreased the probability of attendance by more than half as precipitation ranged from 0 to 0.5 cm (Fig. 9), which was a comparable decrease as with individual male lek attendance. Longer timescales did not change the daily probability of attendance per lek appreciably over the range of data we observed.

Wind on the observation day and previous day was included in top models, although neither had a strong effect on the daily probability of attendance per lek. Wind was also included at several longer time frames, but there was no consistent or strong pattern in how wind influenced daily attendance rates per lek. Daily attendance per lek was lowest at 22 km/hr average wind the previous 10 days in 2013 the opposite pattern occurred in 2014, and daily attendance per lek peaked at 20 km/hr average winds the previous 8 days in 2014 (Fig. 10).

The predictive ability of the models was good in some years, with high Spearman rank correlation coefficients in 2013 and 2014 (Table 8).

Visitation rate per lek

Date and precipitation on the observation day appeared in top models every year, as well as precipitation the previous day in 2011, and several longer time scale wind variables each year (Table 7). The average visitation rate per lek was highest in 2014 (2.044 ± 0.376) and 2013 (1.830 ± 0.213), approximately tripling the frequency of visits in 2011 (0.630 ± 0.252) and quadrupling the frequency of visits in 2012 (0.519 ± 0.126). Higher attendance was also observed in 2013 and 2014 for individual male lek attendance and daily attendance per lek, and predicted peak attendance dates were also similar to both previous analyses. Day of year was the most important predictor for visitation rates per lek (Table 9, Fig. 11) and visitation peaked over a month later in 2011 (12 May) than in 2012 (8 April), with the peak in 2013 (22 April) and 2014 (16 April) falling between the two extremes.

Precipitation on the observation day decreased the number of lek visits per day each year. Visitation per lek was at about twice as high with no precipitation than with 0.5 cm precipitation every year (Fig. 12). In 2011, precipitation the previous day also had a negative effect on individual male lek attendance, although not as strong as precipitation the observed day (Fig. 13).

Wind was included in top models at several longer time frames, but in general visitation rates per lek did not change appreciably over the range of data we observed for most variables. The highest visitation rate per lek peaked at 20 km/hr average winds the previous 12 days and 17 km/hr average winds the previous 8 days. In 2013 visitation rates per lek decreased from 8.385 visits per day to 1.645 visits per day as average wind the previous 8 days increased from 1 km/hr to 21 km/hr.

The models predicted marginally well in some years (Table 8), with Pearson correlation coefficients high in 2011 (Pearson = 0.175, p = 0.0002), with strong positive correlations between observed and predicted attendance in 2012 (Pearson = 0.399, p = <0.0001), 2013 (Pearson = 0.497, p = <0.0001), and 2014 (Pearson = 0.612, p = <0.0001).

DISCUSSION

Weather is rarely studied in relation to daily lek attendance, but was important in our study in addition to time and date. Bradbury et al. (1989b) observed how precipitation and wind can affect count data, both immediately or longer through a lasting depression in attendance for several days. In our study, precipitation and wind negatively affected attendance at different time scales. The negative effects of precipitation were short-term, occurring on the observation day or the next day. Similarly, band-tailed pigeons (*Patagioenas fasciata*) decreased visitation at mineral sites during precipitation events, although their attendance increased following precipitation (Overton et al. 2005). Our data strongly support the current lek count protocols in avoiding counts during precipitation (Connelly et al. 2003), and we additionally suggest avoiding lek counts the day following precipitation due to a lag effect resulting in decreased attendance. Other avian survey techniques also avoid counts during precipitation events because behavior, and therefore detection, can change during rain (Robbins 1981), and the lag effect from precipitation suppresses activity in exposed areas such as leks for an additional day.

Date was influential on all metrics of attendance, and was supported in previous studies as an important factor for the timing of lek attendance (Jenni and Hartzler 1978, Walsh et al. 2004). We observed some variation in the peak attendance date and lek season lengths for different years, likely from different spring weather patterns throughout the study area. Sage-grouse tend to breed earlier at warmer, low elevations and later at high elevations with snow and colder weather (Schroeder et al. 1999, Green 2006). Our data reinforce this previous work because in 2011 the region had high snowfall throughout winter and spring; the lek season was delayed when compared to years with average snowpack and precipitation. In 2012, a mild winter and a warm, dry spring, shifted breeding season timing much earlier compared to an average year and consequently peak attendance was more than a month earlier than in 2011. Precipitation and snowpack was average for the study area during 2013 and 2014, and the peak attendance dates were between the extremes of 2011 and 2012. Some agencies require all lek counts to be completed within a certain time frame (e.g. April 1 to May 10), and inflexible sage-grouse lek count periods could miss peak attendance in years with unusual weather patterns. Elevations varied by over 500 m throughout the study area, so lek season timing was variable with favorable conditions occurring earliest at low elevations and progressing to higher elevations last (Schroeder et al. 1999). In addition to broad scale, season-long lek attendance timing, time of day was also a strong factor predicting individual male lek attendance, with the probability of attendance decreasing as the day progressed. The pattern of decreasing lek attendance from sunrise to mid-day has been shown elsewhere as well (Jenni and Hartzler 1978, Bradbury et al. 1989b).

Attendance metrics were generally lower with high wind speeds averaged over the preceding days (i.e. up to 35 km/hr averaged across the previous 10 days), although various wind variables were included in the highest ranked models they were less influential on lek attendance than precipitation or date. Consistently high wind could decrease attendance because birds might not be able to meet thermoregulation requirements (Gessaman 1972, Sherfy and Pekins 1995). Therefore males may not be able to maintain thermoregulation and engage in energetically costly displays for extended periods of time (Vehrencamp et al. 1989). found songbirds were harder to detect during high winds due to changes in behavior as they often took cover, and recommended counts be avoided when winds exceeded 20 km/hr. We also found behavior, in the form of lek attendance, changed when wind speeds averaged 20 km/hr over several preceding days. The risk of predation might also interact with wind to affect lek attendance rates because eagles, a main predator of sage-grouse may be more active on windy days (Boyko et al. 2004). Additionally, high winds could make male vocal displays hard for females to hear and distinguish between males to pick a mate, potentially making lek displays ineffective at attracting mates (Gibson and Bradbury 1985, Gibson 1989;1996a) and eventually lower reproductive success.

Lek characteristics and bird characteristics were not important for predicting lek visitation or probabilities of attendance per lek in our study. Males in lek-breeding species have high site fidelity and visit the same leks consistently (Campbell 1972, Dunn and Braun 1985, Schroeder and Braun 1992, Schroeder and Robb 2003, Walsh et al. 2010), so characteristics of the leks may not influence visitation rates or attendance. We expected increasing attendance with higher land coverage by sagebrush near the leks because it is their primary food and strutting displays are energetically expensive (Vehrencamp et al. 1989, Barnett and Crawford 1994, Connelly et al. 2000, Gregg 2006, Gregg et al. 2008), but sagebrush did not play an important role in our models of lek attendance. Larger leks may have more dominant males with higher attendance rates (Schroeder and Braun 1992), but lek size did not influence attendance in our study. Other factors such as slope, aspect, or elevation also did not influence attendance per lek, possibly because leks are known to be flat, open areas surrounded by sage (Patterson 1952), so our study area may not have had enough variation in physical landscape characteristics for those features to be important for male sage-grouse behavior. Older males in lek forming birds may attend leks more frequently (Jenni and Hartzler 1978, Höglund and Lundberg 1987, Fiske et al. 1998, Alonso et al. 2010), but we did not find support that age or any other bird characteristics were important variables for attendance.

Date and time were confirmed as the most influential factors determining the probability of lek attendance. However, wind and especially precipitation, when present, negatively affected the probability of lek attendance and the time a male spends at a lek, suggesting it is reasonable to avoid lek counts during high wind or especially during precipitation events (Connelly et al. 2003). In addition, due to the lag effect of one day, we also recommend avoiding lek counts the day following precipitation. Although consistently high winds over several days preceding the lek count may decrease lek attendance as well, there is less support and we do not recommend incorporating it into any protocols. By investigating attendance rates at leks, managers can better estimate numbers of males that were not detected during lek counts because they were not present at the lek, but it is also necessary to understand detection rates during lek counts to relate lek count data to population abundance (Chapter 3).

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Table 1. Variables listed with the structural form best representing their effect on individual male greater sage-grouse lek attendance, daily attendance per lek, and visitation rates per lek. All quadratic terms (Q) are centered on their mean ($(x - \bar{x})^2$), pseudo-thresholds (P) are $ln(x+0.05)$, and linear (L) forms are the untransformed variables. Variables not included in each type of analysis are noted by an "NA."

Variable	**Individual male lek attendance**				**Daily attendance per lek**				**Visitation rate per lek**			
	2011	**2012**	**2013**	**2014**	**2011**	**2012**	**2013**	**2014**	**2011**	**2012**	**2013**	**2014**
Date (Date)	Q	Q	Q	Q	Q	Q	Q	Q	Q	Q	Q	Q
Time of day (Time)	Q	Q	Q	Q	NA	NA	NA	NA	NA	NA	NA	NA
Elevation (Elev)	Q	Q	Q	Q	L	L	Q	Q	L	L	L	L
Wind that day (Wind_d)	Q	Q	Q	Q	L	L	L	Q	L	L	L	Q
Wind the previous day (Wind_p)	L	L	Q	Q	L	L	L	Q	L	L	L	Q
Average wind the previous 4 days (Wind_p4)	Q	Q	Q	Q	L	L	L	Q	L	L	Q	Q
Average wind the previous 6 days (Wind_p6)	Q	Q	Q	Q	L	Q	Q	Q	Q	Q	Q	Q
Average wind the previous 8 days (Wind_p8)	Q	Q	Q	Q	Q	Q	Q	Q	Q	Q	L	Q
Average wind the previous 10 days (Wind_p10)	Q	Q	Q	Q	Q	Q	Q	Q	Q	Q	Q	Q
Average wind the previous 12 days (Wind_p12)	Q	Q	Q	Q	Q	Q	Q	Q	Q	Q	Q	Q
Precipitation that day (Precip_d)	P	Q	P	Q	L	Q	L	Q	L	Q	P	Q
Precipitation the previous day (Precip_p)	P	L	L	Q	L	L	L	Q	L	L	L	Q

Average precipitation the previous 4 days (Precip_4)	Q	L	L	Q	L	L	L	Q	L	L	L	Q
Average precipitation the previous 6 days (Precip_6)	L	P	L	Q	L	L	L	Q	L	Q	L	Q
Average precipitation the previous 8 days (Precip_8)	Q	Q	Q	Q	L	L	Q	Q	L	Q	L	Q
Average precipitation the previous 10 days (Precip_10)	L	L	L	Q	L	L	L	Q	L	P	L	Q
Average precipitation the previous 12 days (Precip_12)	Q	Q	Q	Q	L	L	Q	Q	L	L	Q	Q
Bird mass (Mass)	L	L	L	L	NA	NA	NA	NA	NA	NA	NA	NA
Bird age (Age)	L	L	L	L	NA	NA	NA	NA	NA	NA	NA	NA
Lek area (Lek_area)	NA	NA	NA	NA	L	L	L	L	L	L	L	L
Slope (Slope)	NA	NA	NA	NA	L	L	L	L	L	L	L	L
Aspect (Aspect)	NA	NA	NA	NA	L	L	L	L	L	L	L	L
Percent sage within 603 m of lek (Psage)	NA	NA	NA	NA	L	L	L	L	L	L	L	L

Table 2. Summary of trapping effort and data collected from male greater sage-grouse GPS-PTT transmitters each year (2011-2014) in Carbon County, Wyoming.

	2011	2012	2013	2014
GPS-PTT transmitters deployed	28	37	38	21
Total transmitters deployed per year	108	105	68	31
Active transmitters in spring	22	36	59	55
All GPS-PTT locations in spring[a]	3,318	8,528	22,053	33,195
Days available for marked males to attend[b]	440	1,129	3,015	4,768
Number of leks attended	16	17	25	29
Boundary points used to map lek perimeters	221	221	337	288

[a] GPS-PTT locations in spring were used to assess individual male lek attendance.
[b] Days a marked male was available to attend a lek was used to assess attendance per lek.

Table 3. Top models for each year from *a priori* and *post-hoc* model sets for individual male greater sage-grouse lek attendance in and around the Overland Trail Ranch in Carbon County, Wyoming, 2011 – 2014. For 2013 and 2014 models, we used AIC corrected for overdispersed data (QAIC, $QAIC_C$, and $\Delta QAIC_C$).

***A priori* top models**								
Year	**Model**	**-2 LL**[a]	***K***[b]	***N***[c]	**AIC**[d]	**AIC_C**[e]	**ΔAIC_C**[f]	**w_i**[g]
2011	Date, $Date^2$, Time, $Time^2$, Elev, $Elev^2$	2236.8	8	3318	2252.8	2252.8	0.0	0.998
2012	Date, $Date^2$, Time, $Time^2$, Elev, $Elev^2$	4117.9	8	8528	4134.0	4134.0	0.0	1.000
2013	Date, $Date^2$, *ln*(Precip_d + 0.05), Wind_p, Wind_p8, $Wind\_p8^2$	16974.8	9	22052	16992.8	16992.8	0.0	1.000
2014	Date, $Date^2$, Time, $Time^2$, Elev, $Elev^2$	27546.5	9	33194	21045.9	21045.9	0.0	1.000
***Post-hoc* top models**								
Year	**Model**	**-2 LL**	***K***	***N***	**AIC**	**AIC_C**	**ΔAIC_C**	**w_i**
2011	Date, $Date^2$, Time, $Time^2$, *ln*(Precip_d + 0.05), *ln*(Precip_p + 0.05)	2195.0	8	3318	2211.0	2211.0	0.0	0.886
2012	Date, $Date^2$, Time, $Time^2$, Elev, $Elev^2$	4117.9	8	8528	4134.0	4134.0	0.0	1.000
2013	Date, $Date^2$, Time, $Time^2$, *ln*(Precip_d + 0.05), Wind_p, Wind_p8, $Wind\_p8^2$	16864.6	11	22052	16886.6	16886.6	0.0	1.000
2014	Date, $Date^2$, Time, $Time^2$, Precip_d, $Precip\_d^2$, Wind_p, $Wind\_p^2$, Wind_p10, $Wind\_p10^2$	27108.9	13	33194	20719.9	20719.9	0.0	0.949

[a] LL is log likelihood.
[b] Number of parameters.
[c] Number of observations.
[d] Akaike's Information Criterion (AIC).
[e] AIC adjusted for small sample size.
[f] Change in AIC value from the top model .
[g] Akaike weight.

Table 4. Parameter estimates predicting individual male greater sage-grouse hourly lek attendance 2011 – 2014 in and around the Overland Trail Ranch in Carbon County, Wyoming.

Parameter	*Estimate*	*SE*	*UCL*	*LCL*	*Odds ratio*
2011					
Intercept	3.135	1.097	5.286	0.984	22.989
Date	-0.033	0.007	-0.019	-0.047	0.968
$Date^2$	-0.005	0.001	-0.004	-0.006	0.995
Time	-0.183	0.016	-0.152	-0.214	0.833
$Time^2$	-0.002	0.002	0.003	-0.005	0.999
ln(Precip_p + 0.05)	-0.270	0.074	-0.124	-0.416	0.763
Precip_d	-2.087	0.446	-1.214	-2.960	0.124
2012					
Intercept	27.964	2.5263	32.9157	23.013	1.40×10^{12}
Date	-0.025	0.004	-0.018	-0.033	0.975
$Date^2$	-0.001	0.000	-0.001	-0.001	1.000
Time	-0.071	0.011	-0.051	-0.092	0.932
$Time^2$	-0.006	0.002	-0.003	-0.009	0.994
Elev	-0.012	0.001	-0.010	-0.010	0.988
$Elev^2$	-7.00×10^{-5}	0.000	-7.00×10^{-5}	-7.00×10^{-5}	1.000
2013					
Intercept	-0.059	0.229	0.390	-0.508	0.943
Date	0.003	0.001	0.006	0.001	1.003
$Date^2$	-0.001	4.00×10^{-5}	-0.001	-0.001	0.999
Time	-0.173	0.018	-0.139	-0.208	0.812
$Time^2$	-0.005	0.001	-0.004	-0.007	0.993
ln(Precip_d + 0.05)	-0.400	0.037	-0.328	-0.471	0.623
Wind_p	-0.006	0.002	-0.002	-0.002	0.991
Wind_p8	-0.059	0.005	-0.049	-0.049	0.934
$Wind\_p8^2$	0.004	0.001	0.005	0.003	1.003
2014					
Intercept	-0.623	0.224	-0.184	-1.061	0.536
Date	0.016	0.001	0.018	0.015	1.016
$Date^2$	-0.001	0.000	-0.001	-0.001	0.999
Time	-0.119	0.004	-0.112	-0.126	0.888
$Time^2$	-0.001	0.001	0.000	-0.002	0.999

Precip_d	-3.645	0.387	-2.886	-4.404	0.026
Precip_d^2	3.478	0.701	4.852	2.103	32.395
Wind_p	-0.005	0.001	-0.002	-0.008	0.995
Wind_p^2	-0.000	0.000	-0.000	-0.001	1.000
Wind_p10	-0.004	0.005	0.005	-0.014	0.996
Wind_p10^2	-0.007	0.001	-0.006	-0.007	0.993

Table 5. Goodness-of-fit for top models each year from *a priori* and *post-hoc* model sets for individual male greater sage-grouse lek attendance in and around the Overland Trail Ranch in Carbon County, Wyoming.

***A priori* top models**					
Year	**Model**	**χ^2 / DF[10]**	**K-Fold[11]**	**Spearman[12]**	**Pseudo-R^2[13]**
2011	Date, $Date^2$, Time, $Time^2$, Elev, $Elev^2$	1.08	0.193 ± 0.005	-0.945	0.10361
2012	Date, $Date^2$, Time, $Time^2$, Elev, $Elev^2$	1.10	0.123 ± 0.003	-0.006	0.10808
2013	Date, $Date^2$, *ln*(Precip_d + 0.05), Wind_p, Wind_p8, Wind_p8^2	3.17	0.374 ± 0.001	0.964	0.09728
2014	Date, $Date^2$, Time, $Time^2$, Elev, $Elev^2$	5.51	0.274 ± 0.002	-0.176	0.19936
***Post-hoc* top models**					
Year	**Model**	**χ^2 / DF**	**K-Fold**	**Spearman**	**Pseudo-R^2**
2011	Date, $Date^2$, Time, $Time^2$, *ln*(Precip_d + 0.05), *ln*(Precip_p + 0.05)	1.06	0.181 ± 0.005	-0.778	0.12036
2012	Date, $Date^2$, Time, $Time^2$, Elev, $Elev^2$	1.10	0.126 ± 0.003	-0.006	0.10808
2013	Date, $Date^2$, Time, $Time^2$, *ln*(Precip_d + 0.05), Wind_p, Wind_p8, Wind_p8^2	3.84	0.377 ± 0.002	0.491	0.10315
2014	Date, $Date^2$, Time, $Time^2$, Precip_d, Precip_d^2, Wind_p, Wind_p^2, Wind_p10, Wind_p10^2	2.78	0.269 ± 0.002	-0.103	0.21208

[10] χ^2 / DF is Pearson chi-square divided by degrees of freedom (used to assess goodness-of-fit).
[11] Average ± SE difference between the observed attendance value and the predicted attendance probability.
[12] Spearman rank correlation coefficient.
[13] Pseudo-R^2 calculated as 1-($LL_{TopModel}$ / LL_{Null}).

Table 6. Top models describing factors influencing male greater sage-grouse daily attendance per lek and visitation rates per lek in and around the Overland Trail Ranch in Carbon County, Wyoming 2011-2014. For 2013 and 2014, we used AIC corrected for overdispersed data (QAIC, $QAIC_C$, and $\Delta QAIC_C$).

Daily attendance per lek

Year	**Model**	**-2 LL**	***K***	***N***	**AIC**	**AIC_C**	**ΔAIC_C**	**w_i**
2011	Date, Date^2, Precip_d, *ln*(Precip_p + 0.05)	466.9	7	440	480.9	481.2	0.000	0.724
	Date, Date^2, Precip_d, Wind_d, Wind_p	467.3	8	440	483.3	483.7	2.486	0.209
2012	Date, Date^2, Precip_d, Wind_p12, Wind_p12^2	910.9	9	1129	928.9	929.0	0.000	1.000
2013	Date, Date^2, Precip_d, Wind_p10, Wind_p10^2	2653.2	10	3015	325.3	325.4	0.000	0.248
	Date, Date^2, Precip_d, Wind_p8, Wind_p8^2	2663.4	10	3015	326.5	326.6	1.176	0.138
	Date, Date^2, Precip_d, Wind_d	2688.6	9	3015	327.4	327.5	2.064	0.088
	Date, Date^2, Precip_d, Wind_p6, Wind_p6^2	2671.4	10	3015	327.4	327.5	2.089	0.087
	Date, Date^2, Precip_d	2710.4	8	3015	327.9	327.9	2.556	0.069
	Date, Date^2, Precip_d,Wind_p12, Wind_p12^2	2678.7	10	3015	328.3	328.3	2.938	0.057
	Date, Date^2, Precip_d,Wind_d, Precip_p8, Precip_p8^2	2666.6	11	3015	328.9	328.9	3.558	0.042
	Date (q), Wind_d	2720.7	8	3015	329.1	329.1	3.740	0.038
	Date, Date^2, Precip_d, Wind_d, Precip_p4	2686.3	10	3015	329.1	329.2	3.811	0.037
	Date, Date^2, Precip_d, Precip_p10, Wind_d	2687.3	10	3015	329.2	329.3	3.929	0.035
	Date, Date^2, Precip_d, Precip_p6, Wind_d	2687.7	10	3015	329.3	329.4	3.965	0.034
2014	Date, Date^2, Precip_d, Precip_d^2, Wind_p10, Wind_p10^2	3584.6	11	4768	657.6	657.6	0.000	0.421
	Date, Date^2, Precip_d, Precip_d^2,Wind_p8, Wind_p8^2	3586.0	11	4768	657.8	657.9	0.240	0.373
	Date, Date^2, Precip_d, Precip_d^2, Wind_p12, Wind_p12^2	3596.1	11	4768	659.6	659.7	2.043	0.151

	Date, $Date^2$, Precip_d, $Precip\_d^2$, Wind_p6, $Wind\_p6^2$	3607.6	11	4768	661.6	661.7	4.079	0.055

Visitation rate per lek

Year	**Model**	**-2 LL**	***K***	***N***	**AIC**	**AIC_C**	**ΔAIC_C**	**w_i**
2011	Date, $Date^2$, Precip_d, Precip_p	1100.3	8	440	1116.3	1116.6	0.000	0.577
	Date, $Date^2$, Precip_d, Wind_p6, $Wind\_p6^2$	1101.3	9	440	1119.3	1119.7	3.119	0.121
2012	Date, $Date^2$, Precip_d, $Precip\_d^2$, Wind_p12, $Wind\_p12^2$	2061.5	10	1129	2081.5	2081.7	0.000	0.909
2013	Date, $Date^2$, *ln*(Precip_d + 0.05), Wind_p8, $Wind\_p8^2$	7752.0	9	3015	4098.0	4098.1	0.000	0.791
	Date, $Date^2$, *ln*(Precip_d + 0.05), Wind_p10, $Wind\_p10^2$	7757.1	9	3015	4100.7	4100.7	2.670	0.208
2014	Date, $Date^2$, Precip_d, $Precip\_d^2$, Wind_p8, $Wind\_p8^2$	12573.3	10	4768	5302.9	5302.9	0.000	0.834
	Date, $Date^2$, Precip_d, $Precip\_d^2$, Wind_p10, $Wind\_p10^2$	12581.0	10	4768	5306.1	5306.2	0.197	0.164

Table 7. Parameter estimates for top models predicting daily attendance per lek 2011-2014 in and around the Overland Trail Ranch in Carbon County, Wyoming.

Parameter	*Estimate*	*SE*	*UCL*	*LCL*	*Odds ratio*
2011					
Intercept	3.524	2.197	7.829	-0.781	33.920
Date	-0.036	0.016	-0.005	-0.067	0.965
$Date^2$	-0.006	0.002	-0.003	-0.009	0.994
Precip_d	-1.375	1.024	0.632	-3.382	0.253
ln(Precip_p + 0.05)	-0.559	0.168	-0.229	-0.889	0.572
Wind_d	-0.009	0.016	0.023	-0.041	0.991
Wind_p	0.004	0.009	0.021	-0.013	1.004
2012					
Intercept	5.229	1.170	7.522	2.937	186.61
Date	-0.061	0.008	-0.046	-0.076	0.940
$Date^2$	-0.001	0.000	-0.001	-0.001	1.000
Precip_d	-5.512	2.401	-0.805	-10.218	0.000
$Precip\_d^2$	11.405	5.504	22.193	0.617	89769.450
Wind_p12	0.145	0.032	0.207	0.084	1.160
$Wind\_p12^2$	-0.012	0.002	-0.007	-0.017	0.990
2013					
Intercept	0.817	0.614	2.020	-0.386	2.264
Date	0.017	0.004	0.024	0.010	1.017
$Date^2$	-0.002	9.00×10^{-5}	-0.002	-0.002	0.998
Precip_d	-5.341	0.685	-4.000	-6.683	0.005
Precip_p4	0.000	0.000	0.000	0.000	1.000
Precip_p6	0.000	0.000	0.000	0.000	1.000
Precip_p8	0.002	0.005	0.012	-0.008	1.002
$Precip\_p8^2$	-0.080	0.163	0.240	-0.400	0.923
Precip_p10	0.000	0.000	0.000	0.000	1.000
Wind_d	0.000	2.00×10^{-5}	3.90×10^{-5}	-3.92×10^{-5}	1.000
Wind_p6	0.000	1.00×10^{-5}	2.00×10^{-5}	-1.96×10^{-5}	1.000
$Wind\_p6^2$	0.000	0.000	0.000	0.000	1.000
Wind_p8	0.000	0.001	0.002	-0.002	1.000
$Wind\_p8^2$	0.000	7.00×10^{-5}	1.40×10^{-4}	-1.37×10^{-4}	1.000
Wind_p10	-0.078	0.014	-0.051	-0.105	0.925
$Wind\_p10^2$	0.007	0.001	0.009	0.005	1.007
Wind_p12	0.000	0.000	0.000	0.000	1.000
$Wind\_p12^2$	0.000	0.000	0.000	0.000	1.000
2014					
Intercept	-1.923	0.486	-0.971	-2.875	0.146
Date	0.043	0.002	0.048	0.038	1.044

$Date^2$	-0.001	1.00×10^{-5}	-0.001	-0.001	0.999
Precip_d	-5.130	0.958	-3.252	-7.008	0.006
$Precip\_d^2$	4.464	1.795	7.981	0.947	86.834
Wind_p6	0.000	0.000	0.000	0.000	1.000
$Wind\_p6^2$	0.000	0.000	0.000	0.000	1.000
Wind_p8	-0.003	0.006	0.008	-0.014	0.997
$Wind\_p8^2$	-0.003	0.004	0.004	-0.010	0.997
Wind_p10	0.001	0.008	0.016	-0.014	1.001
$Wind\_p10^2$	-0.006	0.004	0.002	-0.014	0.994
Wind_p12	0.000	7.00×10^{-5}	1.37×10^{-4}	-1.37×10^{-4}	1.000
$Wind\_p12^2$	0.000	4.00×10^{-5}	-7.84×10^{-4}	-7.84×10^{-4}	1.000

Table 8. Goodness-of-fit for top daily attendance per lek and visitation rates per lek models in and around the Overland Trail Ranch in Carbon County, Wyoming 2011-2014 for male greater sage-grouse lek attendance.

Daily attendance per lek					
Year	**Model**	χ^2 **/ DF**	**K-Fold**	**Spearman**	**Pseudo-R^2**
2011	Date, Date^2, Precip_d, *ln*(Precip_p + 0.05)	0.85	0.473 ± 0.011	0.212	0.075
	Date, Date^2, Precip_d, Wind_d, Wind_p	0.86			0.074
2012	Date, Date^2, Precip_d, Wind_p12, Wind_p12^2	0.79	0.301 ± 0.009	0.248	0.161
2013	Date, Date^2, Precip_d, Wind_p10, Wind_p10^2	10.08	0.326 ± 0.045	0.891	0.210
	Date, Date^2, Precip_d, Wind_p8, Wind_p8^2	8.39			0.207
	Date, Date^2, Precip_d, Wind_d	5.11			0.199
	Date, Date^2, Precip_d, Wind_p6, Wind_p6^2	7.92			0.205
	Date, Date^2, Precip_d	7.54			0.193
	Date, Date^2, Precip_d,Wind_p12, Wind_p12^2	9.39			0.202
	Date, Date^2, Precip_d,Wind_d, Precip_p8, Precip_p8^2	3.75			0.206
	Date (q), Wind_d	2.66			0.190
	Date, Date^2, Precip_d, Wind_d, Precip_p4	4.98			0.200
	Date, Date^2, Precip_d, Precip_p10, Wind_d	5.47			0.200
	Date, Date^2, Precip_d, Precip_p6, Wind_d	4.93			0.200
2014	Date, Date^2, Precip_d, Precip_d^2, Wind_p10, Wind_p10^2	5.84	0.251 ± 0.004	0.758	0.391
	Date, Date^2, Precip_d, Precip_d^2,Wind_p8, Wind_p8^2	8.32			0.391
	Date, Date^2, Precip_d, Precip_d^2, Wind_p12, Wind_p12^2	5.76			0.389
	Date, Date^2, Precip_d, Precip_d^2, Wind_p6, Wind_p6^2	15.10			0.387
Visitation rate per lek					
Year	**Model**	χ^2 **/ DF**	**K-Fold**	**Pearson**	**Pseudo-R^2**
2011	Date, Date^2, Precip_d, Precip_p	0.99	1.046 ± 0.047	0.179	0.043

	Date, $Date^2$, Precip_d, Wind_p6, $Wind\_p6^2$	0.99			0.042
2012	Date, $Date^2$, Precip_d, $Precip\_d^2$, Wind_p12, $Wind\_p12^2$	0.89	0.714 ± 0.032	0.399	0.092
2013	Date, $Date^2$, *ln*(Precip_d + 0.05), Wind_p8, $Wind\_p8^2$	2.12	1.1067 ± 0.0204	0.49741	0.11095
	Date, $Date^2$, *ln*(Precip_d + 0.05), Wind_p10, $Wind\_p10^2$	2.00			0.11023
2014	Date, $Date^2$, Precip_d, $Precip\_d^2$, Wind_p8, $Wind\_p8^2$	2.05	1.1837 ± 0.0206	0.61192	0.19456
	Date, $Date^2$, Precip_d, $Precip\_d^2$, Wind_p10, $Wind\_p10^2$	1.96			0.19406

Table 9. Parameter estimates predicting visitation rates per lek for male greater sage-grouse 2011-2014 in and around the Overland Trail Ranch in Carbon County, Wyoming.

Parameter	*Estimate*	*SE*	*UCL*	*LCL*	*Odds ratio*
2011					
Intercept	3.053	1.154	5.315	0.791	21.179
Date	-0.023	0.007	-0.009	-0.037	0.977
$Date^2$	-0.004	0.001	-0.003	-0.005	0.996
Precip_d	-1.262	0.394	-0.490	-2.034	0.283
Precip_p	-0.740	0.457	0.156	-1.636	0.477
Wind_p6	-0.011	0.020	0.028	-0.050	0.989
$Wind\_p6^2$	0.003	0.005	0.014	-0.008	1.003
2012					
Intercept	3.088	0.670	4.401	1.776	21.933
Date	-0.041	0.004	-0.033	-0.049	0.960
$Date^2$	-0.001	0.000	-0.001	-0.001	0.999
Precip_d	-3.107	1.197	-0.761	-5.453	0.045
$Precip\_d^2$	5.810	2.391	10.497	1.124	333.619
Wind_p12	0.094	0.017	0.128	0.060	1.099
$Wind\_p12^2$	-0.009	0.002	-0.006	-0.012	0.991
2013					
Intercept	-0.971	0.285	-0.412	-1.530	0.379
Date	0.012	0.002	0.015	0.009	1.012
$Date^2$	-0.001	0.000	-0.001	-0.001	0.999
ln(precip_d + 0.05)	-0.034	0.039	-0.264	-0.416	0.712
Wind_p10	0.000	0.000	0.000	0.000	1.000
$Wind\_p10^2$	0.000	0.000	0.000	0.000	1.000
Wind_p8	-0.041	0.005	-0.032	-0.050	0.960
$Wind\_p8^2$	0.005	0.001	0.006	0.004	1.005
2014					
Intercept	-0.982	0.206	-0.578	-1.386	0.375
Date	0.025	0.001	0.027	0.023	1.025
$Date^2$	-0.001	0.000	-0.001	-0.001	0.999
Precip_d	-2.877	0.361	-2.169	-3.585	0.056
$Precip\_d^2$	3.253	0.658	4.542	1.964	25.868
Wind_p10	0.000	0.001	0.002	-0.002	1.000
$Wind\_p10^2$	0.000	0.000	0.000	-0.000	1.000
Wind_p8	-0.018	0.004	-0.010	-0.026	0.982
$Wind\_p8^2$	-0.005	0.001	-0.004	-0.006	0.995

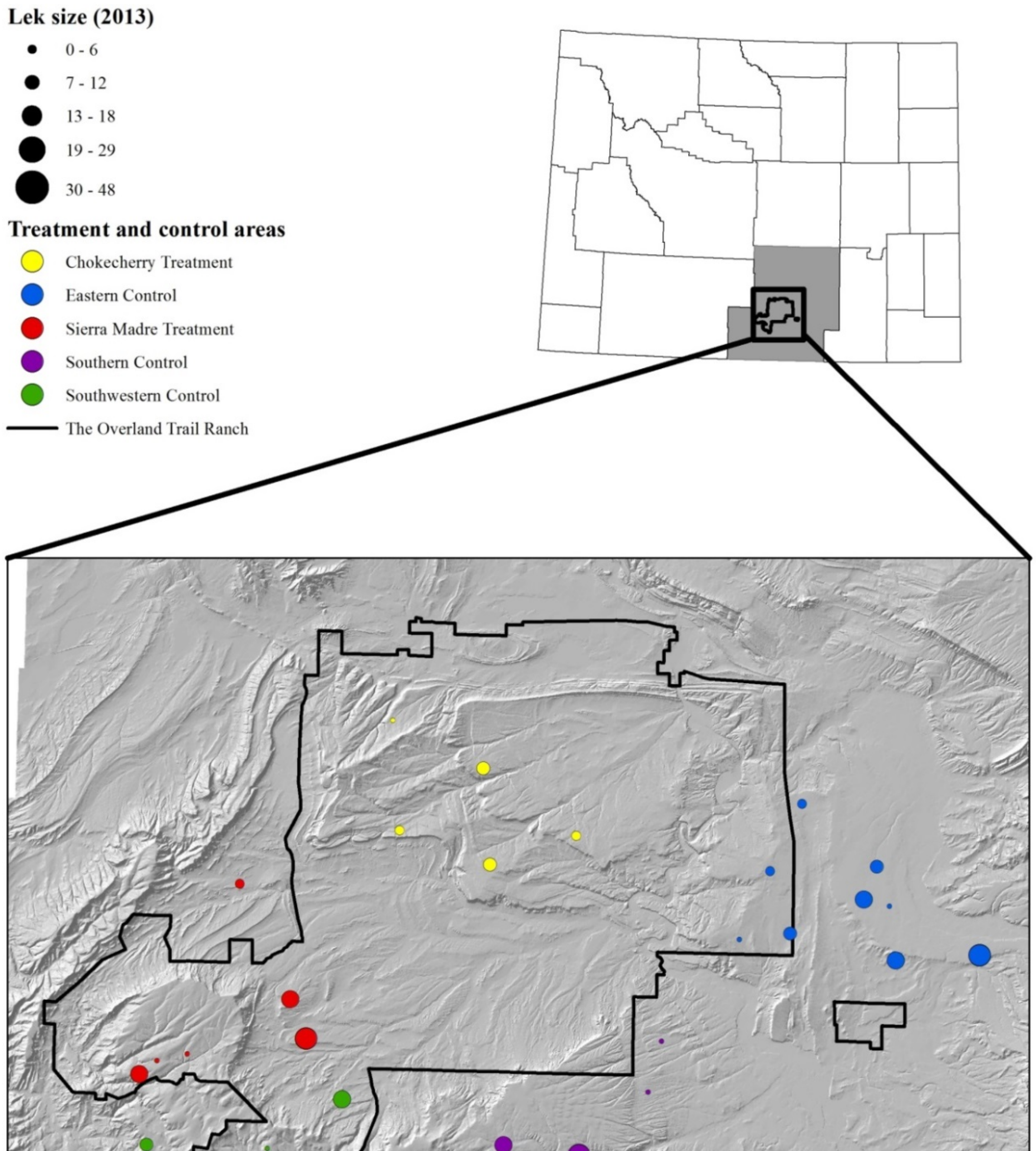

Figure 1. Study area in Carbon County, Wyoming for evaluating male lek attendance 2011 – 2014. The treatment areas, Chokecherry and Sierra Madre, are in the turbine footprint whereas the control areas are away from the turbine footprint. Lek sizes shown are from 2013 counts.

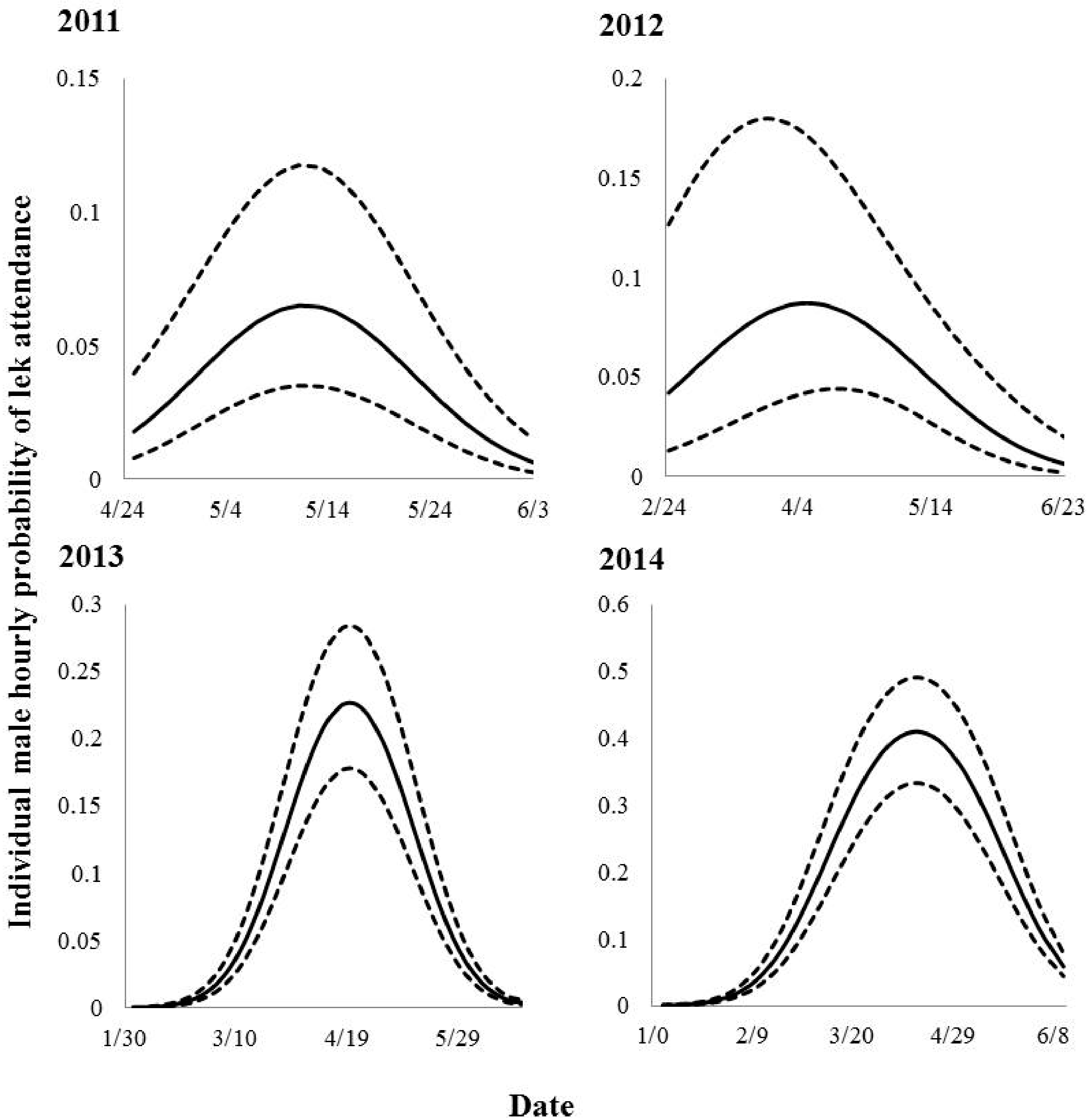

Figure 2. Date strongly influenced individual male greater sage-grouse hourly lek attendance on and around the Overland Trail Ranch in Carbon County, Wyoming 2011 – 2014 for *a priori* and *post-hoc* models.

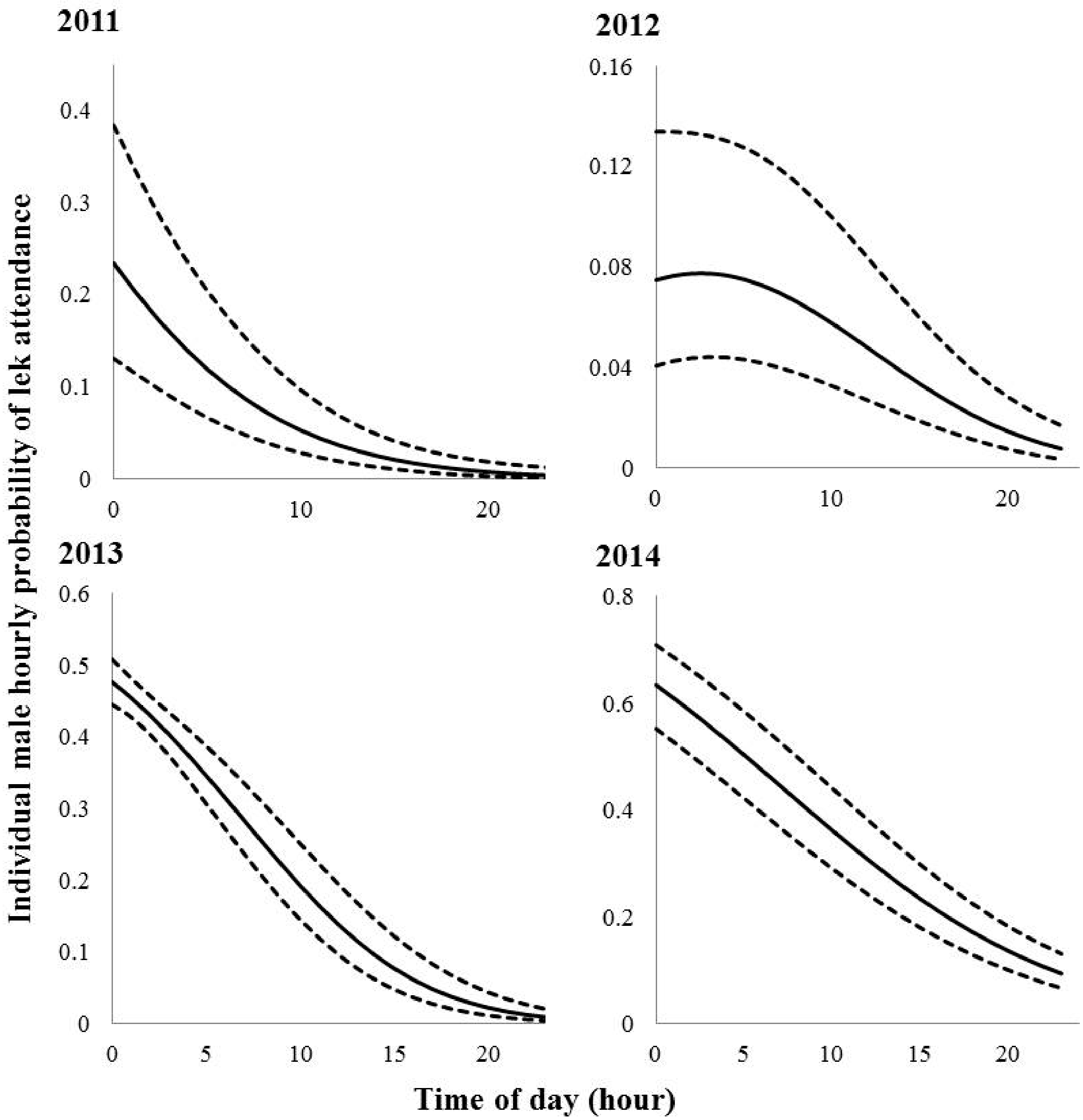

Figure 3. Time of day strongly influenced individual male greater sage-grouse hourly lek attendance on and around the Overland Trail Ranch in Carbon County, Wyoming 2011 – 2014 in *post-hoc* models, with attendance decreasing as the day progressed.

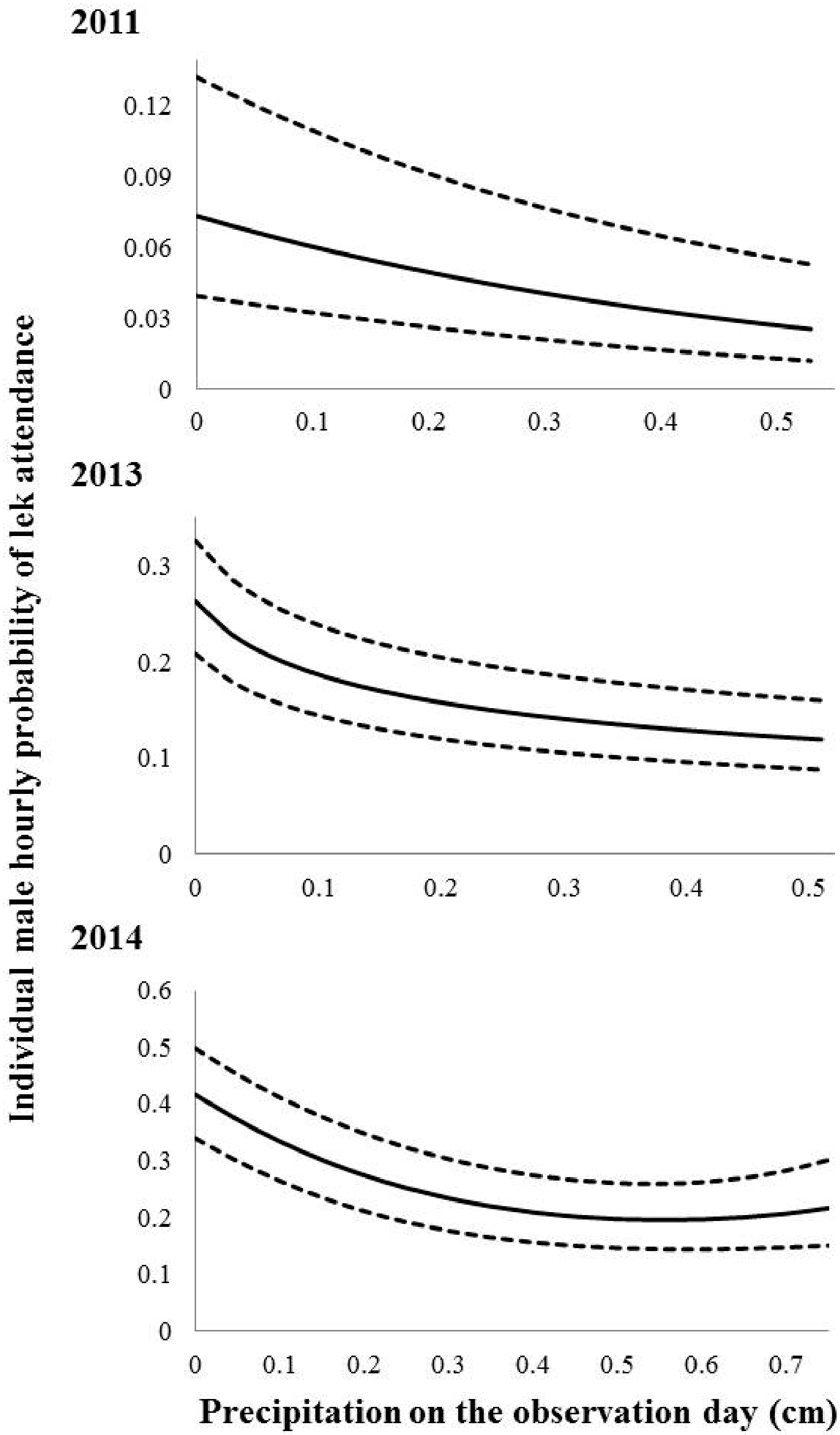

Figure 4. Individual male greater sage-grouse hourly lek attendance was 2-3 times lower with 0.5 cm of precipitation than with no precipitation on and around the Overland Trail Ranch in Carbon County, Wyoming 2011 – 2014.

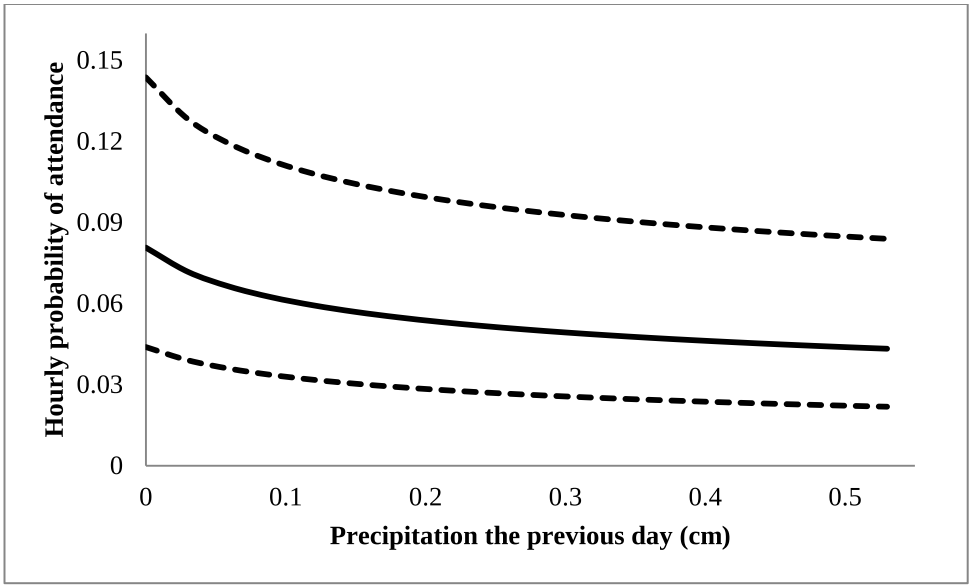

Figure 5. Individual male greater sage-grouse hourly lek attendance was lower when precipitation fell on the previous day than with no precipitation the previous day in and around the Overland Trail Ranch in Carbon County, Wyoming 2011 – 2014.

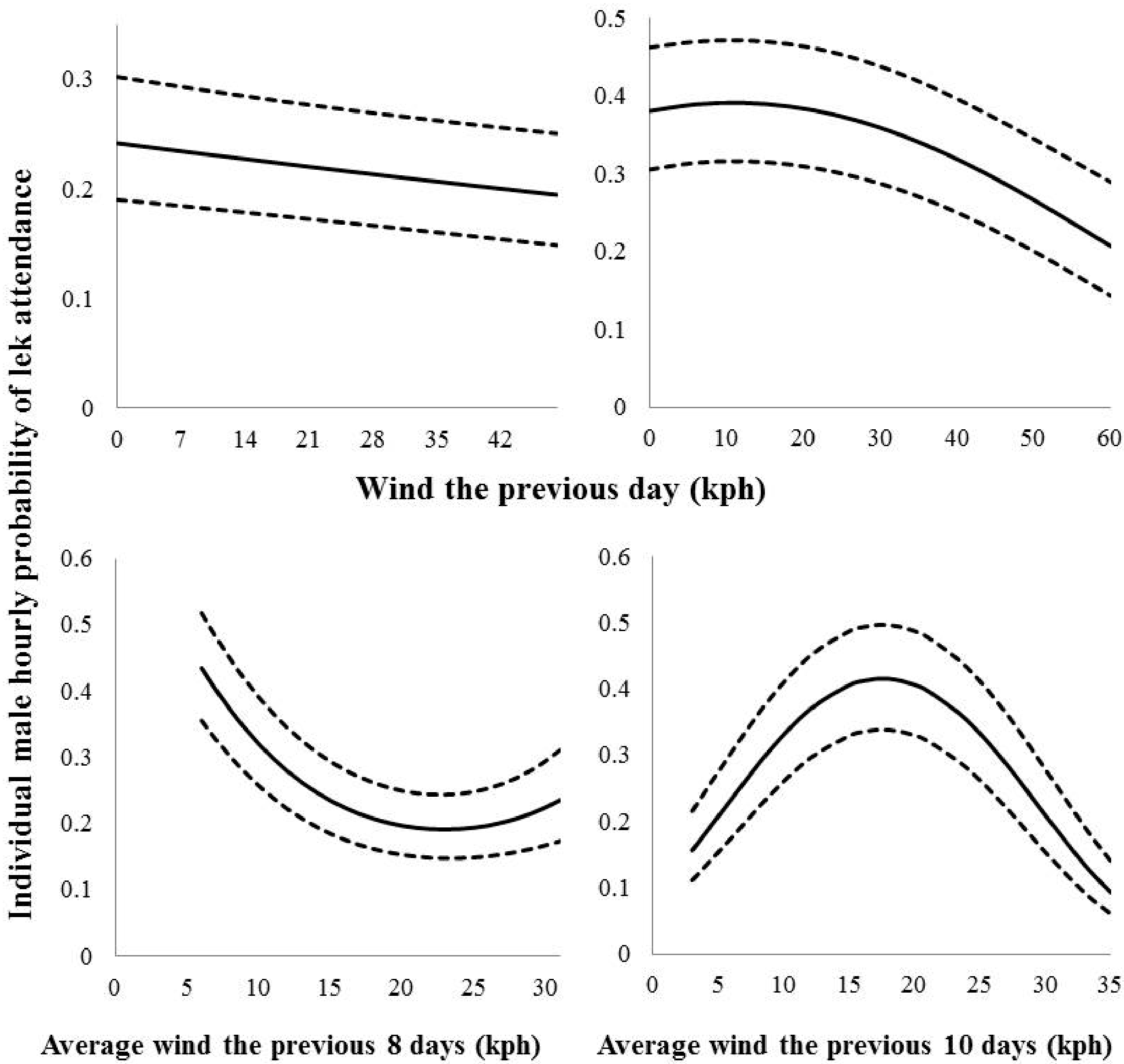

Figure 6. Individual male greater sage-grouse hourly lek attendance was affected by winds at several time scales on and around the Overland Trail Ranch in Carbon County, Wyoming 2011 – 2014. Attendance was lower with increasing wind speeds the previous day and previous 8 days.

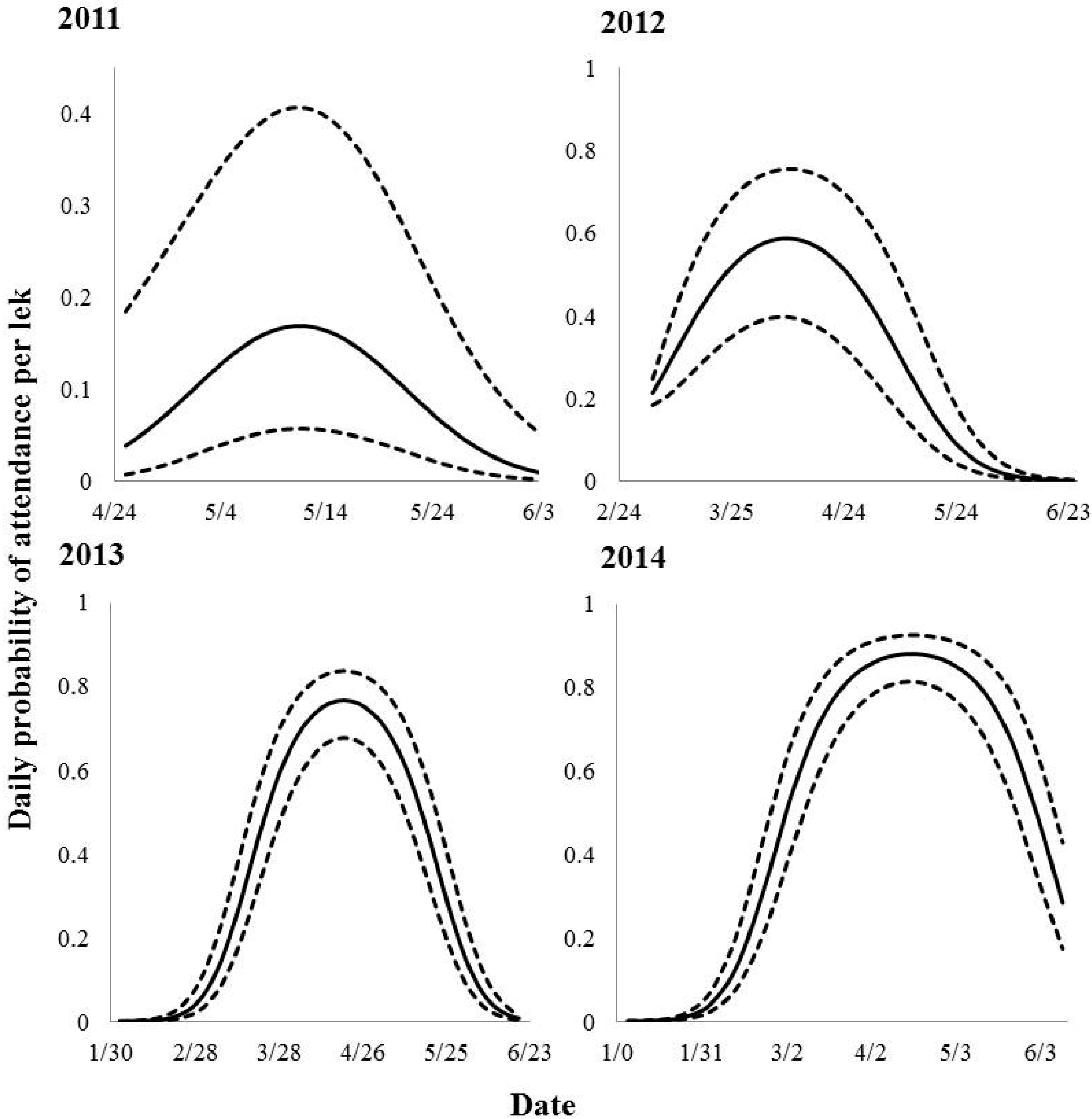

Figure 7. Date strongly influenced daily attendance per lek for male greater sage-grouse in Carbon County, Wyoming 2011 – 2014.

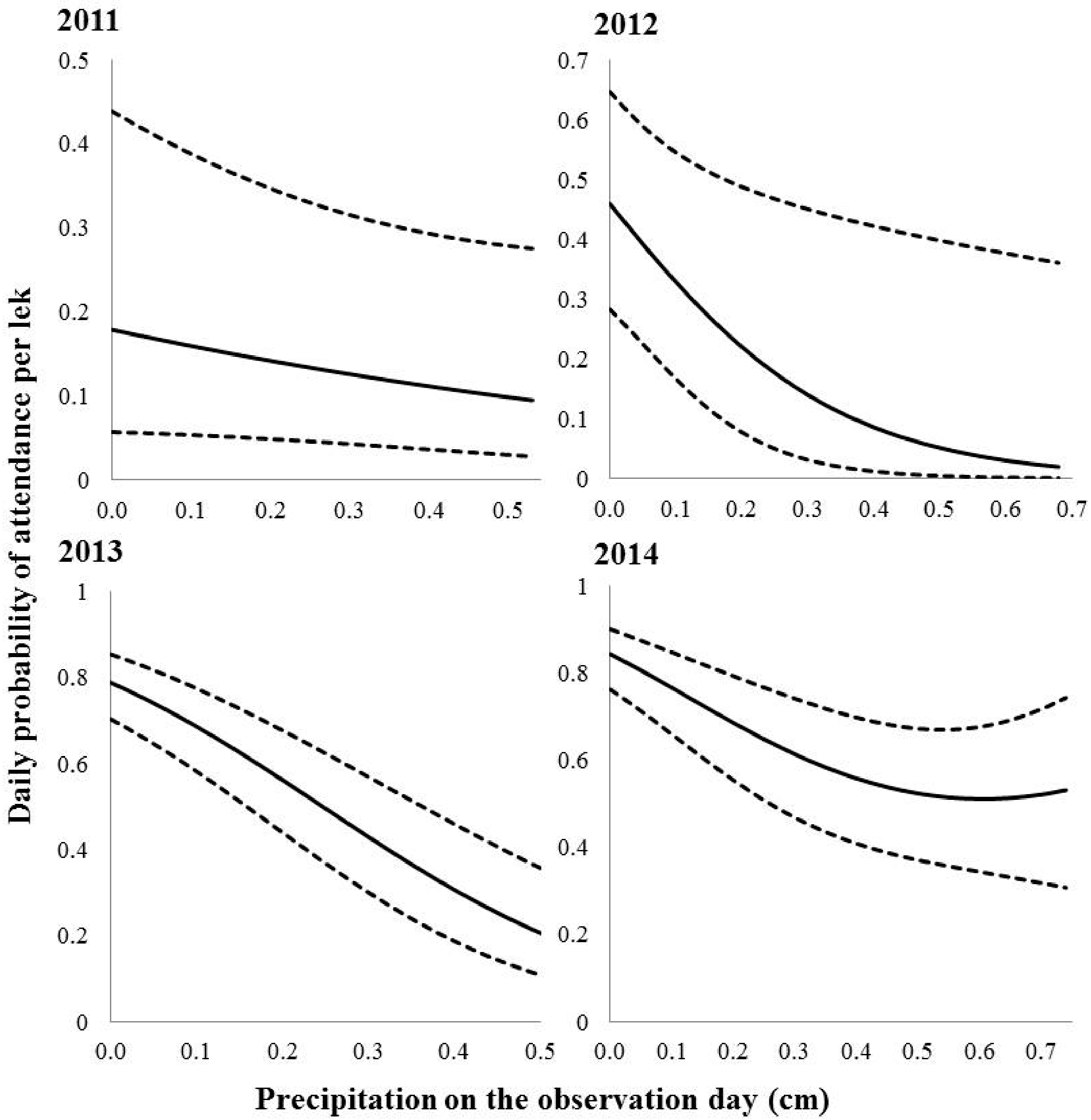

Figure 8. Daily attendance per lek for male greater sage-grouse in Carbon County, Wyoming 2011 – 2014 decreased as precipitation on the observation day increased.

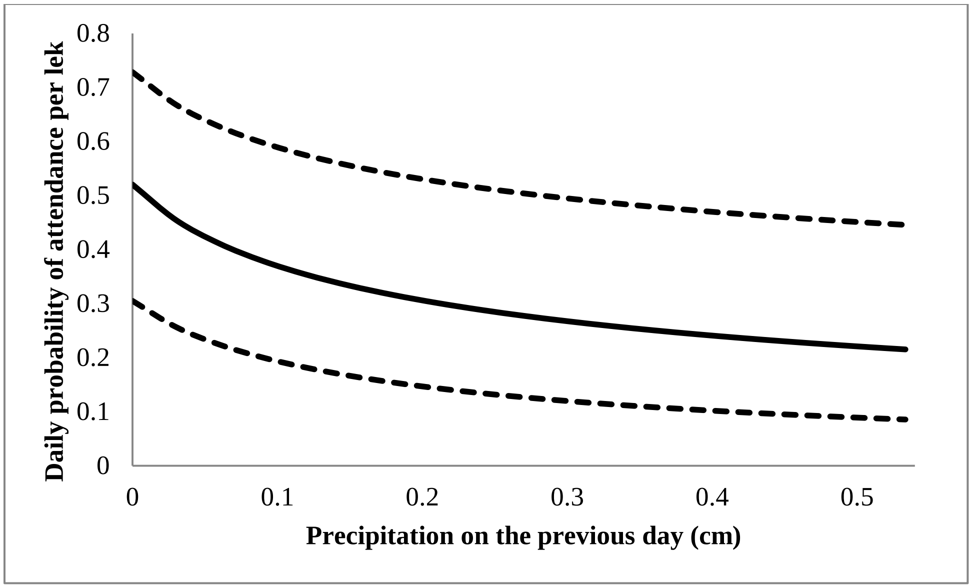

Figure 9. Daily attendance per lek was lower with precipitation the previous day than when there was no precipitation the previous day for male greater sage-grouse in Carbon County, Wyoming in 2011.

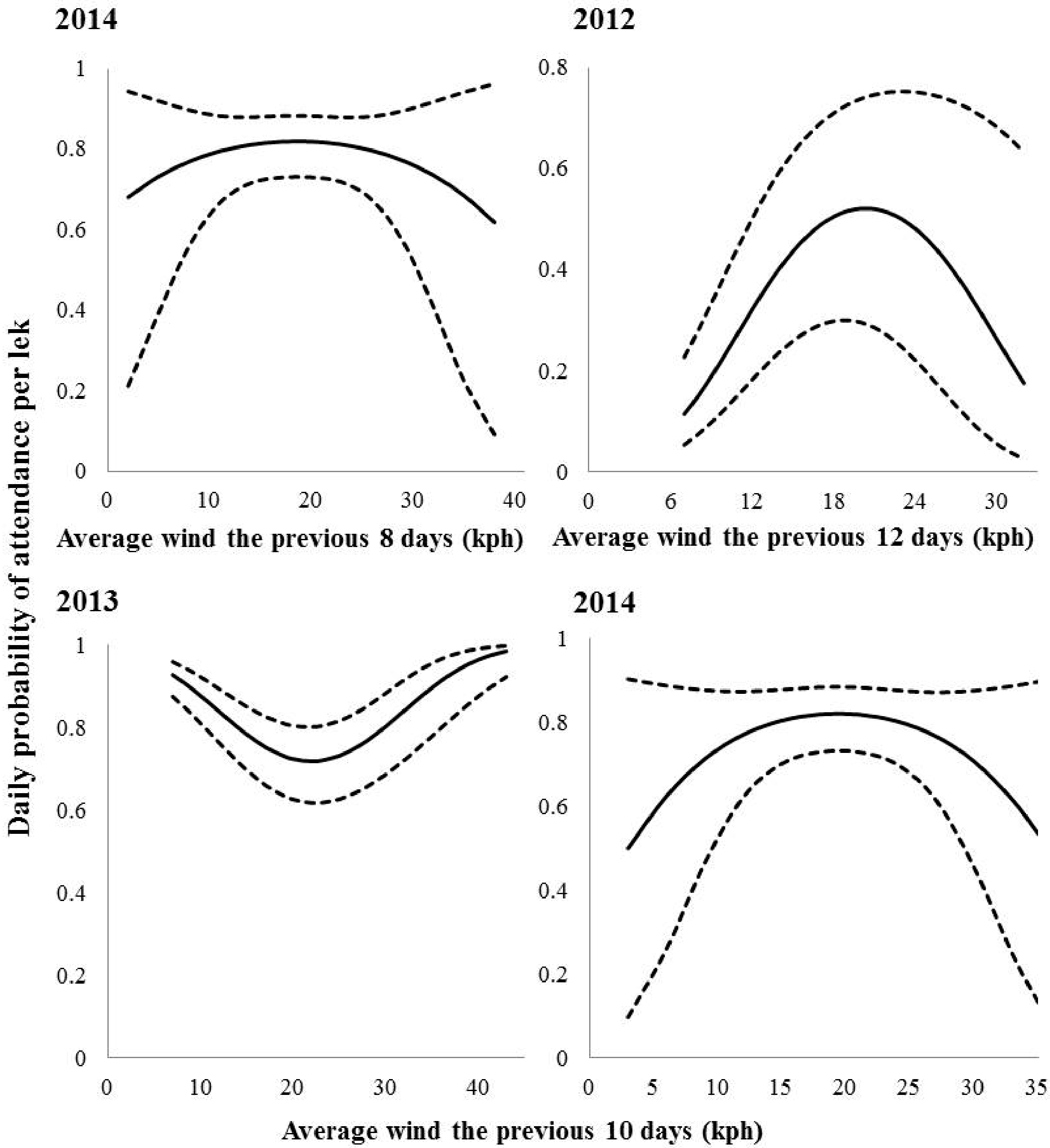

Figure 10. Wind affected daily attendance per lek for male greater sage-grouse in Carbon County, Wyoming 2012 – 2014, although patterns and timescales varied by year.

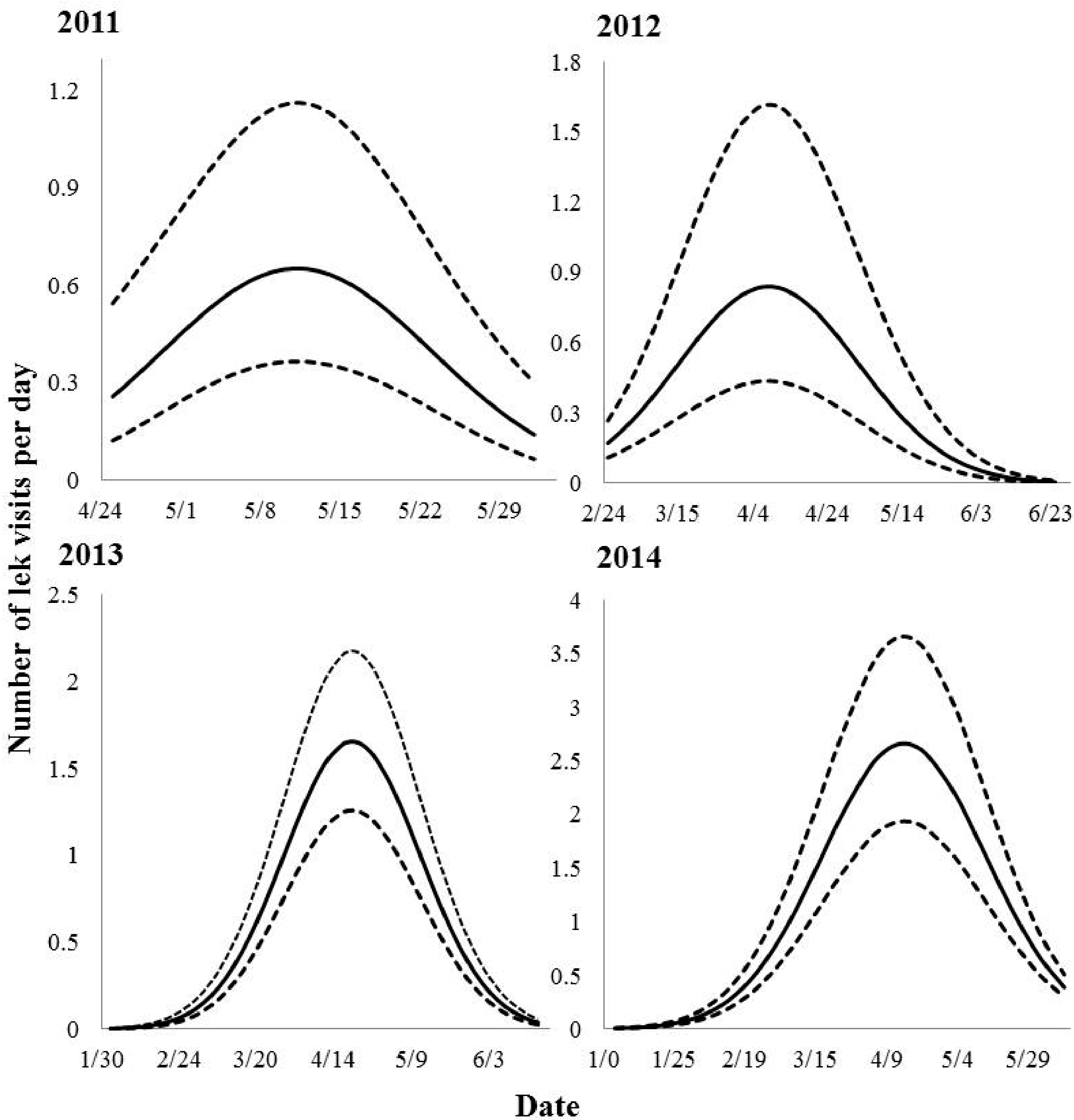

Figure 11. Date strongly influenced the visitation rate per lek for male greater sage-grouse in Carbon County, Wyoming 2011 – 2014.

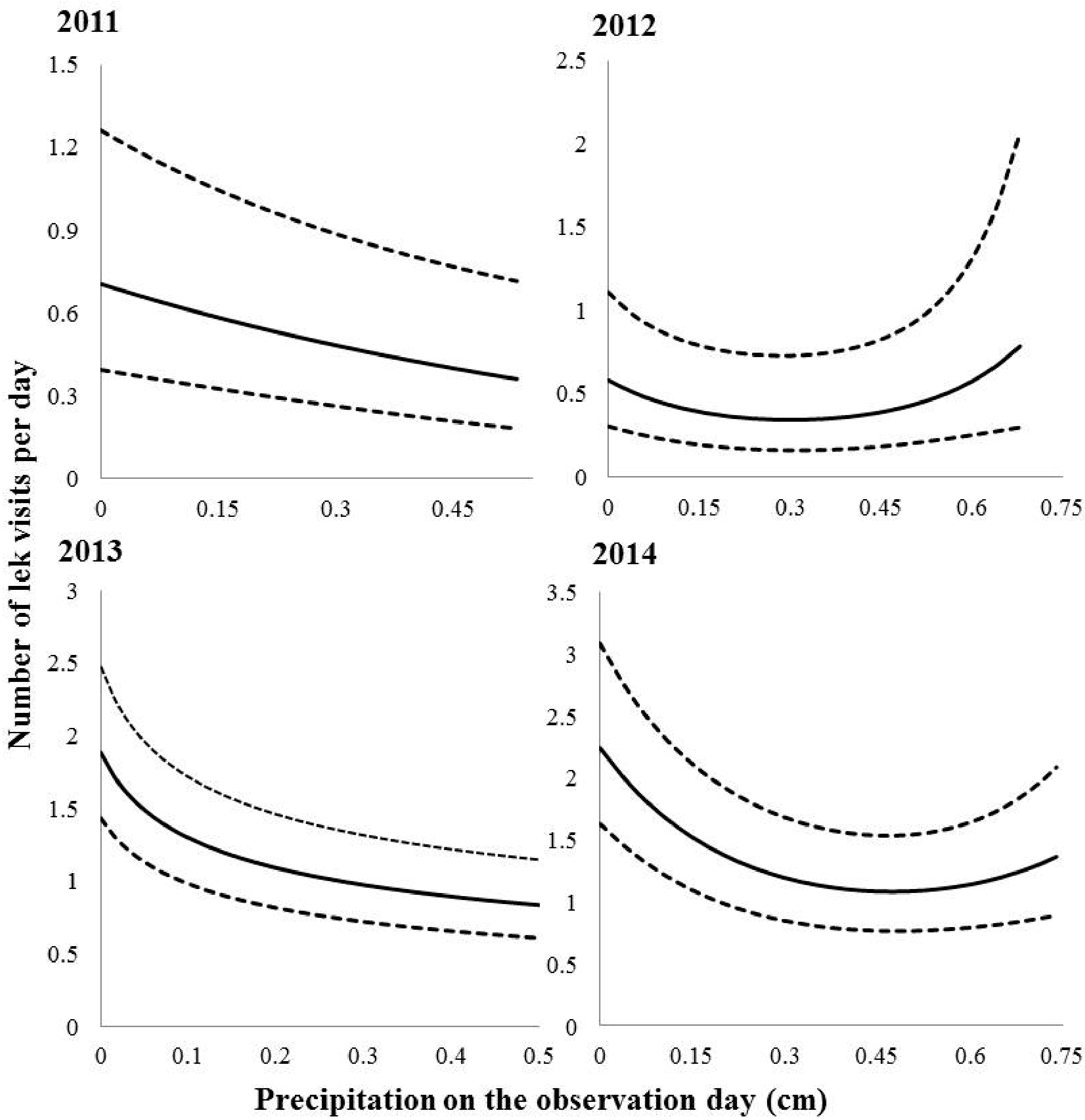

Figure 12. Visitation rates per lek decreased with increasing precipitation on the observation day for male greater sage-grouse in Carbon County, Wyoming 2011 – 2014.

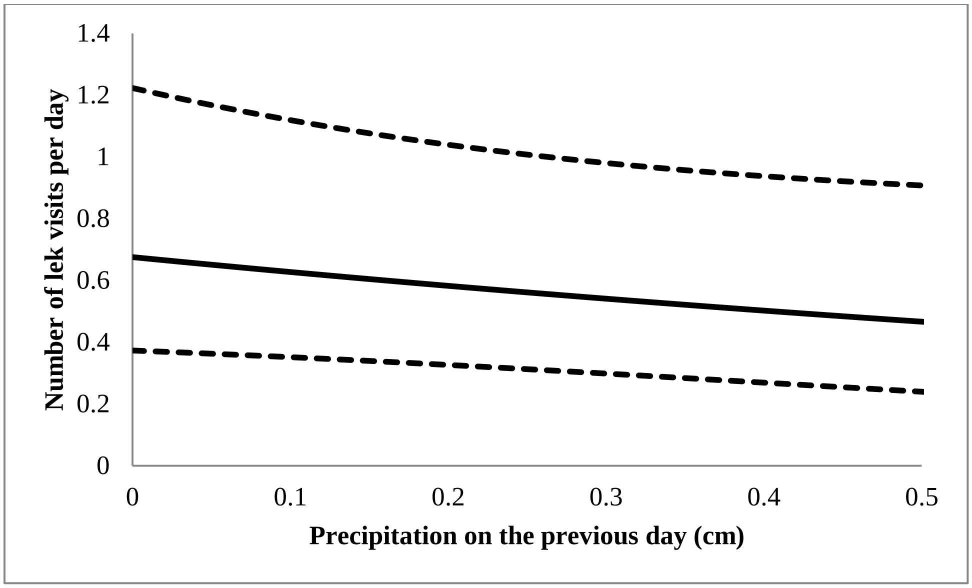

Figure 13. Visitation rates per lek were lower the day following precipitation for male greater sage-grouse in Carbon County, Wyoming in 2011.

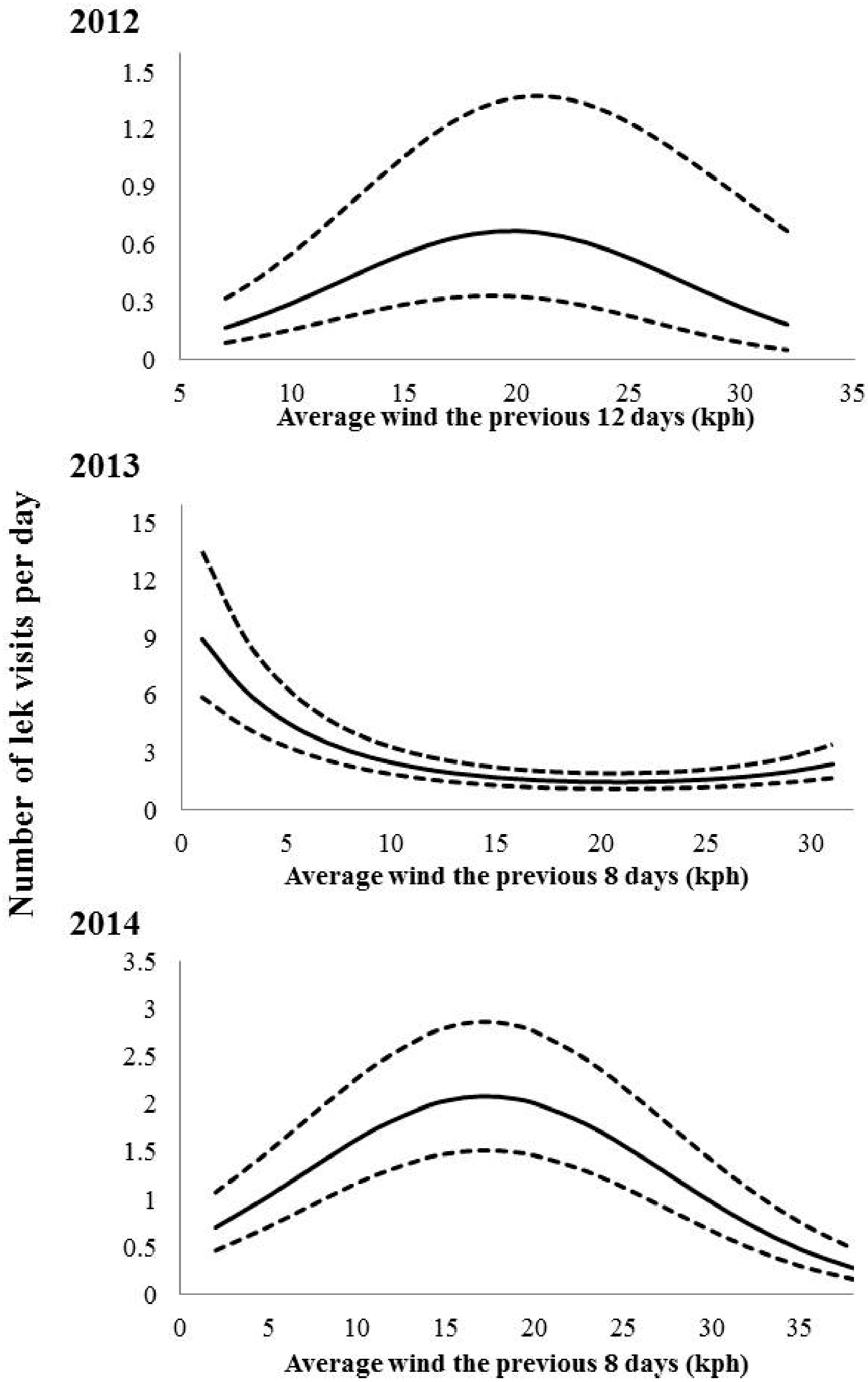

Figure 14. Visitation rate per lek for male greater sage-grouse in Carbon County, Wyoming 2012 – 2014 was influenced by wind at several longer time scales.

CHAPTER 2: USE OF MULTI-STATE MARK-RECAPTURE MODELS TO ASSESS MALE GREATER SAGE-GROUSE MOVEMENTS AMONG LEKS

ABSTRACT

Interlek movements of lek breeding birds are important to understand because they could affect genetic flow in a population, complicate the use of lek counts as a population index, and might be indicative of a change in breeding behavior following a disturbance. Previous research on male greater sage-grouse (*Centrocercus urophasianus,* hereafter sage-grouse) evaluated interlek movement frequencies as proportions of marked males that attended multiple leks during a single season, but daily interlek movement probabilities had not been extensively investigated but are especially useful to inform managers when males move most frequently, which could confound lek counts. Factors that may affect movements among leks by males include bird age and mass, weather, date, and lek characteristics and these have not been explored despite their potential influence on lek counts and genetic connectivity of populations. We used a Bayesian multi-state mark-recapture model to assess the daily probability of interlek movements and to determine factors that influenced interlek movement rates for male sage-grouse in Wyoming. We fit 145 males with Solar Argos Global Positioning Systems Platform Transmitter Terminals over 4 years in Carbon County, Wyoming. We assessed the importance of bird characteristics, lek characteristics, date, anthropogenic disturbances, and weather on the daily probability of interlek movements. The daily probability of a male sage-grouse moving among leks ranged from 1.04% [95% CI: 0.72%, 1.40%] in 2014 to 2.22% [95% CI: 1.60%, 2.90%] in 2013, indicating high daily fidelity for a single lek throughout the season, although there was a 38.6% to 69.9% chance that a male would move at some point throughout the season. We observed years with higher lek

fidelity also had higher survival by all male sage-grouse. Smaller individuals, juveniles, or individuals with low lek attendance were most likely to move to another lek. Movement probabilities were positively associated with the extent of sagebrush surrounding the lek and precipitation the previous day, and negatively associated with current day precipitation. Due to high lek fidelity, interlek movements are unlikely to bias lek counts, but other factors such as attendance rates should also be considered.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) have undergone substantial population declines, primarily from habitat degradation and fragmentation (Braun 1998, Connelly et al. 2004). Although sage-grouse were previously widespread in semiarid sagebrush (*Artemisia spp.*) steppe habitats, their range has been constricted to approximately 56% of their pre-settlement distribution (Schroeder et al. 2004) and they have suffered range-wide declines in abundance averaging 33%, with declines up to 92% in some populations (Connelly and Braun 1997, Braun 1998, Aldridge and Brigham 2003). Currently, sage-grouse are considered “warranted but precluded” from listing as endangered in the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service [USFWS] 2010). As a result, it is important to accurately monitor population sizes and male lek ecology, such as interlek movements (i.e. movements among leks during the breeding season), for changes in breeding behavior. A lek is a traditional breeding ground where males display and females come to mate. Interlek movements are uncommon due to high fidelity exhibited by males to leks (Campbell 1972, Dunn and Braun 1985, Schroeder and Braun 1992, Schroeder and Robb 2003, Walsh et al. 2010). Interlek movements by males could impact long-term reproductive success at a lek and gene flow among leks, or complicate lek count data for use as a population index. Although previous research has examined the influence of age on interlek movements (Schoenbrg 1982, Emmons and Braun 1984, Dunn and Braun 1985, Schroeder and Robb 2003), many factors remain unexplored such as characteristics that may make leks attractive, weather conditions that may influence interlek movements, small scale disturbances, or seasonal timing.

Interlek movements may reflect breeding effort or gene flow among leks and these movements likely vary by age of birds or body condition. Because few males on the lek mate (Jenni and Hartzler 1978, Gibson and Bradbury 1985), if dominant males move less frequently among leks they may contribute more strongly to the gene pool at a single lek because they may establish themselves at territories more successfully and mate. Dominant males typically have high rates of lek attendance (Gibson and Bradbury 1985), have more mass (Bowyer et al. 2007, Natoli et al. 2007), and are often older (Wiley 1974, Pelletier and Festa-Bianchet 2006). Conversely, larger males may have more energy to move among leks than smaller males because the strutting display is energetically expensive and causes males to lose mass throughout the season (Beck and Braun 1978, Vehrencamp et al. 1989). Adult males may move among leks less frequently than juvenile males (Schoenbrg 1982, Emmons and Braun 1984, Schroeder and Robb 2003), although age may not affect interlek movements in some areas (Dunn and Braun 1985). Many factors could influence movements among leks and which leks they favor, and these factors could ultimately influence reproduction on different leks or for different males and have implications to monitoring approaches, including lek counts.

Other factors such as vegetation or topographic characteristics of leks, weather, timing during the breeding season, or disturbances could also influence interlek movements. Some leks may be more desirable display sites based on their topographic attributes (Patterson 1952) or have higher proportions of sagebrush in the immediate proximity (Vehrencamp et al. 1989, Barnett and Crawford 1994, Connelly et al. 2000, Gregg 2006, Gregg et al. 2008). Males that do move may have more energy for breeding by only moving to the next closest lek (Schroeder and Robb 2003). Additionally males may be attracted to leks that have high concentrations of females (Bradbury et al. 1989a), or they may be attracted to leks with high concentrations of other successful males (Beehler and Foster 1988). Precipitation can decrease lek attendance (Bradbury et al. 1989b) and lower activity levels, so males may be less likely to move to another lek during precipitation events. Male sage-grouse may be more likely to move among leks in the beginning or end of the lek season (Emmons and Braun 1984, Wegge and Larsen 1987). Finally, small scale disturbances such as lek counts, trapping near leks, or the presence of observation blinds are frequently found at sage-grouse leks and the effects of these disturbances have not been assessed. However, it is important to understand how research methodology may influence breeding behavior (Dougherty 2008, Ibáñez-Álamo et al. 2012).

Understanding interlek movements could improve the reliability of lek counts. Lek counts are the only long-term data set available for sage-grouse population assessments, and have been used by state and federal management agencies as early as the 1940s (Connelly and Schroeder 2007, Johnson and Rowland 2007). However, lek counts might not be a useful index of population size if males move among leks at different rates and therefore cannot be detected by lek counters or are double counted (Anderson 2001). Counting a male during a lek count only occurs if the male is available for detection at the lek and has not moved to a different lek, and the observer detects the male when present on the lek (Alldredge et al. 2007, Schmidt et al. 2013, Chapter 3). Therefore, daily interlek movement probabilities can be modeled to understand factors influencing movement direction and frequency, which can be used to inform managers when males are most likely to move and therefore when counts should be avoided. Previous research that assessed male interlek movements (Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985, Schroeder and Robb 2003) had small sample sizes and birds were often captured on leks, possibly biasing the sample towards dominant males with high site fidelity (Walsh et al. 2004), and few studies examined the frequency of movements in relation to factors other than age. Interlek movements were summarized as the number of leks a male was observed at per year with 15 – 27% of adults moving to a new lek (Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985), but no research has examined factors influencing movements and timing of the movements except age. Recent interlek movement research incorporated larger sample sizes and found there was a 3% chance annually that a male might move from the lek it was captured at, but examined movements at a coarse temporal scale and did not examine factors influencing movements (Gibson et al. 2014). An evaluation of daily interlek movement probabilities and circumstances influencing movements would provide insight about sage-grouse breeding ecology and lek preferences at a fine temporal scale such as a day, which can be used to examine factors such as precipitation and wind that occur over short time periods but likely influence movements. Understanding factors influencing interlek movements at a daily scale could improve lek count protocols to more accurately relate the lek count index to population size by avoiding counts during days with high interlek movement rates.

Interlek movements are not well documented but are necessary to understand lek ecology, long-term reproductive success, to relate lek counts to population size, and to understand how disturbances influence male sage-grouse behavior on leks during spring. We hypothesized that male interlek movements may be affected by bird characteristics, lek characteristics, timing within the breeding season, environmental conditions such as weather, and anthropogenic disturbances. We estimated interlek movement probabilities for male sage-grouse and examined the factors affecting interlek movements in Carbon County, Wyoming.

STUDY AREA

This research was part of a larger, long-term study with a Before-After Control-Impact design to assess the relationship between male sage-grouse ecology and wind energy development. The 1,000 turbine development was proposed on The Overland Trail Ranch (OTR), a 320,000 acre (1,295 km^2) checkerboard of private and public land (BLM and Wyoming Game and Fish Department [WGFD]) ownership south of Rawlins, WY. There were 57 known leks throughout the study area, with 20 – 33 leks active each year during research (Fig. 1). The OTR lies within a basin with rocky ridges to the north and northeast, and sagebrush steppe foothills to the south and southwest. Elevations ranged from 1,890 m to 2,590 m above sea level.

The climate was semiarid, with short, hot summers and long, cold winters (Bailey 1995). The highest temperatures occur in July (average maximum 31 °C) and the lowest temperatures occur in December and January (average maximum -1 °C) (Western Regional Climate Center [WRCC] 2008). Annual precipitation was 19-26 cm in the basin and higher in the foothills and ridges, with most precipitation falling between April and October (WRCC 2008). Growing seasons were about 120 days, from late April to early October (Bailey 1995).

Vegetation consisted primarily of sagebrush (*Artemisia spp*.) with short grasses (Bailey 1995). Willows (*Salix spp*.) and sedges (*Carex spp*.) lined streams and valley bottoms, and greasewood (*Sarcobatus vermiculatus*) grew in moist alkaline flats, and some shadscale (*Atriplex confertifolia*) grew throughout the lower elevations (Bailey 1995). Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*) dominated higher elevations, with silver sagebrush (*A. cana*) in lowlands and black sagebrush (*A. nova*) in rocky, exposed soils (Connelly et al. 2004, Welch 2005).

METHODS

Trapping and Marking

We trapped male sage-grouse near active leks. High site fidelity by dominant males captured near leks in spring could bias results towards increased lek attendance and fewer interlek movements (Walsh et al. 2004). To avoid bias for dominant male birds, we captured birds primarily in late fall, which we supplemented with spring captures to maintain desired sample sizes.

We captured male sage-grouse using spotlighting and hoop-netting techniques (Giesen et al. 1982, Wakkinen et al. 1992) facilitated by All-Terrain Vehicles (ATV). Two-person groups visited sage-grouse roosting sites at night. Once a bird was located, one person approached on the ATV while shining a light in the bird's eyes, and the other person approached behind the ATV on foot, carrying a 75 cm diameter hoop net with 1.75 cm nylon mesh netting, captured the grouse, and restrained it to reduce injuries. We weighed captured males and classified them as adults (≥ 2 years old) or yearlings (<1 year old) based upon primary wing feather characteristics (Eng 1955, Crunden 1963). Trapping and handling procedures were approved through the University of Missouri Institutional Animal Care and Use Committee (Protocol #6750).

Trapping began May 2011 with a phased-in approach. Our goal was to mark 20 males in 2011, 20 males in 2012, and 10 males in 2013 with 30 g solar powered platform transmitter terminal (PTT-100) Global Positioning System (GPS) transmitters (accuracy ± 18 m, Microwave Telemetry, Inc., Columbia, MD). We attached GPS-PTT transmitters using the Rappole and Tipton (1991) method. Each bird also received a uniquely identifiable colored and aluminum leg band combination. During spring, GPS-PTT transmitters recorded locations every hour from 0400 to 0900, and after 0900 transmitters collected 3 more locations throughout the day on 5 schedules to ensure locations were during different periods in the 24-hour cycle.

To determine a GPS-PTT tagged male bird's location in relation to the lek, we mapped the perimeters of all known active leks. We mapped lek perimeters annually because leks may shift over time (Bergerud and Gratson 1988). We mapped boundaries after the breeding season ended and after watching the lek several times during lek counts following standard protocols (Connelly et al. 2003), to incorporate temporal variation in lek shape and size throughout the year. We recorded an azimuth and distance to birds on lek edges (average 9 – 13 locations per lek per year) and used these locations as well as concentrations of cecal tar, droppings, and feathers to demarcate lek boundaries, to which we added a 40 m buffer in ArcMap Geographic Information System (GIS; Environmental Systems Research Institute, Redlands, California, USA) to accommodate individuals on the boundary periphery that were likely attending leks. We applied 2012 lek boundaries to location data collected in 2011 and additionally applied 2013 lek boundaries for 6 leks we were unable to accurately demarcate in either 2011 or 2012. We considered a bird to be attending the lek when a location was within the mapped lek boundaries.

Multi-State Mark-Recapture Estimates

We estimated daily interlek movement probabilities of individual male sage-grouse. We assumed males were associated with the closest lek (measured by Euclidean distance) and that a male attended a lek if they were recorded within that lek's boundary. For males that attended 1 or 2 leks throughout the season, we only considered them to be associated with leks they attended. We considered an interlek movement to occur on the date that the closest lek to the bird was a different lek. If a male attended two leks in a single day, we assigned the male to the lek association that showed a movement between leks. If a male attended 3 or more leks throughout the season, we based lek associations on distance to the closest lek. We considered the lek season to start with the arrival of the first marked male on a lek, and ended with the departure of the last marked male on a lek. We included all data immediately after a male was captured because many males began to attend leks and behave normally within 1 – 2 mornings after being captured and we wanted to include all possible data. We used locations of birds to locate unknown leks in the study area, to ensure interlek movements were not biased. Model convergence was poor with data pooled across years and using year as an additive effect, and we wanted to include annual variability so we modeled interlek movements separately by year.

To evaluate the influence of lek characteristics on interlek movements, we calculated several covariates using the Geospatial Modelling Environment (GME; Beyer 2012) with ArcMap. For each lek, we estimated average slope, aspect, and elevation within the lek boundaries using a 10 m digital elevation model (DEM). For aspect, we first converted DEM aspect cells to radians, took the sine and cosine of each cell, and averaged the values of the sine and cosine cells within the lek perimeter. We converted back to degrees using the arctan transformation. We also used the GME and a 30 x 30 m land cover layer (Wyoming Geographic Information Science Center [WyGISC] 2004) reclassified as sagebrush or "other" to determine the percent of sage within 603 m of the lek; 603 m was the median distance from the lek boundary to each GPS-PTT transmitter location in our study site in spring 2011 – 2013 and represents the average distance from the lek of radio marked males. We recorded daily precipitation and average wind speed at sunrise from the National Oceanic and Atmospheric Administration (NOAA) weather station in Rawlins, WY. We also calculated seasonal lek attendance as the proportion of days a male attended a lek during the breeding season.

We used a Bayesian multi-state mark-recapture (MSMR) model (Williams et al. 2002, Lebreton et al. 2009, Kéry and Schaub 2012) to estimate daily probabilities of interlek movements. We classified birds into 3 states: Lek, Lek', and Dead (Fig. 2). All birds were initially within the Lek state. Those birds that moved to a different lek were assigned the state Lek', where they remained until they moved to yet a different lek (and transitioned back the state Lek) or died. We used a transition matrix to describe the probability of transitioning from the state at time $t - 1$ (the rows) to the state at time t (the columns) during a single time step (i.e. day):

		State at time step t		
		Lek	**Lek'**	**Dead**
State at time step $t - 1$	**Lek**	$(1 - \psi_{it})\ \phi$	$(\psi_{it})\ \phi$	$1 - \phi$
	Lek'	$(\psi_{it})\ \phi$	$(1 - \psi_{it})\ \phi$	$1 - \phi$
	Dead	0	0	1

where ψ_{it} is the probability of sage grouse i moving to a new lek during time step t and ϕ is the daily survival probability. We held ϕ constant across all time steps and states.

A male sage-grouse's state at time t was modeled as a categorical random variable:

$$state_t \sim categorical(\mathrm{M}_{t-1})$$

where M_{t-1} is the row of the transition matrix associated with the sage-grouse's state at time $t - 1$. We assumed vague normal ($\mu = 0$, $\sigma 2 = 100$) prior distributions for covariate parameters and a uniform(0, 1) prior distribution for the ϕ parameter. We imputed missing states and covariates when transmitters temporarily failed to collect locations.

W modeled the probability of moving among leks as a function of bird characteristics, lek characteristics, environmental conditions, and anthropogenic disturbances as:

$$\mathrm{logit}(\psi_{it}) = \beta_0 + \beta_1 age_{i,t-1} + \beta_2 mass_{i,t-1} + \beta_3 attendance_{i,t-1} + \beta_4 slope_{i,t-1} + \beta_5 aspect_{i,t-1} + \beta_6 elevation_{i,t-1} + \beta_7 psage_{i,t-1} + \beta_8 lekarea_{i,t-1} + \beta_9 date_{i,t-1} + \beta_{10} datequadratic_{i,t-1} +$$

$\beta_{11} malecount_{i,t-1} + \beta_{12} femalecount_{i,t-1} + \beta_{13} PPT_{i,t-1} + \beta_{14} PPTprev_{i,t-1} + \beta_{15} wind_{i,t-1} +$

$\beta_{16} windPrev_{i,t-1} + \beta_{17} blinds_{i,t-1} + \beta_{18} counts_{i,t-1} + \beta_{19} trapping_{i,t-1}$

Covariates related to bird characteristics included bird mass, seasonal attendance rate, and age modeled as dummy variable = 1 if the male was an adult and 0 if the male was a juvenile. For lek characteristics we modeled transitions to leks with certain physical characteristics including average slope, average aspect, average elevation, proportion of surrounding sagebrush within 603 m of the lek boundary, and lek area. Additionally we considered lek characteristics related to the lek formation hypotheses (i.e. hotshots and hotspots theories) by testing movements to male and female high counts (i.e. maximum number of males and females seen on the lek during lek counts) for the lek each year. We included environmental conditions by modeling day of year and its quadratic term, precipitation on the day of movement and precipitation the day preceding movement, and wind on the day of movement and wind the day preceding movement. Finally we considered anthropogenic disturbances by modeling the presence of ground blinds at leks, lek counters, or trapping near leks as dummy variables = 1 if a disturbance occurred, 0 otherwise. Models were created using biologically reasonable combinations of these variables (Appendix 1), to assess the influences of bird characteristics, lek characteristics, environmental conditions and date, and anthropogenic disturbances on male interlek movements. Covariates were recorded every day and for every state a male was in.

Model Building and Selection Process

We fit models in WinBUGS (Gilks et al. 1994) using the R2WinBUGS interface (Sturtz et al. 2005). We used 3 Markov chains to simulate posterior distributions of all parameters. We ran each chain for 10,000 iterations after discarding the first 5,000 iterations as burn-in, and kept every 10^{th} sample to minimize correlation between draws. The Brooks-Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998) indicated satisfactory convergence ($\hat{R} \approx 1$) for all parameter estimates, with 3,000 random samples from the posterior distribution for each parameter (1,000 per chain). We used the Deviance Information Criterion (DIC) to select the most parsimonious model (Spiegelhalter et al. 2003), keeping analysis separated by each year, and used only the top model for inference if no other model weights were ≥1/8 the weight of the top model. If one or more additional models had a weight ≥1/8 the weight of the top model, and parameter estimates and standard errors from the top model were similar to parameter estimates and standard errors from the global model, we based inference off the global model in lieu of multi-model inference. We assessed goodness-of-fit by examining standardized residual plots comparing the observed interlek movement histories to predicted movement histories (Dupuis and Schwarz 2007).

RESULTS

Trapping and Marking

Each year we deployed 31 ± 4 (mean ± standard error) GPS-PTT transmitters and 43 ± 9 birds were active each spring (Table 1). The GPS-PTT transmitters recorded locations during 2,338 ± 976 days each spring. We recorded 138 interlek movements to another lek by any male during our study. Throughout our study, we had 92 males that never moved to a new lek and 57 males that made at least one interlek movement. Lek sizes varied substantially (59806 ± 48729 m^2, range = 5915 m^2 – 268594 m^2).

Lek Transitions

There was a 1.04% [95% CI: 0.72%, 1.40%] probability a male would move among leks during a day in 2014, and males were more than twice as likely to move during 2013 (2.18% [95% CI: 1.55%, 2.87%]). Daily movement probabilities in 2012 were intermediate (1.60% [95% CI: 0.80%, 2.55%]). The highest average probability of moving to a new lek at any point in the breeding season was during 2013 (69.17% [95% CI: 56.66%, 78.97%]) as well as the lowest average probability of surviving throughout the breeding season (68.69% [95% CI: 61.81%, 76.33%]). The lowest probability of moving to a new lek at any time in the breeding season occurred in 2012 (38.64% [95%CI: 54.26%, 21.59%]), which was also the year with the highest probability of surviving through the season (83.34% [95% CI: 73.94%, 93.89%]). Interlek movement rates (61.36% [95% CI: 48.17%, 72.26%]) and survival rates (76.09% [95% CI: 63.62%, 90.97%]) throughout the 2014 breeding season were intermediate to the other years. In 2012 and 2014, there was no model uncertainty whereas 2013 showed considerable uncertainty (Table 2). In 2013, parameter estimates for top models were similar to the global model parameter estimates so the global model was used for inference.

Bird characteristics including mass, age, and attendance largely influenced interlek movements, but the magnitude and direction of the results differed across years. In 2012, males were more likely to move if they were smaller (Fig. 3), adults, or attended leks infrequently whereas in 2013 males that were smaller, juveniles, or attended leks regularly were more likely to move although the patterns were not as strong in 2012. In 2012, males that weighed 2300 g were 15 times more likely to move to a new lek than a male weighing 3000 g (Table 3), adults were about 5 times more likely to move than juveniles, and males that rarely attended a lek were 28 times more likely to move among leks than a male that attended every day. Pooling data across years could provide a more consistent understanding of how male characteristics influence interlek movement rates.

Several physical lek characteristics and male and female high counts were also included in the highest ranked models although their effects were not as strong as bird characteristics. Elevation was included in the models from 2013 and 2014 but showed opposite association with probability of movement to a different lek. In 2013 males were over 4 times more likely to move towards a low elevation lek, whereas in 2014 males were about 12 times more likely to move to a high elevation lek. Surrounding sagebrush cover also was included in 2013 and males were 3 times less likely to move to a lek with 30% surrounding sagebrush cover versus a lek with 100% surrounding sagebrush cover (Fig. 4). In 2013 males moved to leks with more males and fewer females (Fig. 5). Male sage-grouse were 4 times less likely to move to a lek with 60 hens than a lek with 0 hens, and 4 times less likely to move to a lek with 2 males than 50 males.

Environmental conditions also had some influence on interlek movements. Interlek movements were 4 to 12 times more likely to occur in the beginning of the breeding season than at the end of the season (Fig. 6). Male sage-grouse were almost 5 times more likely to stay at their current lek when there was precipitation, but on a day following precipitation, males were >2 times more likely to transition to a new lek (Fig. 7). Wind did not have a meaningful influence on male interlek movement probabilities. Anthropogenic disturbances, including ground blinds near the lek, lek counts from foot, and spotlighting and hoop-netting trapping near a lek did not have any detectable influence on male sage-grouse interlek movements. Residual plots indicated model fit was good for all years (Figure 7), although there were some extreme residuals from small observed counts.

DISCUSSION

Males showed high daily fidelity to a single lek, although there was a high probability of interlek movement at least once throughout the breeding season. Males of many grouse species, including sage-grouse, have high fidelity to their lek site for life (Campbell 1972, Dunn and Braun 1985, Schroeder and Braun 1992, Schroeder and Robb 2003, Walsh et al. 2010) and leks can persist yearly in the same sites because of high fidelity (Patterson 1952, Jenni and Hartzler 1978, Connelly et al. 2003). Although we observed high daily fidelity, about 40% of the males in our study made an interlek movement at least once during the breeding season, indicating interlek movements may be more common in spring than previously reported (e.g., Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985). High daily fidelity could help males establish territories at a lek over time, and also build knowledge of predators and competitors in the area (Bergerud and Gratson 1988). As a result, males with high fidelity could establish central territories and therefore may be more attractive to mates (Hovi et al. 1994) and also may have higher survival. Within our study we also observed survival was highest in years with high lek fidelity, and survival was lowest when lek fidelity was low. This suggests a cost of moving among leks in terms of lower survival, so it is important to recognize the drivers for interlek movements to understand benefits of interlek movements.

Physical characteristics of male sage-grouse had the strongest influence on the probability of interlek movements. In particular, heavier males were least likely to make interlek movements. This likely occurs because heavier males are more likely to mate and may be established at successful territories on a lek (Beck and Braun 1978, Vehrencamp et al. 1989). Juvenile male sage-grouse have less mass than adults and are subdominant to adults in lek mating systems (Owen-Smith 1993, McElligott et al. 1999, Pelletier and Festa-Bianchet 2006, Natoli et al. 2007, Alonso et al. 2010). Although we did observe some annual variation, adult males displayed high fidelity for a single lek in 2013. In lek-forming species, dominant males typically have high lek attendance rates (Höglund and Lundberg 1987, Apollonio et al. 1989), and in general we found males that attended every day were less likely to move than males that attended rarely, suggesting dominant male sage-grouse have high fidelity to their lek. As a result, it is unlikely that dominant males provide substantial gene flow among leks although they may strongly contribute to the reproductive success at a single lek. Gene flow may primarily occur from dispersing male and female yearlings (Bush et al. 2010), and from females that move among leks more frequently (Wallestad and Schladweiler 1974). Additionally, strong lek fidelity explains why lek abandonment does not immediately occur in oil and gas developments, because adult males return to their leks despite disturbance for several years after development, and leks are only abandoned after yearling males stop dispersing to disturbed leks (Holloran 2005, Walker et al. 2007, Holloran et al. 2010). As a result, interlek movements should be monitored at least 3 years post-construction in developments for changes that may indicate lek abandonment over time.

The migration to leks at the beginning of the breeding season may depend on snowpack and improving weather conditions (Schroeder et al. 1999, Green 2006); just as weather influences when breeding begins, weather can also influence the probability of interlek movements. At the beginning of the lek season movements were more likely and males in 2014 moved towards high elevation leks potentially as the snowpack melted early in the season. However, in 2013males were more likely to move towards low elevation leks, potentially to avoid variable and severe weather at high elevation sites (Boyle et al. 2010). We observed several GPS-PTT marked males regularly attending a high elevation lek until snow displaced them to lower elevation leks where they displayed for several days before returning to the high elevation lek (A. L. Fremgen, C. P. Hansen, *personal observation*). During lek counts immediately following a large precipitation event, especially at lower elevation leks in close proximity to high elevation leks, lek counts can have inflated high counts for males and females at lower elevations with less precipitation (A. L. Fremgen, C. P. Hansen, *personal observation*). Therefore, we recommend waiting two days following precipitation (and in particular snow) to conduct lek counts to avoid biased high count data as males move leks. Lek counts could also be avoided in areas with substantial topographic relief when snowpack at higher elevation leks is melting, as males may be more likely to move at that time in the beginning of the breeding season. Examining interlek movements averaged across all years, rather than analyzing by each year, could help managers incorporate interlek movement rates into lek count protocols for all years. The frequency and direction of interlek movements contributes to an availability bias, in which males are not present at the lek during lek counts, which is important to quantify if relating lek counts to population abundance

(Alldredge et al. 2007, Schmidt et al. 2013). In addition, managers must know detection rates on leks to enumerate the number of males not seen during counts on the lek (Chapter 3).

The combination of social and physical lek characteristics may make some leks more desirable than others, and may explain why males choose to move to a new lek despite potentially lower survival. Theories of lek formation are controversial, and our results could provide support for the “hotshot” theory of lek formation, in which males gather around dominant males in groups and females move to those concentrations (e.g., Moyles and Boag 1981, Beehler and Foster 1988, Partecke et al. 2002). We observed higher probability of lek transition toward leks with high male counts (Bradbury et al. 1989a, Westcott 1994, Gibson 1996b). Testing female interlek movement patterns in addition to male interlek movement patterns could provide additional insight to lek formation mechanisms. We also observed several males moving towards leks with higher proportions of sagebrush near the lek, potentially because there may be more food resources available in those areas and sage-grouse strutting displays are energetically expensive (Vehrencamp et al. 1989, Barnett and Crawford 1994, Connelly et al. 2000, Gregg 2006, Gregg et al. 2008). Sage-grouse require large intact sagebrush habitats across the landscape (Patterson 1952, Connelly et al. 2004).

Nearly all sage-grouse leks have some form of anthropogenic disturbance in spring from personnel conducting lek counts. Although other lek count methods are being explored, such as aerial imagery and thermal imagery from small aircraft or unmanned aircraft systems, lek counts remain the most effective and common method so it is important to recognize the potential impacts field personnel may have (Booth et al.

2009, McRoberts 2009, Gillette et al. 2013). Most sage-grouse research involves trapping and marking sage-grouse, often near leks in spring, and research sometimes involves ground blinds near the lek for observation purposes. If the effects of these disturbances are considered, they are generally assumed to be insignificant (Jenni and Hartzler 1978, Gibson and Bradbury 1985, Walsh et al. 2004, Patricelli and Krakauer 2010) although we were unaware of any research assessing the impacts of lek counts, trapping, or ground blind presence on male sage-grouse behavior. Our analysis suggested movements rates were the same in the presence of blinds, trapping, or lek counters but additional research should examine the effects of these disturbances on other aspects of male sage-grouse behavior on leks.

We were able to confirm dominant males move among leks less frequently than subordinates and male movements are affected by precipitation. Current lek count protocols should continue to avoid counts during precipitation and should consider avoiding counts the day following precipitation events. Interlek movements appear to have a cost in terms of decreased survival and leks with substantial sagebrush surrounding them are more attractive to males that move, as are leks that have more females in attendance. Interlek movements may occur more frequently than previously reported.

LITERATURE CITED

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Table 1. Trapping effort and data collected from GPS-PTT transmitters on male greater sage-grouse each year (2011-2014) in Carbon County, Wyoming.

	2011	2012	2013	2014
GPS-PTT transmitters deployed	28	37	38	21
Active transmitters in spring	22	36	59	55
All GPS-PTT locations in spring	3,318	8,528	22,053	33,195
Days used to assess movements, sum for all males	440	1,129	3,015	4,768
Number of leks with a GPS-PTT transmitter male	16	17	25	29
Observed transitions[14]	3	9	56	70

[14] Observed transitions are an interlek movement by any GPS-PTT transmitter male from attending one lek to attending another lek in the study area.

Table 2. Top models[15] describing factors influencing male greater sage-grouse daily interlek movement probabilities in and around the Overland Trail Ranch in Carbon County, Wyoming 2011-2014. Factors used to select the top model included the Deviance Information Criterion (DIC), change in DIC value from the top model (ΔDIC), and the DIC model weight (w_i).

Model	*DIC*	*ΔDIC*	w_i
2012			
Age, attendance, and mass	289.9	0.0	0.911
2013			
Precipitation the day of movement	1043.1	0.0	0.223
Null	1044.5	1.4	0.111
Date	1045.6	2.5	0.0639
Wind the day of movement	1045.7	2.6	0.0608
Age, Attendance, and Mass	1045.8	2.7	0.0578
Wind the previous day	1046.1	3.0	0.0498
Max Male	1046.2	3.1	0.0474
Mass	1046.3	3.2	0.0450
Max Hen	1046.4	3.3	0.0428
Age	1046.6	3.5	0.0388
Precipitation the previous day	1046.9	3.8	0.0334
Blinds all days (movement away from)	1047.0	3.9	0.0317
Age and Attend	1047.2	4.1	0.0287
2014			
Date (quadratic) and elevation	1023.1	0.0	1.000

[15] All models shown are ≥ 1/8 the DIC w_i of the top model.

Table 3. Parameter estimates for top models predicting male greater sage-grouse interlek movement probabilities 2012-2014 in and around the Overland Trail Ranch in Carbon County, Wyoming. Included are the standard deviation for the estimate (*SD*), as well as lower and upper credible interval limits (*LCI*, *UCI*). 2013 parameter estimates were from the global model.

Predictor	*Estimate*	*SD*	*LCI*	*UCI*
2012				
Intercept	-4.16	0.289	-4.72	-3.59
Age	0.718	0.294	0.142	1.29
Attendance	-1.12	0.324	-1.75	-0.483
Mass	-0.836	0.302	-1.43	-0.244
2013				
Intercept	-3.810	0.543	-4.972	-2.819
Age	-0.008	0.553	-1.015	1.176
Attendance	0.592	0.179	0.259	0.941
Mass	-0.233	0.136	-0.491	0.038
Date	-0.289	0.173	-0.638	0.043
$Date^2$	-0.140	0.163	-0.459	0.166
Precipitation during movement	-0.305	0.161	-0.654	-0.021
Precipitation day previous to movement	0.103	0.094	-0.095	0.275
Wind during movement	-0.040	0.129	-0.301	0.208
Wind day previous to move	-0.118	0.123	-0.362	0.124
Maximum hen count	-0.435	0.238	-0.893	0.034
Maximum male count	0.398	0.204	-0.012	0.791
Aspect	-0.339	0.124	-0.457	0.039
Slope	0.046	0.210	-0.371	0.436
Percent sage within 603 meters of lek	0.362	0.164	0.040	0.682
Elevation of lek	-0.450	0.180	-0.822	-0.098
Lek area (m^2)	-0.127	0.234	-0.590	0.330
Count at lek	0.022	0.667	-1.458	1.195
Trapping at/near lek	-0.692	1.293	-3.669	1.250
Blinds at lek	-0.466	0.336	-1.155	0.176
2014				
Intercept	-4.57	0.171	-4.91	-4.24
Date	2.86	1.70	-0.464	6.19
$Date^2$	-8.79	1.75	-12.2	-5.36
Elevation	0.645	0.0960	0.457	0.833

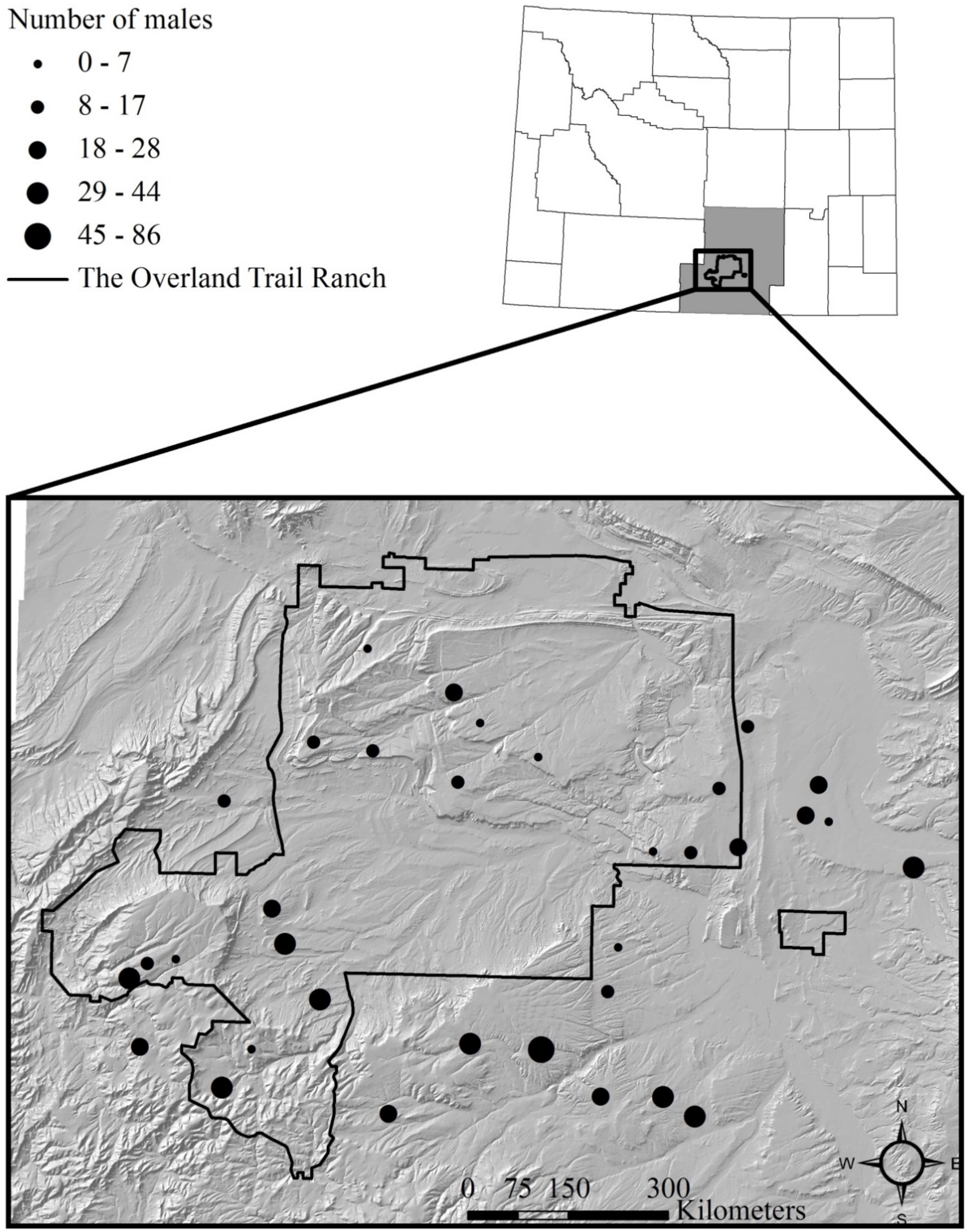

Figure 1. Study area for male greater sage-grouse interlek movements in Carbon County, Wyoming 2011-2014. Lek sizes shown are from 2013 lek counts.

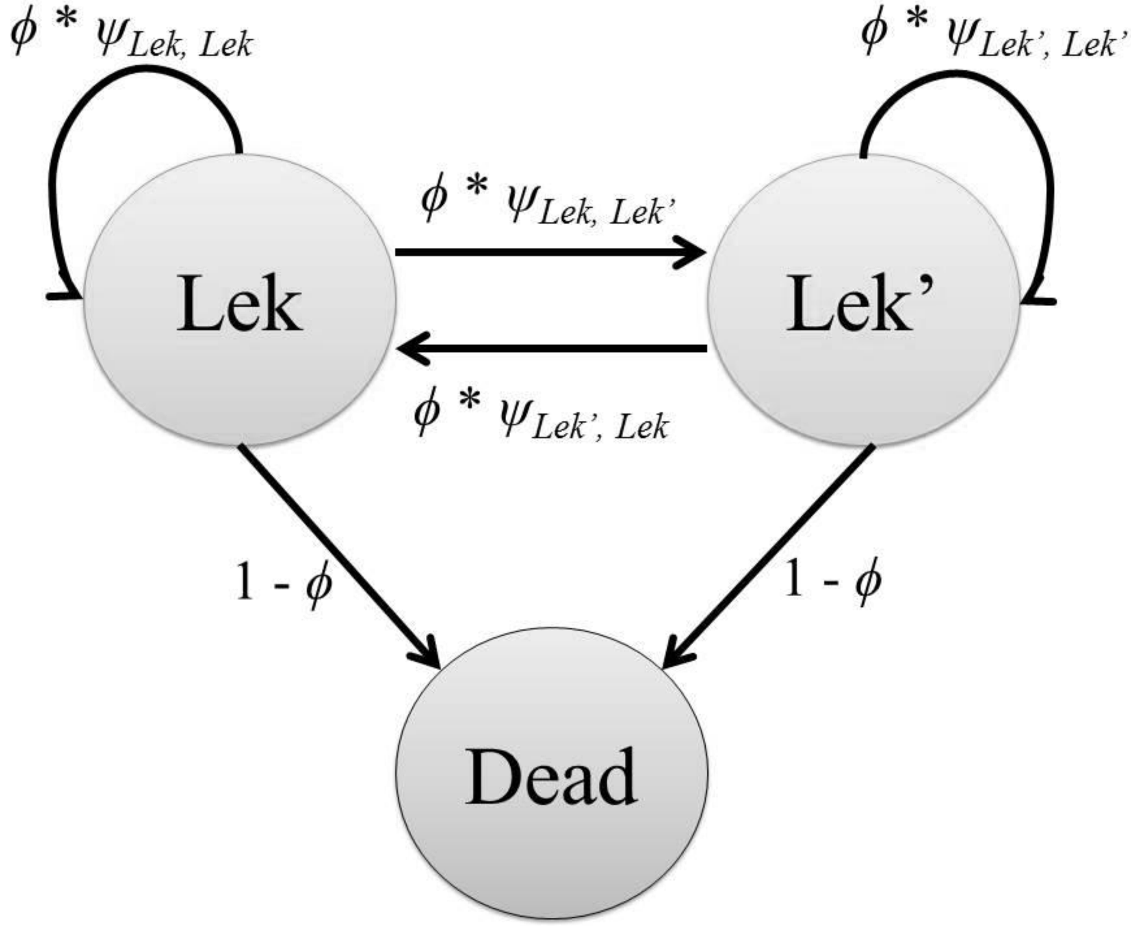

Figure 2. Schematic diagram for the probability of transitioning (ψ) and the probability of surviving (ϕ) from one time step to the next, for male sage-grouse interlek movements in Carbon County, Wyoming 2012-2014. Each circle represents a state in the multi-state mark-recapture model, with Lek representing the first lek a male attended, and any transition to a new lek is to Lek'.

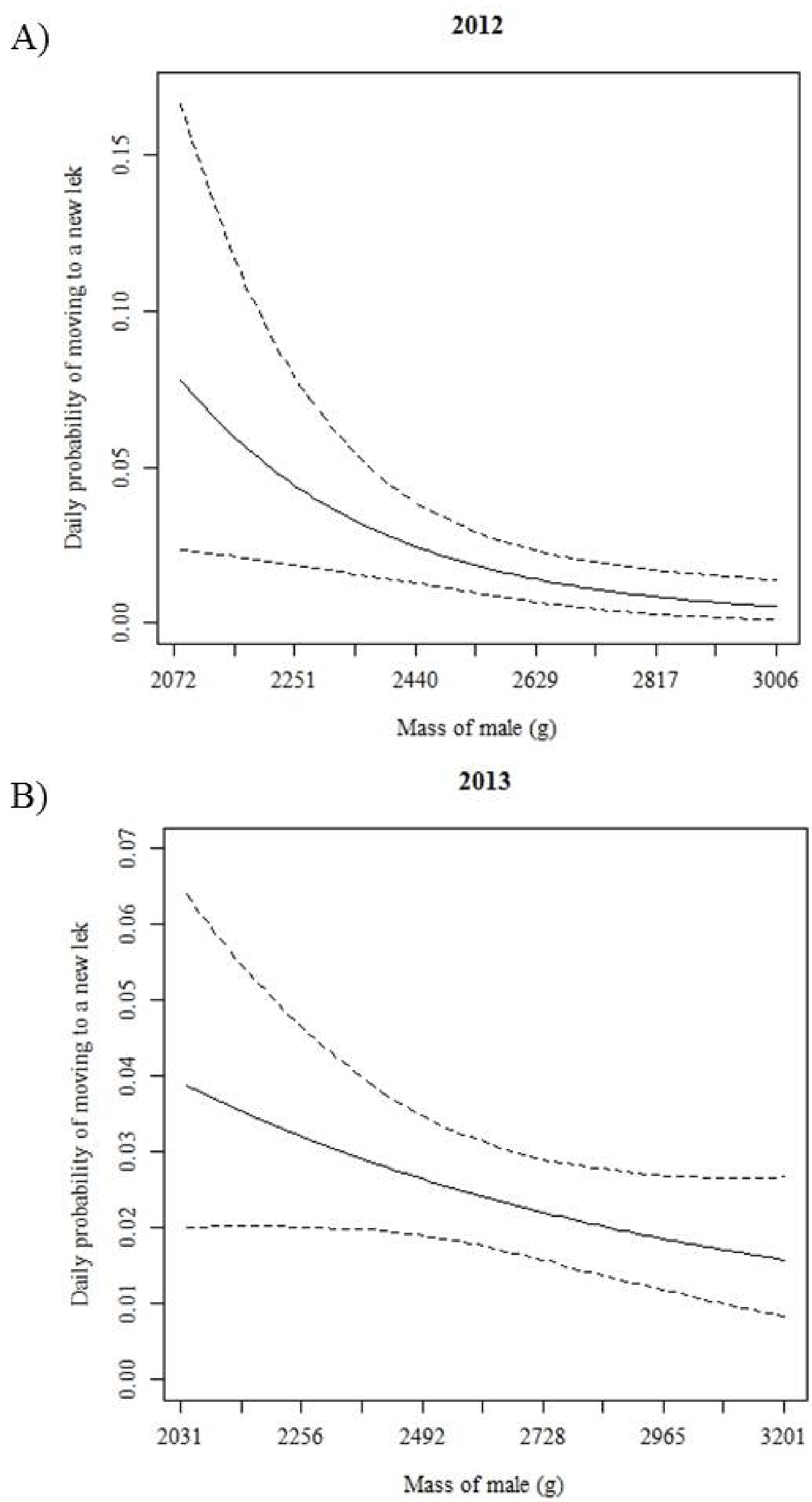

Figure 3. Males with less mass were more likely to move to a new lek in A) 2012 and B) 2013 in Carbon County, Wyoming.

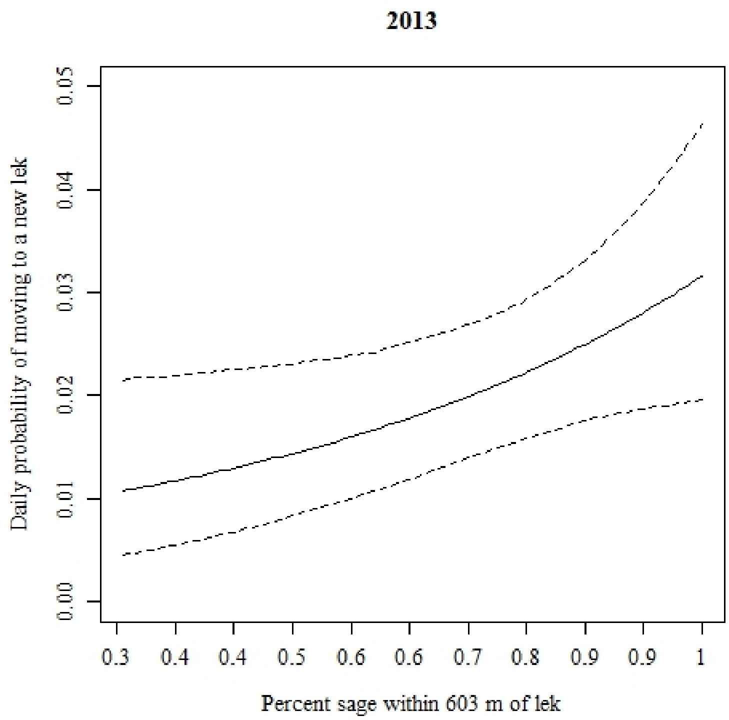

Figure 4. Males were had a higher daily probability of movement towards leks with more surrounding sagebrush than leks with less sagebrush within a 603 m extent in Carbon County, Wyoming 2013.

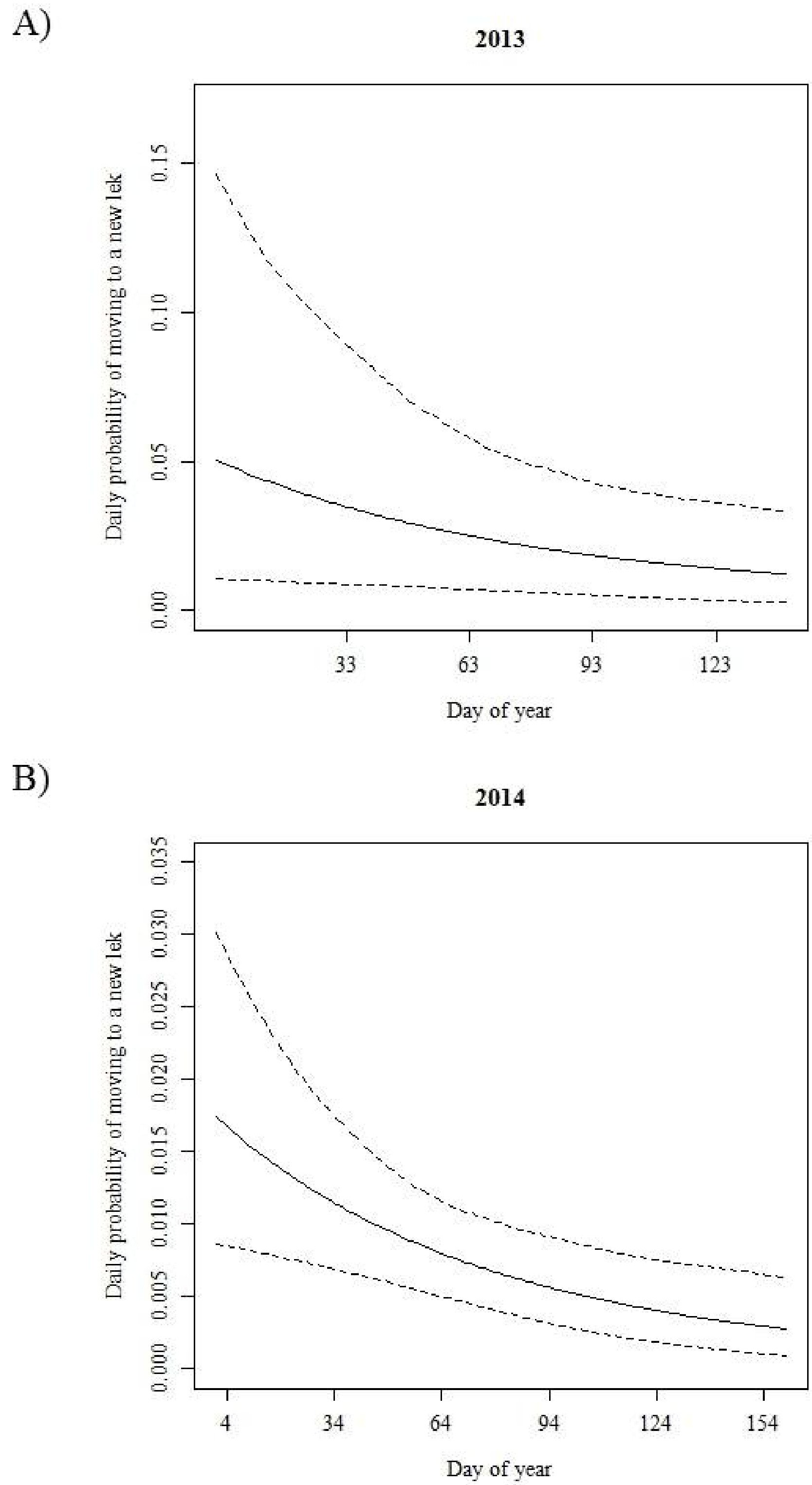

Figure 5. Male greater sage-grouse in Carbon County, Wyoming were more likely to move among leks earlier in the breeding season in both A) 2013 and B) 2014.

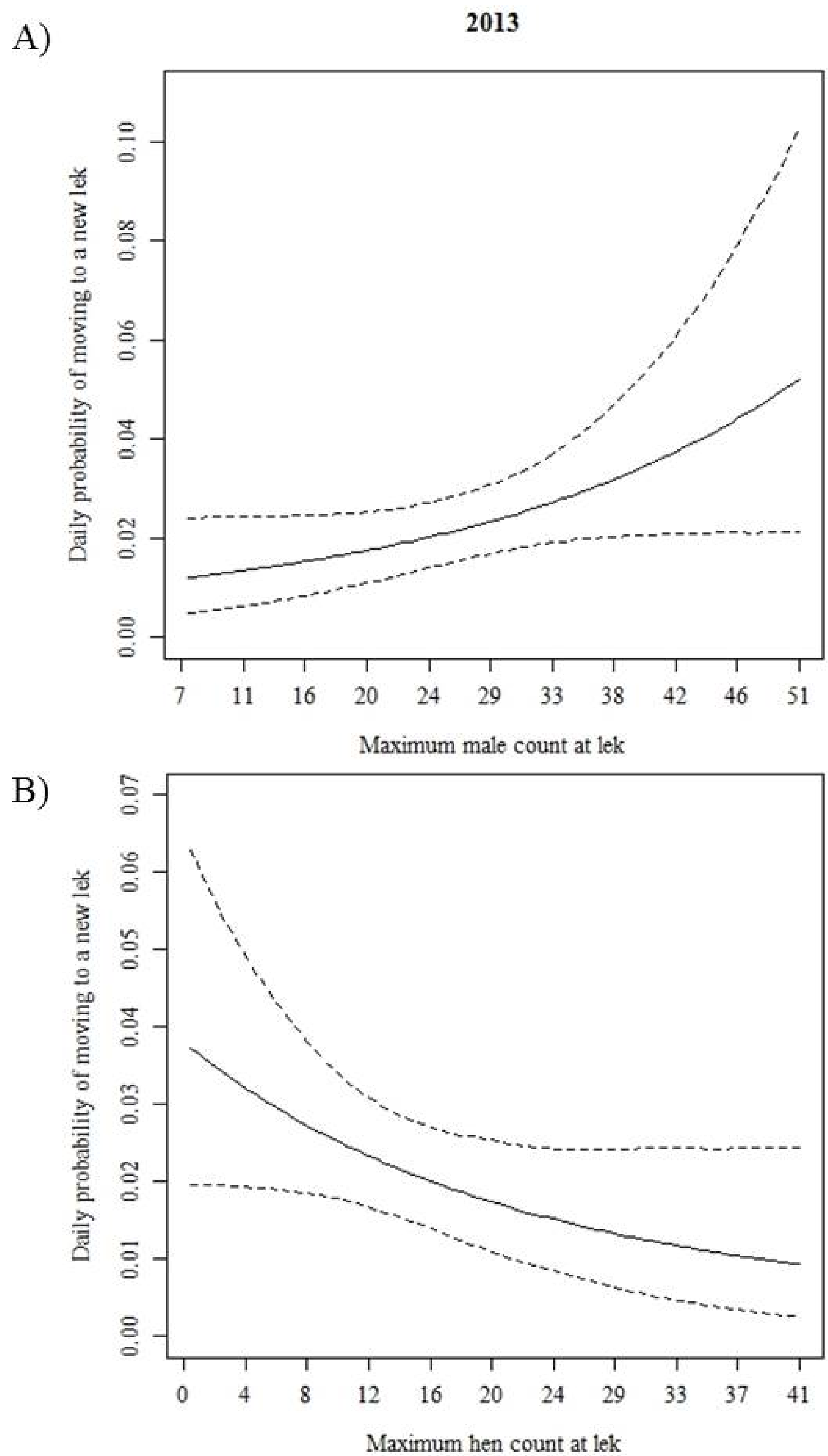

Figure 6. Male greater sage-grouse in Carbon County, Wyoming in 2013 were more likely to move to leks with A) more males and B) fewer hens.

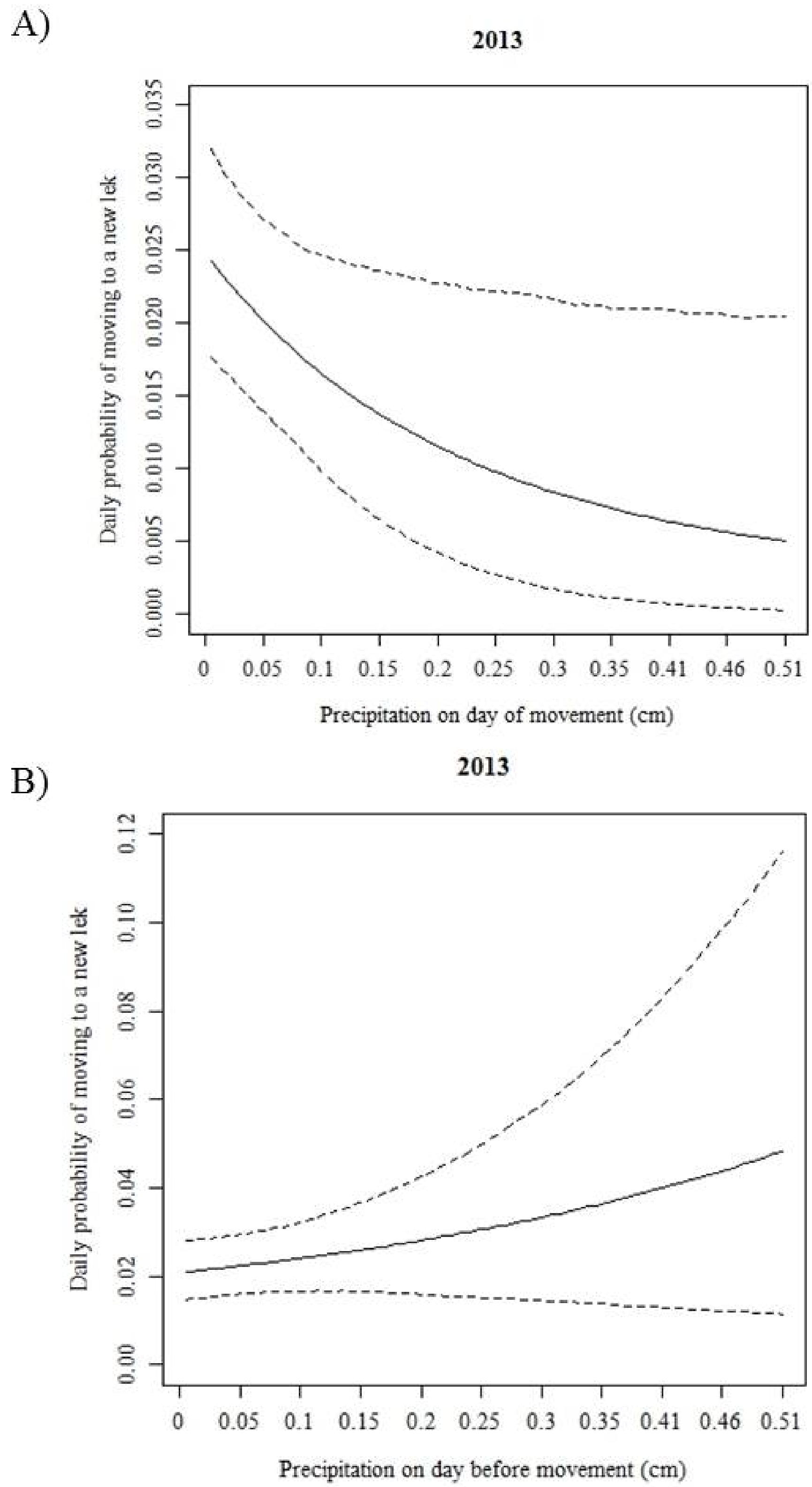

Figure 7. Males in Carbon County, Wyoming 2013 were A) less likely to move on a day with precipitation and B) more likely to move on a day following precipitation.

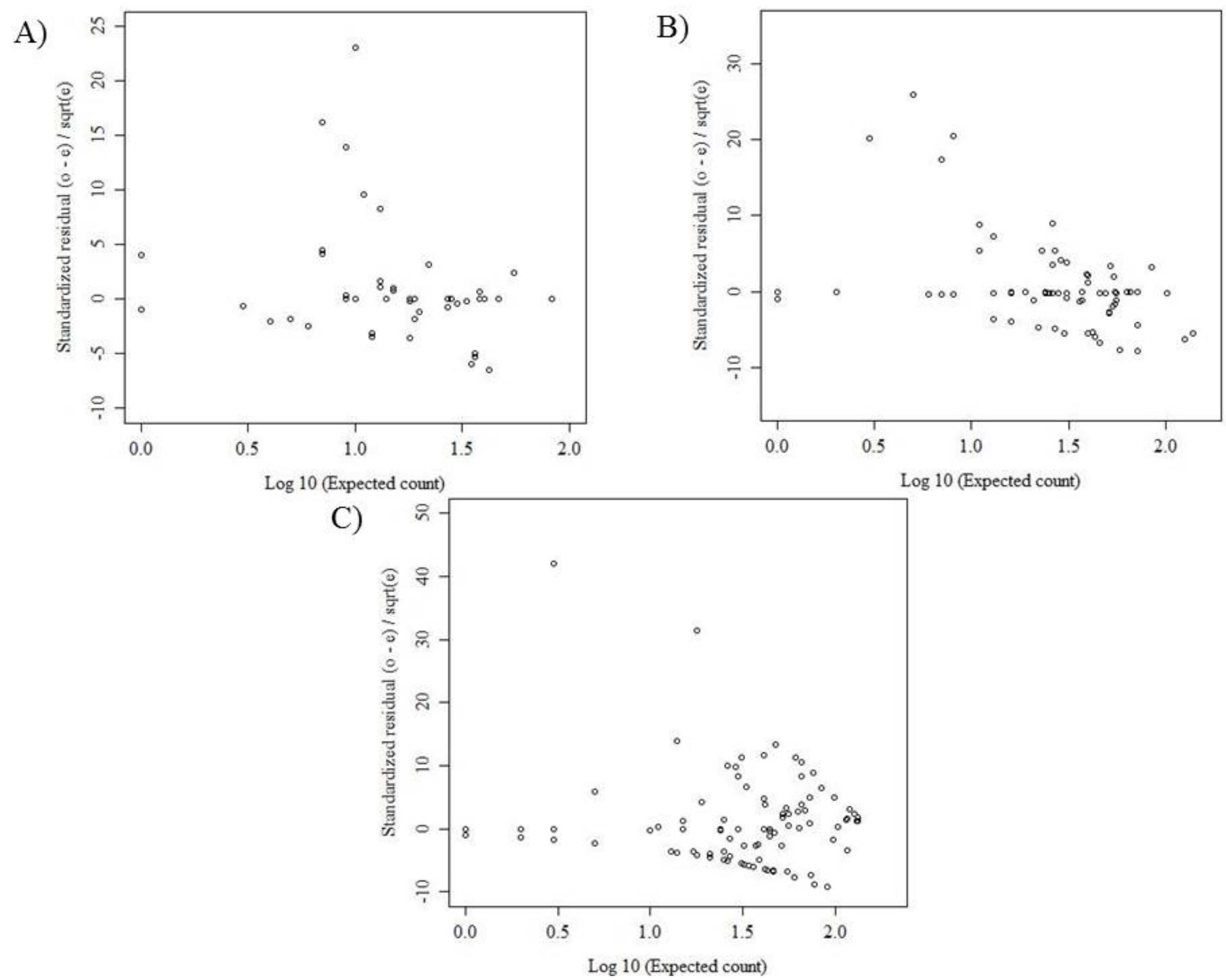

Figure 8. Residual plots for each year for the 3-state analysis of male greater sage-grouse interlek movements in Carbon County, Wyoming, using the top model in 2012 (A), global model in 2013 (B), and top model in 2014 (C).

CHAPTER 3: DETERMINING MALE SAGE-GROUSE DETECTABILITY ON LEKS IN CARBON COUNTY, WYOMING USING SIGHTABILITY SURVEYS

ABSTRACT

All male sage-grouse are not likely detected during lek counts, which could complicate the use of lek counts as a male population index if variation in detection probabilities cannot be accounted for. By assessing factors that influence detection probabilities, managers can revise lek count protocols so lek counts are made when the highest detection probabilities occur, and can correct counts using lek-specific detection probabilities to more accurately estimate the number of birds present on leks. We fit 410 males with GPS and VHF transmitters and uniquely identifiable leg-bands over 4 years in Carbon County, Wyoming. We counted male sage-grouse using accepted lek-count protocols on 21 leks and evaluated variables associated with our ability to detect marked males by observers. We evaluated detection probabilities of male sage-grouse based on factors related to bird characteristics, lek and group size, lek characteristics, light conditions, and observer. We then applied the detection probability to correct lek count data. Detection probabilities were high (0.870 [95% CL: 0.777, 0.928) and varied among leks from 0.771 (95% CL: 0.575, 0.893) to 0.928 (95% CL: 0.734, 0.983). Male sage-grouse detection declined with increasing sage height and bare ground and decreasing snow cover. Detection probability was also lower when the observer could not make observations from a higher elevation than the lek. Sightability models predicted detection well and can be used to accurately estimate population sizes from lek counts, which is especially useful where precise abundance estimates are required. The variation in predicted detection probabilities across leks was relatively small (15.7%) so a single

average correction of 87.0% detection across all leks could be applied to lek counts in our study area.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) were previously widespread in semiarid sagebrush (*Artemisia spp.*) steppe habitats, but they have experienced extensive population declines averaging at least 30% throughout their range since 1985 (Connelly and Braun 1997, Braun 1998, Connelly et al. 2004). As peripheral and small populations are extirpated, the sage-grouse range has constricted to 56% of their pre- European settlement distribution (Schroeder et al. 2004). Sage-grouse are considered “warranted but precluded” from listing as endangered in the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service [USFWS] 2010). Biologists and managers must be able to accurately estimate populations to monitor status and trends of this species that depends on the sagebrush steppe ecosystem.

State and federal management agencies have been counting male sage-grouse on leks since the 1940s to evaluate sage-grouse population status and trends, and these data represent the only long-term data set available for sage-grouse population assessments (Connelly and Schroeder 2007, Johnson and Rowland 2007). Lek locations and the timing of the breeding season are predictable because of high site fidelity to leks by sage-grouse annually (Patterson 1952, Jenni and Hartzler 1978, Connelly et al. 2003) and within a breeding season (Campbell 1972, Dunn and Braun 1985, Schroeder and Braun 1992, Schroeder and Robb 2003, Walsh et al. 2010). Lek counts are also valuable because leks are relatively high concentrations of the population that can be easily and inexpensively surveyed every year in the same location (Patterson 1952, Dalke et al. 1963, Beck and Braun 1980, Walsh et al. 2004, Sedinger 2007).

Although lek counts are commonly used to survey the male population and review trends through time, lek counts may not provide a reliable index to population size because of imperfect detection and variability in detection among leks (Samuel et al. 1987, Anderson 2001). Birds that are not easily observed but are still present on the lek, such as foraging males or yearlings that do not actively display (Garton et al. 2007), may not be counted during a lek survey, which could bias the population estimate if not accounted for. When detection is imperfect, detection probabilities can be used to estimate the number of males missed during a lek survey (White and Shenk 2001, White 2005). So called sightability studies have been extensively applied to ungulates and other large game species (Samuel et al. 1987, Steinhorst and Samuel 1989, Bodie et al. 1995, Udevitz et al. 2006, Vander Wal et al. 2011), but have only recently been proposed for use in upland game birds (Walsh et al. 2004, Clifton and Krementz 2006, Baumgardt 2011, Guttery et al. 2011). However, the observer's ability to detect the male when present on the lek provides an incomplete estimate of population abundance unless availability bias is accounted for to determine whether or not a male is present on the lek to be detected (Alldredge et al. 2007, Schmidt et al. 2013, Chapter 1).

Factors that affect sage-grouse sightability include light conditions (Vander Wal et al. 2011), bird behavior, bird location within the lek and in relation to other birds, observer experience and location in relation to the animal, and vegetative cover (Samuel et al. 1987, Vander Wal et al. 2011, Walsh et al. 2011). The lek's physical size and the group size of displaying birds may impact the observer's ability to effectively search the area, and observers may have difficulty accurately counting birds on leks with high numbers of bird versus those with fewer birds (Samuel et al. 1987, Rice et al. 2009). A bird's movement or posture can increase an observer's ability to notice the animal (Bodie et al. 1995, Garton et al. 2007). Topography and lek characteristics could influence detection by either increasing detection when an observer looks down on a lek located on a slope, or inhibiting detection when an observer looks across a flat landscape. The observer's location in relation to the bird could also influence detection, such as higher detection probabilities for bighorn sheep (*Ovis candensis*) at or above the same altitude as the observer and lower detection for animals below the observer (Bodie et al. 1995). Sightability studies determine the degree to which various factors influence detection, and can be used to estimate a detection probability for each lek based on the characteristics of a lek, conditions of the count, and characteristics of the sage-grouse. Sightability studies can also be used to identify the best conditions to conduct lek surveys so that detection of individuals is maximized and lek counts can be corrected.

We estimated detection probabilities on leks in the pre-construction phase of a wind energy development in Carbon County, Wyoming. We evaluated how vegetation, bird characteristics and activity, lek size, lek characteristics, light conditions, and observer affected detection probabilities. We then applied the estimated detection probabilities to lek count data for a more accurate population estimate.

STUDY AREA

This research was part of a larger, long-term study using a Before-After Control-Impact design to assess the relationship between wind energy development and male sage-grouse ecology. The wind energy development was proposed on The Overland Trail Ranch (OTR), a 320,000 acre (1,295 km^2) checkerboard of private and public land (BLM and Wyoming Game and Fish Department [WGFD]) ownership south of Rawlins, WY. There were 57 leks throughout the study area (Fig. 1). About 20-33 leks were active each year throughout the study period. The OTR lies within a basin with sagebrush steppe foothills to the south and southwest and rocky ridges to the north and northeast, with elevations ranging from 1,890 m above sea level to 2,590 m. The study area is in the intermountain semidesert province (Bailey 1995).

The climate was semiarid, with long, cold winters and short, hot summers (Bailey 1995). Highest temperatures were in July (average maximum 31 °C) and lowest temperatures in December and January (average maximum -1 °C) (Western Regional Climate Center [WRCC] 2008). Typical annual precipitation was 19-26 cm in the basin, with most precipitation falling between April and October (WRCC 2008). Growing seasons were about 120 days, and last from late April to early October (Bailey 1995).

Vegetation predominantly consisted of sagebrush (*Artemisia spp*.) or shadscale (*Atriplex confertifolia*) with short grasses (Bailey 1995). Greasewood (*Sarcobatus vermiculatus*) grew in moist alkaline flats, and willows (*Salix spp*.) and sedges (*Carex spp*.) lined streams and valley bottoms (Bailey 1995). Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*) dominated higher elevations, with silver sagebrush (*A. cana*) in lowlands and black sagebrush (*A. nova*) in rocky, exposed soils (Connelly et al. 2004, Welch 2005).

METHODS

Trapping and marking

We trapped birds and distributed transmitters equally among active leks on and around the OTR. High site fidelity by dominant males captured near leks in spring could bias results towards active, frequently displaying adult males with high detection (Walsh et al. 2004). To avoid bias of dominant males we captured birds in late fall when the rugged terrain was accessible, and in spring to maintain adequate sample sizes.

We captured male sage-grouse using spotlighting and hoop-netting techniques (Giesen et al. 1982, Wakkinen et al. 1992) facilitated by All-Terrain Vehicles (ATV). Two-person groups visited sage-grouse roosting sites at night. Once a bird was located, one person approached on the ATV while shining a light in the bird's eyes. The other person approached behind the ATV on foot, carrying a 75 cm diameter hoop net with 1.75 cm nylon mesh netting, captured the grouse and restrained it to reduce injuries. We weighed captured males and classified them as adults (≥ 2 years old) or yearlings (<1 year old) based upon primary wing feather characteristics (Eng 1955, Crunden 1963). Trapping and handling procedures were approved through the University of Missouri Institutional Animal Care and Use Committee (Protocol #6750).

We began trapping in May 2011 and increased our sample size of marked birds each year. We attempted to mark 20 males in 2011, 20 additional males in 2012, and 10 additional males in 2013 with 30 g solar powered platform transmitter terminal (PTT-100) Global Positioning System (GPS) transmitters (accuracy ± 18 m, Microwave Telemetry, Inc., Columbia, MD). We marked an additional 50 males in 2011 with very high frequency (VHF) transmitters and attempted to maintain a sample size of 70 males

(20 with GPS-PTT transmitters and 50 with VHF transmitters) in 2011, 90 males (20 with GPS-PTT transmitters and 50 with VHF transmitters) in 2012, and 100 males (50 with GPS-PTT transmitters and 50 with VHF transmitters) in 2013 and 2014. All adult and yearling males tagged in spring with VHF transmitters received 30 g transmitters (Model A1150, Advanced Telemetry Systems [ATS], Isanti, MN), whereas juveniles tagged in fall with VHF transmitters received 15 g ATS transmitters (Model A1260, ATS, Isanti, MN) or15 g Telonics (LB-35, Telonics, Mesa, AZ) transmitters. We replaced a portion of VHF transmitters with GPS-PTT transmitters in spring to achieve a balance of adult and juvenile males marked with GPS-PTT transmitters. We attached GPS-PTT and VHF transmitters using the Rappole and Tipton (1991) method. Each bird also received uniquely identifiable size 16 colored leg band combinations to facilitate resighting on leks (Walsh 2002, National Band and Tag Company 2011). Unique leg band combinations were made using 6 possible colors with a minimum of 2 bands on the right leg and a maximum of 2 bands on each leg.

Sightability surveys

We performed sightability surveys of males marked with color-bands and males with transmitters at least twice each year and included leks with a range of displaying males. We did not survey leks visible to major roads to avoid equipment theft. Sightability surveys began 1 April in 2012, 28 March in 2013, and 20 March in 2014 and continued until most leks were inactive or 3 lek counts were completed on each lek (early May in 2012, mid-May in 2013, and late May in 2014). To minimize disturbance on the lek, ground blinds were placed at an observation point 1 week prior to sightability surveys to allow the grouse to habituate to its presence.

One observer (Observer 1) performed a lek count with knowledge of marked bird locations, via telemetry, and a second observer (Observer 2) counted with no prior knowledge of bird locations. Observer 1 was in a blind on the lek perimeter, able to observe marked birds at close proximity and use telemetry to locate unseen marked birds. Observer 1 entered the blind 2 hours before sunrise and counted the birds at 15 minute intervals starting as soon as it was light, approximately 30 minutes before sunrise, until all birds left the lek (usually before 10:00). Counts were used to identify lek high counts for males and females, and determine the amount of time spent surveying the lek. Between counts, Observer 1 used telemetry equipment to scan radio frequencies and detect unseen radio-marked birds on the lek, and once they were visually confirmed the male was present on the lek, Observer 1 would note the marked male's location and covariates. Once a bird was detected by Observer 1, it was not considered again.

Observer 2 followed Wyoming Game and Fish Department (WGFD) protocols for the lek survey, conducting counts simultaneously in time with Observer 1 but independently. Observer 2 counted the lek on foot without a blind, from approximately 100-200 m from the lek to avoid flushing grouse, with >90% of the lek visible. Observer 2 noted the time they spent surveying for marked individuals and the total time they were present at the lek to calculate sampling intensity. Observer 2 recorded male and female counts, as well as color band identities, locations, and covariates for marked birds.

Once the survey was complete, the observers compared data. Grouse that Observer 2 located were considered "detected." Grouse that Observer 1 noted, but Observer 2 failed to detect were considered "undetected." Covariates recorded by

Observer 2 were used when the marked male was detected by Observer 2, and covariates recorded by Observer 1 were used when the marked male was undetected by Observer 2.

Covariates included date, location (UTMs), time the count was conducted, wind speed, and sky condition. Sky condition was recorded as a code: clear/few clouds (0), partly cloudy (1), cloudy or overcast (2), fog or haze (3), drizzle (4), showers (5), flurries (6), or snow showers (7). For each marked bird, observers recorded the bird's activity (sitting, foraging/ standing without strutting, or strutting), time the bird was observed, and group size (number of grouse within 5 m of the marked bird). We determined marked bird locations using a compass and rangefinder (accuracy ± 1 yard from 5 to 750 yards, Leupold RX-750) to determine an azimuth and distance from a known location. After the lek season ended, observers mapped leks using known locations of marked and unmarked birds on the lek boundaries noted during lek counts, as well as sign such as feathers and droppings.

We recorded vegetation measurements after all grouse left the lek. Using the grouse location as the center point, the observers made two 10-m perpendicular bisecting transects (4 5-m transects in each cardinal direction) and recorded visual obstruction, vegetation height, and canopy cover data in Allegro MX data loggers (Juniper Systems Inc. 2010). We measured visual obstruction (VOR) using a modified Robel pole with 1.27 cm increments (Robel et al. 1970, Benkobi et al. 2000) at the plot center and every meter up to 5 m from the plot center with a VOR reading in each cardinal direction (n = 84). We recorded the lowest height at which an increment on the Robel pole was completely obscured. We estimated canopy cover using a 0.1 m^2 Daubenmire frame placed parallel to the transect (Daubenmire 1959). Estimates were taken every meter (0-

5) away from the plot center (*n* = 28). In each frame observers estimated cover classes for sagebrush, other shrubs, grasses and forbs, snow, and bare ground. Cover classes were 1 = 0-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = 96-100%. We also measured natural droop height for sagebrush, other shrubs, and grasses or forbs by selecting the plant in each category closest to the corner of the frame. We averaged Robel pole readings for each grouse location, cover class midpoints across all Daubenmire plots per site, and averaged vegetation heights per location.

In addition, we calculated several additional covariates. We used a seasonal lek attendance rate calculated per male as a covariate by dividing the number of days each bird attended the lek by the number of days the bird was available to attend the lek throughout the season (Walsh et al. 2004). VHF-tagged birds were only available for resight during lek counts. We also used the number of males present on the lek during the count as a covariate. We used a GIS (GIS; Environmental Systems Research Institute, Redlands, California, USA) with a 30 x 30 m land cover layer (Wyoming Geographic Information Science Center [WyGISC] 2004) to calculate the percent of sagebrush within 50 m of the marked male and used a 30 x 30 m digital elevation model (DEM) to determined elevation for the observation point(s) and the marked male, and we subtracted the elevation of the marked male's location from Observer 2's elevation to model the effects of the observer's position in relation to the lek. We calculated total lek area (m^2) using mapped lek perimeters.

Sightability model data analysis

We created *a priori* models (Appendix 1) to test predictions related to observer characteristics, vegetation, lek characteristics and size, light conditions, and bird characteristics. Models were created using biologically reasonable combinations of variables. We tested for correlation among covariates (PROC CORR, SAS Institute, Inc., Cary, NC) and when variables were highly correlated ($r > 0.8$) we kept only the one that was most biologically meaningful. We evaluated whether data could be combined across years by comparing model rank with and without year as a covariate for multiple models; year did not influence detection so we analyzed data pooled across all years.

We modeled sightability using covariates at sites where birds were and were not detected logistic regression (White and Shenk 2001):

$$\hat{y} = \frac{\exp(u)}{1+\exp(u)}$$

where ŷ is the sighting probability and $u = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots \beta_k x_k$ contains the parameter coefficients (β_i) and covariate values (x_i). We used logistic regression in a generalized linear mixed model with observer identity as a random effect in SAS 9.3 (PROC GLIMMIX, SAS Institute).

We used second-order small sample size AIC_C (Burnham and Anderson 2002) to identify the most parsimonious model. Our model selection process involved two stages, including a screening process first to select the structural form of each variable that best represented its effect on detection, and then fitting *a priori* models using the best structural form (Franklin et al. 2000, Washburn et al. 2004). We tested the structural form of each variable using AIC_C to rank linear, quadratic, and pseudothreshold forms with the quadratic term centered on its mean to avoid multicollinearity between the linear and the quadratic terms in the polynomial (Bonnot et al. 2011). For simplicity we selected the linear structural form unless a nonlinear form was > 2 ΔAIC_C units of the linear form for that variable. We tested our *a priori* model set and averaged parameter estimates for all models with an Akaike weight (w_i) more than 1/8 the weight of the top model.

We evaluated goodness of fit using the Pearson Chi-Square statistic divided by degrees of freedom (Pearson χ^2 / DF). We evaluated the predictive ability of the most supported model using k-fold cross validation (Boyce et al. 2002). We divided data into 10 random subsets, each with about 10% of the data. We removed one subset for the testing data, and refit the model using the remaining 9 subsets as training data. We estimated detection probabilities for the testing set based on the model parameter estimates from the corresponding training set, and found the average difference between predicted probability of detection and observed detection. We also evaluated predictive ability using the Spearman-rank correlation coefficient. We divided our detected bird observations into 10 bins based on their predicted probability of detection, and found the Spearman-rank correlation between the predicted probability and the frequency of observed detection in each bin.

We used the averaged model parameter estimates to calculate detection probabilities at each lek using the characteristics of that lek. For leks in the study area that were not used in sightability sampling, we averaged values for each variable across all leks. Once the detection probability ($\hat{y}$) was calculated for each lek, we used it to obtain a more accurate estimate of males present on the lek from count data. The estimated number of males on the lek ($\widehat{N}$) was:

$$\widehat{N} = \sum_{1}^{i} \frac{l_i}{\hat{y}_i}$$

where l_i is the number of birds counted on lek i and $\hat{y}_i$ is the detection probability on lek i. Variance for the population estimate was calculated using bootstrap methods. At each active lek we sampled from the estimated detection probability and used the high count at a single lek to calculate the population estimate for 1,000 iterations. Estimated numbers of males at each lek were summed for the total male population throughout the study area.

RESULTS

We deployed an average of 78 ± 18 (mean ± SE) transmitters each year (31 ± 4 GPS-PTT transmitters and 47 ± 16 VHF transmitters). Lek size and sightability survey effort are summarized in Table 1. Combining 2012 – 2014, we detected 222 marked birds; 44 birds were undetected.

Most marked grouse were detected quickly, and longer searches produced few additional marked males. The majority of males were detected in the first half hour before sunrise through the first hour after sunrise (Fig. 2). We detected 7 marked males later than 1 hour after sunrise.

Initially, the two top models included sampling intensity and time since 30 minutes before sunrise but those variables were not interpretable because they were strongly related to their sample distribution, with most males being detected early in the morning. After removing those two variables, the top model for sightability included sage height and snow cover, but there was model uncertainty so the top 3 models were averaged (Table 2). Variables included in the averaged model were percent bare ground, sage height, snow cover, and elevation difference from observer to grouse (Fig. 3).

Although no variables had a strong influence on detection based on parameter coefficients and their precision, variables included in the averaged model had consistent influences on detection in all models. Detection increased with increasing snow cover, whereas sage height, bare ground, and elevation difference all showed a negative relationship with detection.

The average probability of bird detection across all leks using the averaged model was high (0.870 [95% CL: 0.777, 0.928]) and detection probabilities varied among occupied leks from 0.771 (95% CL: 0.575, 0.893) to 0.928 (95% CL: 0.734, 0.983) (Table 4). The averaged model predicted male sage-grouse detection well. The Pearson χ^2 / DF statistic indicated adequate model fit for the top 3 models, ranging from 0.81 (χ^2_{266} = 216.15) to 0.83 (χ^2_{266} = 220.05). The difference between observed detection and the expected detection was 0.265 ± 0.280 and the Spearman rank correlation coefficient was 0.964 (p = <0.0001).

Detection probabilities and the associated population estimates varied throughout the study area. When accounting for undetected males during lek counts, the population in 2012 increased 16.2% from 481 to 559 ± 0.117 estimated males; the population in 2013 increased 16.6% from 493 to 575 ± 0.088 estimated males; and the population in 2014 increased 15.7% from 717 to 830 ± 0.110 estimated males. Counts were corrected by as much as 13 males on a larger lek (detection rate 79.0%) with relatively tall and dense sagebrush. Although lek high counts and lek detection probabilities varied among leks, the estimated male population size was similar in our study area if a constant average detection probability of 0.870 was applied to all leks rather than incorporating the lek-specific detection probabilities (553 males in 2012, 567 males in 2013, 824 males in 2014).

DISCUSSION

Our models for lekking male sage-grouse in Carbon County, Wyoming indicate that detection probabilities are high and that the most important factors affecting detection are sage height and snow cover. Our hypothesis that vegetation cover may inhibit detection was most strongly supported relative to other hypotheses. Vegetation is consistently shown to be a factor affecting detectability from sighting surveys of wildlife. Previous research on ungulate sightability has indicated that increasing vegetative cover can conceal animals and decrease detection (Samuel et al. 1987, Anderson and Lindzey 1996, Rice et al. 2009, Vander Wal et al. 2011). We observed that less bare ground and shorter sagebrush predicted higher detection probabilities; taller sage obscured the observer's view and decreased detection of individuals. The elevation difference between the observer and the grouse affected detection as well. Males below the observer were sometimes obscured by dips in the landscape such as drainages (Guttery et al. 2011). Higher snow cover also increased sightability of grouse. Most snowfall in our study occurred as several heavy storms, creating a white background on the lek that contrasted the male's dark plumage, making them easily visible. Previous studies with elk support that snow cover increases contrast with dark brown animals and therefore increases their detection (Samuel et al. 1987).

We did not find evidence that sage-grouse activity, a lek's physical characteristics, light conditions, or lek size affected detection. Previous research with ungulates found movement or animal posture, increased an observer's ability to detect the animal (Samuel et al. 1987, Bodie et al. 1995) but lek counters had high resight probabilities with all sage-grouse postures, possibly because a male can be completely obscured by vegetation regardless of his activity. We expected better light conditions, with clear skies and direct sunlight later in the morning, to yield higher detection probabilities (Bodie et al. 1995, Baumgardt 2011, Vander Wal et al. 2011). We may not have observed a great enough range in sky conditions to find an effect, because we did not conduct lek counts during heavy precipitation (Connelly et al. 2003) and few males were present on the lek during precipitation events that limited visibility. We anticipated larger leks would be more difficult to search and would have lower detection probabilities (Baumgardt 2011), but displaying males could be visible at leks with little ground cover regardless of the number of birds present or the lek area. Resight could be higher with sage-grouse than ungulates because male sage-grouse were displaying as opposed to elusive, and sage-grouse leks are typically flat, open landscapes (Patterson 1952) that may have less habitat diversity and landscape type diversity than areas frequented by large game species.

Several other factors could make lek counts unreliable as a population index. Not all leks are known and those that are known may not be a representative sample from all leks (Anderson 2001, Johnson and Rowland 2007). Even if all leks were known, generally not all leks are counted every year because of logistical constraints (Johnson and Rowland 2007), although most state agencies only monitor male population trends using leks that have been surveyed consistently through time (S. Gamo, *personal communication*). Often not all males will be present on the lek during counts because date, time of day, weather, or predators all affect lek attendance (Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh et al. 2004, Johnson and Rowland 2007, Chapter 1), and occasionally birds visit different leks than they are normally present on (Emmons and Braun 1984, Schroeder and Robb 2003, Chapter 2). Finally, despite being present, not all males are accurately counted (Walsh et al. 2004). We attempted to quantify the accuracy of counts, but these other aspects of lek counts should also be assessed for their influence on count accuracy prior to using lek counts as a male population index because there is likely an availability bias in addition to the detection bias (Alldredge et al. 2007, Schmidt et al. 2013). However we also found most marked males were detected during the time frame recommended for sage-grouse lek counts, so protocols may already maximize realistic detection probabilities (Connelly et al. 2003). Only 3% of marked males were observed past1 hour after sunrise, and many of those marked males may have been counted earlier without observers identifying color bands or transmitters.

Because we observed detection probabilities that were specific to individual leks and conditions, we recommend performing sightability surveys in conjunction with lek counts when an accurate male population estimate is critical, especially for small regional populations, or when there is great variation at a site in lek characteristics, or variation in bird numbers on leks. However, detection probabilities were fairly consistent and only varied by about 16%, so lek counts could be corrected by a detection probability of 0.870 when estimating number of males in our study area. We would not recommend using the model to predict detection outside our study area and conditions (White and Shenk 2001). Collecting data in a wider range of conditions might increase model selection certainty and predictive ability.

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Table 1. Lek sizes and sightability survey effort to assess male greater sage-grouse detectability in Carbon County, Wyoming, in 2012 – 2014.

	2012	2013	2014
Start date of sightability surveys	2 April	28 March	20 March
End date of sightability surveys	23 May	23 May	22 May
Number of leks counted	50	53	58
Number of occupied leks	25	29	33
Average number of males on occupied leks	20 ± 3.11	17 ± 2.35	22 ± 3.00
Minimum-maximum number of males on an occupied lek	1-63	1-48	1-86
Lek high counts, total for all leks	481	493	718
Number of sightability surveys completed	50	55	60
Leks with sightability surveys	20	20	22
Number of observations of marked males	33	112	121
Number marked males that were detected by Observer 2	23 (69.70%)	99 (88.39%)	100 (82.64%)
Number of unique marked males observed	28	67	68

Table 2. Evaluation of sightability models, ranked by ΔAIC_C predicting male sage-grouse detectability in Carbon County, Wyoming, 2012 – 2014. All variables took a linear structural form except variables noted with (p), which were best represented as a pseudo-threshold.

Model	-2 LL[a]	K[b]	AIC[c]	AIC_c[d]	ΔAIC_c[e]	w_i[f]
Sage height (p) + snow cover*	221.761	4	229.761	229.915	0.000	0.420
Elevation difference (p)*	226.927	3	232.927	233.019	3.104	0.089
Sage height (p) + bare ground (p)*	225.105	4	233.105	233.259	3.344	0.079
Sage cover + grass/forb cover + other shrub cover	224.219	5	234.219	234.450	4.535	0.043
Slope + elevation	226.456	4	234.456	234.609	4.695	0.040
Sage cover + VOR	226.838	4	234.838	234.992	5.077	0.033
Sage cover	228.979	3	234.979	235.070	5.156	0.032
Sage cover + grass/forb cover	226.950	4	234.950	235.103	5.188	0.031
Sage cover + grass/forb cover + VOR	225.011	5	235.011	235.242	5.327	0.029
Sage height (p)	229.333	3	235.333	235.425	5.510	0.027
Sage cover + grass/forb height (p) + VOR	225.286	5	235.286	235.517	5.602	0.026
Sage height (p) + grass/forb cover	227.525	4	235.525	235.678	5.764	0.024
Activity + attendance (p)	225.869	5	235.869	236.101	6.186	0.019
Sage height (p) + grass/forb height (p)	228.308	4	236.308	236.461	6.546	0.016
Grass/forb cover	230.637	3	236.637	236.728	6.814	0.014
Aspect (p)	230.912	3	236.912	237.004	7.089	0.012
Grass/forb height (p)	231.496	3	237.496	237.587	7.673	0.009
Grass/forb cover + other shrub height	229.905	4	237.905	238.058	8.143	0.007

[a] LL is log likelihood
[b] Number of parameters in model
[c] Akaike Information Criterion (AIC)
[d] AIC with second order bias correction for small sample size
[e] ΔAIC_C= difference (Δ) in AIC_C between the most parsimonious model in the set and the model of interest
[f] w_i= the model probability

Males present at lek	232.590	3	238.590	238.681	8.767	0.005
Group size	232.693	3	238.693	238.785	8.870	0.005
Slope	232.772	3	238.772	238.864	8.949	0.005
Proportion sage in 50 m (p)	232.890	3	238.890	238.981	9.067	0.005
Lek area (p)	232.924	3	238.924	239.016	9.101	0.004
Slope + aspect (p)	230.874	4	238.874	239.027	9.112	0.004
Proportion sage in 50 m (p) + aspect (p)	230.893	4	238.893	239.046	9.132	0.004
Sky conditions	222.560	8	238.560	239.120	9.206	0.004
Activity + age	229.199	5	239.199	239.430	9.515	0.004
Activity	231.940	4	239.940	240.093	10.179	0.003
Males present at lek + group size	232.247	4	240.247	240.400	10.486	0.002
Males present at lek + lek area (p)	232.460	4	240.460	240.614	10.699	0.002
Group size + lek area (p)	232.632	4	240.632	240.786	10.871	0.002
Males present at lek + lek area (p) + group size	232.102	5	242.102	242.332	12.418	0.001
Null	232.981	2	236.981	237.026	49.165	0.000

Table 3. Model-averaged parameter estimates with unconditional standard errors (SE), odds ratio, and confidence intervals (LCL, UCL) for detection probabilities of male greater sage-grouse on leks in Carbon County, Wyoming, 2012 – 2014. All variables took a linear structural form except variables noted with (p), which were best represented as a pseudo-threshold.

Parameter	Estimate	SE	Odds Ratio	LCL	UCL
Bare ground (p)	-0.0202	0.0375	0.9800	-0.0937	0.0533
Elevation difference[a] (p)	-0.2174	0.3967	0.8046	-0.9949	0.5600
Intercept	2.3693	1.6479	10.6902	-0.8606	5.5993
Sage height (p)	-0.1639	0.1145	0.8488	-0.3883	0.0605
Snow cover	0.0146	0.0112	1.0147	-0.0074	0.0366

[a] Elevation difference is observer – grouse

Table 4. Detection probabilities and greater sage-grouse male populations estimated for each active lek in the study area in Carbon County, Wyoming, 2012 – 2014.

Lek name	$\hat{y}^a$	LCL	UCL	2012 Max[b]	2012 $\hat{N}$	2012 SE($\hat{N}$)	2013 Max	2013 $\hat{N}$	2013 SE($\hat{N}$)	2014 Max	2014 $\hat{N}$	2014 SE($\hat{N}$)
1784314	0.870	0.777	0.928	1	1	0.001	6	7	0.005	39	45	0.034
1785042	0.870	0.777	0.928	18	21	0.016	1	1	0.001	17	20	0.015
1785331	0.790	0.604	0.903	50	63	0.100	35	44	0.065	22	28	0.043
1785362	0.872	0.772	0.932	45	52	0.040	34	39	0.031	38	44	0.034
1786163	0.903	0.783	0.961	19	21	0.015	21	23	0.016	33	37	0.026
1786252	0.928	0.734	0.983	63	68	0.041	48	52	0.033	86	93	0.056
1885223	0.870	0.777	0.928	0	0	0.000	3	3	0.003	2	2	0.002
1983074	0.870	0.777	0.928	20	23	0.018	15	17	0.013	21	24	0.019
1983323	0.870	0.777	0.928	0	0	0.000	23	26	0.020	23	26	0.020
1984172	0.903	0.811	0.953	24	27	0.017	10	11	0.007	12	13	0.009
1984312	0.870	0.777	0.928	7	8	0.006	3	3	0.003	13	15	0.011
1984332	0.900	0.769	0.960	21	23	0.018	15	17	0.012	19	21	0.016
1985352	0.870	0.777	0.928	0	0	0.000	0	0	0.000	3	3	0.002
2084341	0.914	0.810	0.964	11	12	0.008	9	10	0.006	14	15	0.009
Ault Ditch	0.851	0.711	0.930	NC	0	0.000	32	38	0.037	43	51	0.048
Chokecherry Bench	0.870	0.777	0.928	0	0	0.000	3	3	0.003	0	0	0.000
Deadman Creek	0.832	0.694	0.916	32	38	0.041	22	26	0.029	28	34	0.038
Gravel Pits	0.870	0.777	0.928	8	9	0.007	0	0	0.000	3	3	0.003

[a] Detection probability ($\hat{y}$), shown with corresponding 95% confidence limits (LCL, UCL)
[b] For each year, the maximum count per lek (Max) is compared to the estimated population ($\hat{N}$) given the maximum count and the detection probability, and the population standard error based on bootstrapping [SE($\hat{N}$)]. NC denotes when a lek was not counted during that year.

Grove Meadow	0.803	0.522	0.938	5	6	0.000	4	5	0.008	10	12	0.020
Hugus Draw	0.825	0.597	0.938	0	0	0.000	18	22	0.030	24	29	0.039
Junction	0.897	0.806	0.948	13	14	0.010	7	8	0.005	5	6	0.004
Little Sage Creek	0.870	0.777	0.928	19	22	0.017	11	13	0.010	16	18	0.014
Little Beaver	0.775	0.604	0.886	14	18	0.027	18	23	0.036	19	25	0.037
Lone Tree Creek	0.853	0.755	0.916	NC	0	0.000	38	45	0.037	44	52	0.042
Low Reservoir	0.870	0.777	0.928	NC	0	0.000	NC	0	0.000	22	25	0.019
McKinney Crossing	0.854	0.757	0.917	8	9	0.008	1	1	0.001	0	0	0.000
Miller Hill	0.862	0.771	0.921	10	12	0.009	26	30	0.023	36	42	0.032
Rawlins Reservoir	0.771	0.575	0.893	7	9	0.016	4	5	0.009	4	5	0.009
Sage Creek Basin	0.833	0.717	0.907	25	30	0.029	29	35	0.032	38	46	0.045
Sage Creek Ranch	0.835	0.732	0.904	32	38	0.035	27	32	0.029	37	44	0.040
Sheep Mountain	0.870	0.777	0.928	0	0	0.000	0	0	0.000	11	13	0.010
South Hugus	0.870	0.777	0.928	0	0	0.000	0	0	0.000	7	8	0.006
Upper Iron Springs	0.865	0.765	0.927	21	24	0.019	18	21	0.016	16	18	0.014
Wild Horse Canyon	0.891	0.718	0.963	8	9	0.007	12	13	0.011	12	13	0.011
Total, all leks	0.870	0.777	0.928	481	559	0.117	493	575	0.088	717	830	0.110

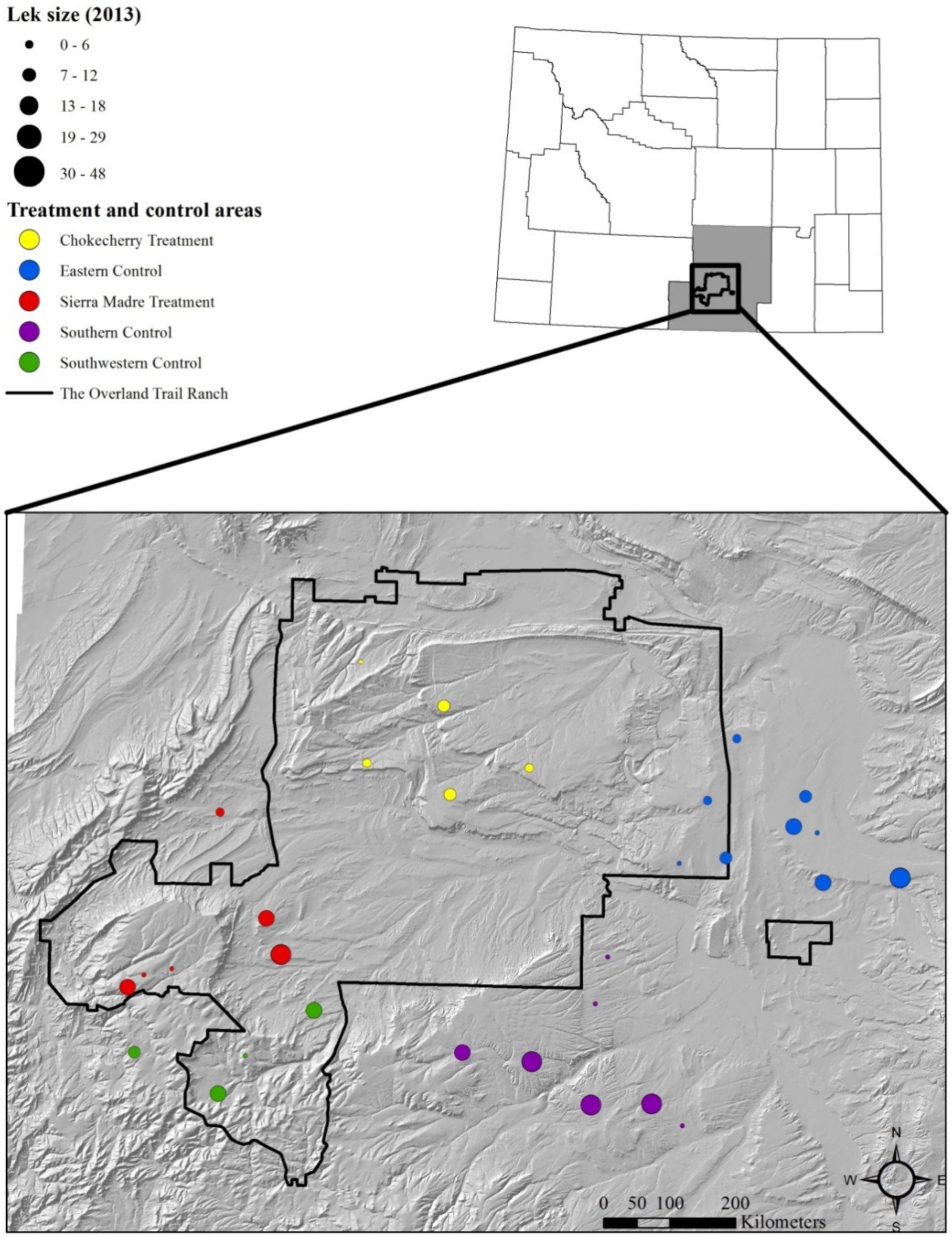

Figure 1. The Overland Trail Ranch in Carbon County, Wyoming, with all active leks in the study area. Treatment areas include the Sierra Madre and Chokecherry areas, and the controls are the southwest, south, and eastern areas. Symbol size represents relative lek size based on 2013 count data.

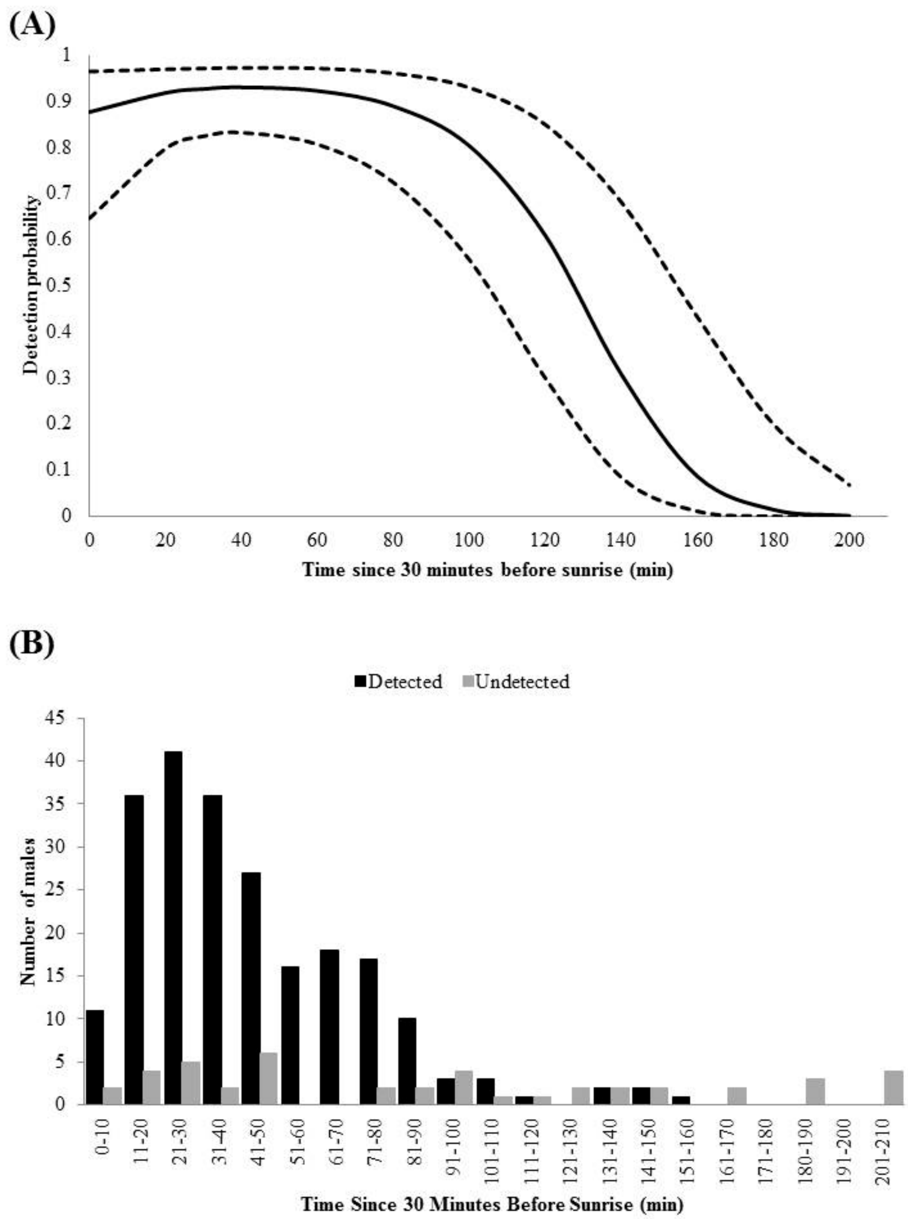

Figure 2. Time since 30 minutes before sunrise during sightability surveys in Carbon County, Wyoming, including (A) the probability of detection predicted from the logistic regression with a random effect for observer identity, modeled across the range of times we observed and (B) counts of males that were detected or undetected through different time intervals. The time since 30 minutes before sunrise for males that were undetected by Observer 2 was calculated as the time spent searching the lek without finding the marked male.

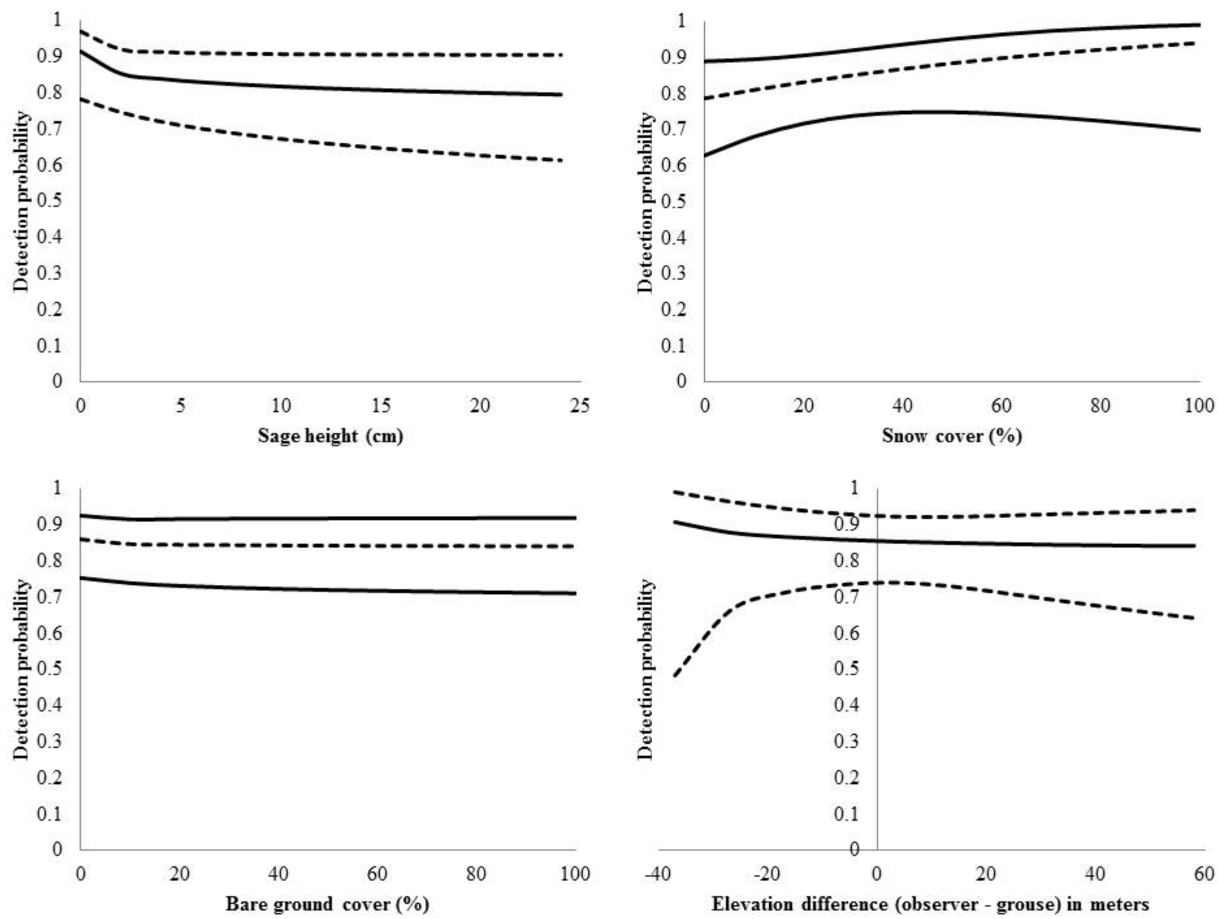

Figure 3. Variables included in the model averaged top model for male greater sage-grouse detectability in Carbon County, Wyoming from 2012 – 2014. Variables are graphed across the range observed throughout the study, and include 95% upper and lower confidence limits as dotted lines.

APPENDIX A

Appendix A. *A priori* models for individual male daily lek attendance. Average precipitation or wind the previous X days was replaced with precipitation the previous 4, 6, 8, 10, or 12 days depending on which time scales were most relevant based on preliminary testing.

Prediction	Model	Written Model	Model Structure	Expected Result(s)
Null	A_0	Null (attendance is random)	β_0	$\beta_0 = 0$
Weather	$A_{W(D)+J}$	Negative effect of wind that day and quadratic effect of ordinal date	$\beta_0 + \beta_1(W_D) + \beta_2(J)^2$	$\beta_1 < 0, \beta_2 > 0, \beta_{(2)}{}^2 < 0$
	$A_{P(D)+J}$	Negative effect of precipitation during that day and quadratic effect of ordinal date	$\beta_0 + \beta_1(P_D) + \beta_2(J)^2$	$\beta_1 < 0, \beta_2 > 0, \beta_{(2)}{}^2 < 0$
	$A_{P(P)+J}$	Quadratic effect of precipitation the previous X days and ordinal date	$\beta_0 + \beta_1(P_P)^2 + \beta_2(J)^2$	$\beta_1 < 0, \beta_{(1)}{}^2 < 0, \beta_2 > 0, \beta_{(2)}{}^2 < 0$
	$A_{P(D)+P(Y)+J}$	Negative effect of precipitation that day and previous day, quadratic effect of ordinal date	$\beta_0 + \beta_1(P_D) + \beta_2(P_Y) + \beta_3(J)^2$	$\beta_1 < 0, \beta_2 < 0, \beta_3 > 0, \beta_{(3)}{}^2 < 0$
	$A_{P(D)+W(Y)+W(P)+J}$	Negative effects of precipitation that day and wind the previous day, quadratic effects of wind the previous X days and ordinal date	$\beta_0 + \beta_1(P_D) + \beta_2(W_Y) + \beta_3(W_P)^2 + \beta_4(J)^2$	$\beta_1 < 0, \beta_2 < 0, \beta_3 > 0, \beta_{(3)}{}^2 < 0, \beta_4 > 0, \beta_{(4)}{}^2 < 0$
	$A_{P(D)+W(D)+J}$	Negative effects of precipitation and wind on that day, quadratic effect of ordinal date	$\beta_0 + \beta_1(P_D) + \beta_2(W_D) + \beta_3(J)^2$	$\beta_1 < 0, \beta_2 < 0, \beta_3 > 0, \beta_{(3)}{}^2 < 0$
	$A_{W(D)+P(P)+W(Y)+J}$	Negative effect of wind that day. Quadratic effects of precipitation the previous X days, wind the previous day, and ordinal date.	$\beta_0 + \beta_1(W_D) + \beta_2(P_P)^2 + \beta_3(W_Y)^2 + \beta_4(J)^2$	$\beta_1 < 0, \beta_2 > 0, \beta_{(2)}{}^2 < 0, \beta_3 > 0, \beta_{(3)}{}^2 < 0, \beta_4 > 0, \beta_{(4)}{}^2 < 0$
	$A_{P(D)+W(D)+P(P)+J}$	Negative effects of precipitation and wind that day, quadratic effects of precipitation the previous X days and ordinal date	$\beta_0 + \beta_1(P_D) + \beta_2(W_D) + \beta_3(P_P)^2 + \beta_4(J)^2$	$\beta_1 < 0, \beta_2 < 0, \beta_3 > 0, \beta_{(3)}{}^2 < 0, \beta_4 > 0, \beta_{(4)}{}^2 < 0$
Time and elevation	A_J	Quadratic effect of ordinal date	$\beta_0 + \beta_1(J)^2$	$\beta_1 > 0, \beta_{(1)}{}^2 < 0$
	A_{J+E}	Quadratic effect of ordinal date and elevation	$\beta_0 + \beta_1(J)^2 + \beta_2(E)^2$	$\beta_1 > 0, \beta_{(1)}{}^2 < 0, \beta_2 > 0, \beta_{(2)}{}^2 < 0$

Bird characteristics	$A_{O + J}$	Positive effect of bird age, quadratic effect of ordinal date	$\beta_0 + \beta_1(O_{juvenile}) + \beta_2(O_{adult}) + \beta_3(J)^2$	$\beta_1 < \beta_2$, $\beta_3 > 0$, $\beta_{(3)}^2 < 0$
	$A_{O + M + J}$	Positive effect of bird age and bird mass, quadratic effect of ordinal date	$\beta_0 + \beta_1(O_{juvenile}) + \beta_2(O_{adult}) + \beta_3(M) + \beta_4(J)^2$	$\beta_1 < \beta_2$, $\beta_3 < 0$, $\beta_4 > 0$, $\beta_{(4)}^2 < 0$
Full model for individual attendance	$A_{P(D) + W(D) + O + W(P) + P(P) + P(Y) + W(Y) + M + E + J + TIME}$	Negative effects of precipitation and wind that day and bird age. Quadratic effects of wind and precipitation the previous X days, and precipitation the previous day. Pseudo-threshold effect of wind yesterday. Positive effect of bird mass. Quadratic effects of elevation, ordinal date, and time.	$\beta_0 + \beta_1(P_D) + \beta_2(W_D) + \beta_3(O_{juvenile}) + \beta_4(O_{adult}) + \beta_5(W_P)^2 + \beta_6(P_P)^2 + \beta_7(P_Y)^2 + \beta_8(\ln(W_Y)) + \beta_9(M) + \beta_{10}(E)^2 + \beta_{11}(J)^2 + \beta_{12}(TIME)^2$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 < \beta_4$, $\beta_5 > 0$, $\beta_{(5)}^2 < 0$, $\beta_6 > 0$, $\beta_{(6)}^2 < 0$, $\beta_7 > 0$, $\beta_{(7)}^2 < 0$, $\beta_8 < 0$, $\beta_9 > 0$, $\beta_{10} > 0$, $\beta_{(10)}^2 < 0$, $\beta_{11} > 0$, $\beta_{(11)}^2 < 0$, $\beta_{12} < 0$, $\beta_{(12)}^2 > 0$

APPENDIX B

Appendix B. *A priori* models for lek attendance per lek. Average precipitation or wind the previous X days was replaced with precipitation the previous 4, 6, 8, 10, or 12 days depending on which time scales were most relevant based on preliminary testing.

Prediction	**Model**	**Written Model**	**Model Structure**	**Expected Result(s)**
Null	A_0	Null (attendance is random)	β_0	$\beta_0 = 0$
Weather	$A_{W(D) + J}$	Negative effect of wind that day and quadratic effect of ordinal date	$\beta_0 + \beta_1(W_D) + \beta_2(J)^2$	$\beta_1 < 0$, $\beta_2 > 0$, $\beta_{(2)}{}^2 < 0$
	$A_{P(D) + J}$	Negative effect of precipitation during that day and quadratic effect of ordinal date	$\beta_0 + \beta_1(P_D) + \beta_2(J)^2$	$\beta_1 < 0$, $\beta_2 > 0$, $\beta_{(2)}{}^2 < 0$
	$A_{P(P) + J}$	Quadratic effect of precipitation the previous X days and ordinal date	$\beta_0 + \beta_1(P_P)^2 + \beta_2(J)^2$	$\beta_1 < 0$, $\beta_{(1)}{}^2 < 0$, $\beta_2 > 0$, $\beta_{(2)}{}^2 < 0$
	$A_{P(D) + P(Y) + J}$	Negative effect of precipitation that day and previous day, quadratic effect of ordinal date	$\beta_0 + \beta_1(P_D) + \beta_2(P_Y) + \beta_3(J)^2$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 > 0$, $\beta_{(3)}{}^2 < 0$
	$A_{P(D) + W(Y) + W(P) + J}$	Negative effects of precipitation that day and wind the previous day, quadratic effects of wind the previous X days and ordinal date	$\beta_0 + \beta_1(P_D) + \beta_2(W_Y) + \beta_3(W_P)^2 + \beta_4(J)^2$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 > 0$, $\beta_{(3)}{}^2 < 0$, $\beta_4 > 0$, $\beta_{(4)}{}^2 < 0$
	$A_{P(D) + W(D) + J}$	Negative effects of precipitation and wind on that day, quadratic effect of ordinal date	$\beta_0 + \beta_1(P_D) + \beta_2(W_D) + \beta_3(J)^2$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 > 0$, $\beta_{(3)}{}^2 < 0$
	$A_{W(D) + P(P) + W(Y) + J}$	Negative effect of wind that day. Quadratic effects of precipitation the previous X days, wind the previous day, and ordinal date	$\beta_0 + \beta_1(W_D) + \beta_2(P_P)^2 + \beta_3(W_Y)^2 + \beta_4(J)^2$	$\beta_1 < 0$, $\beta_2 > 0$, $\beta_{(2)}{}^2 < 0$, $\beta_3 > 0$, $\beta_{(3)}{}^2 < 0$, $\beta_4 > 0$, $\beta_{(4)}{}^2 < 0$
	$A_{P(D) + W(D) + P(P) + J}$	Negative effects of precipitation and wind that day, quadratic effects of precipitation the previous X days and ordinal date	$\beta_0 + \beta_1(P_D) + \beta_2(W_D) + \beta_3(P_P)^2 + \beta_4(J)^2$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 > 0$, $\beta_{(3)}{}^2 < 0$, $\beta_4 > 0$, $\beta_{(4)}{}^2 < 0$
Time	A_J	Quadratic effect of ordinal date	$\beta_0 + \beta_1(J)^2$	$\beta_1 > 0$, $\beta_{(1)}{}^2 < 0$
Lek characteristics	$A_{J + E}$	Quadratic effect of ordinal date and elevation	$\beta_0 + \beta_1(J)^2 + \beta_2(E)^2$	$\beta_1 > 0$, $\beta_{(1)}{}^2 < 0$, $\beta_2 > 0$, $\beta_{(2)}{}^2 < 0$
	$A_{J + S + PS}$	Positive effect of slope and percent sage cover within 603 m of lek. Quadratic effect of ordinal date	$\beta_0 + \beta_1(J)^2 + \beta_2(S) + \beta_3(PS)$	$\beta_1 > 0$, $\beta_{(1)}{}^2 < 0$, $\beta_2 > 0$, $\beta_3 > 0$

	$A_{J + A + PS}$	Quadratic effect of aspect and ordinal date, and positive effects of percent sage within 603 m of lek	$\beta_0 + \beta_1(J)^2 + \beta_2(A)^2 + \beta_3(PS)$	$\beta_1 > 0$, $\beta_{(1)}^2 < 0$, $\beta_2 > 0$, $\beta_{(2)}^2 < 0$, $\beta_3 > 0$
	$A_{J + PS}$	Quadratic effect of ordinal date, positive effect of percent sage within 603 m of the lek	$\beta_0 + \beta_1(J)^2 + \beta_2(PS)$	$\beta_1 > 0$, $\beta_{(1)}^2 < 0$, $\beta_2 > 0$
	$A_{J + A + S + PS}$	Quadratic effects of date and aspect, positive effect of slope and percent sage within 603 m of lek	$\beta_0 + \beta_1(J)^2 + \beta_2(A)^2 + \beta_3(S) + \beta_4(PS)$	$\beta_1 > 0$, $\beta_{(1)}^2 < 0$, $\beta_2 > 0$, $\beta_{(2)}^2 < 0$, $\beta_3 > 0$, $\beta_4 > 0$
	$A_{J + LA + PS}$	Quadratic effect of ordinal date, positive effect of lek area and percent sage within 603 m of the lek	$\beta_0 + \beta_1(J)^2 + \beta_2(LA) + \beta_3(PS)$	$\beta_1 > 0$, $\beta_{(1)}^2 < 0$, $\beta_2 > 0$, $\beta_3 > 0$
	$A_{J + LA}$	Quadratic effect of ordinal date, positive effect of lek area	$\beta_0 + \beta_1(J)^2 + \beta_2(LA)$	$\beta_1 > 0$, $\beta_{(1)}^2 < 0$, $\beta_2 > 0$

APPENDIX C

Appendix C. *A priori* models for male sage-grouse movements among leks in Carbon County, Wyoming 2011-2014.

Prediction	Model	Written Model	Model Structure	Expected Result(s)
Null	ψ_0	Null (interlek movement is random)	β_0	$\beta_0 = 0$
Anthropogenic disturbances	ψ_B	Positive effect of ground blind at lek	$\beta_0 + \beta_1(Blinds)$	$\beta_1 > 0$
	ψ_C	Positive effect of counting a lek	$\beta_0 + \beta_1(Counts)$	$\beta_1 > 0$
	ψ_T	Positive effect of trapping at a lek	$\beta_0 + \beta_1(Trapping)$	$\beta_1 > 0$
Bird characteristics	ψ_O	Negative effect of bird age	$\beta_0 + \beta_1(O_{juvenile}) + \beta_2(O_{adult})$	$\beta_1 > \beta_2$
	ψ_A	Positive effect of lek attendance rates	$\beta_0 + \beta_1(A)$	$\beta_1 > 0$
	ψ_{M+O}	Positive effect of bird weight, negative effect of bird age	$\beta_0 + \beta_1(M) + \beta_2(O_{juvenile}) + \beta_3(O_{adult})$	$\beta_1 > 0$, $\beta_2 > \beta_3$
	ψ_{A+O}	Negative effects of individual lek attendance rates and bird age	$\beta_0 + \beta_1(A) + \beta_2(O_{juvenile}) + \beta_3(O_{adult})$	$\beta_1 < 0$, $\beta_2 > \beta_3$
	ψ_{A+O+M}	Negative effects of individual lek attendance rates and bird age, positive effect of bird weight	$\beta_0 + \beta_1(A) + \beta_2(O_{juvenile}) + \beta_3(O_{adult}) + \beta_4(M)$	$\beta_1 < 0$, $\beta_2 > \beta_3$, $\beta_4 > 0$
Lek characteristics (physical attributes)	ψ_{ASP}	Quadratic effect of aspect	$\beta_0 + \beta_1(ASP)^2$	$\beta_1 > 0$, $\beta_{(1)}{}^2 < 0$
	ψ_{VC}	Positive effect of percent sage within 603 m of lek	$\beta_0 + \beta_1(VC)$	$\beta_1 > 0$
	ψ_{VC+SLO}	Positive effect of percent sage within 603 m of lek and negative effect of slope	$\beta_0 + \beta_1(VC) + \beta_2(SLO)$	$\beta_1 > 0$, $\beta_2 < 0$
	$\psi_{ASP+SLO}$	Quadratic effect of aspect, negative effect of slope	$\beta_0 + \beta_1(ASP)^2 + \beta_2(SLO)$	$\beta_1 > 0$, $\beta_{(1)}{}^2 < 0$, $\beta_2 < 0$
	$\psi_{ASP+SLO+VC}$	Quadratic effect of aspect, negative effect of slope and positive effect of percent sage within 603 m of lek	$\beta_0 + \beta_1(ASP)^2 + \beta_2(SLO) + \beta_3(VC)$	$\beta_1 > 0$, $\beta_{(1)}{}^2 < 0$, $\beta_2 < 0$, $\beta_3 > 0$
(lek formation hypotheses)	ψ_C	Positive effects of maximum male count at the lek that year	$\beta_0 + \beta_1(C)$	$\beta_1 > 0$
	ψ_F	Positive effects of maximum female count at the lek that year	$\beta_0 + \beta_1(F)$	$\beta_1 > 0$

Environmental characteristics	ψ_{J}	Quadratic effect of ordinal date	$\beta_0 + \beta_1(J)^2$	$\beta_1 < 0, \beta_{(1)}^2 < 0$
	$\psi_{J + E}$	Quadratic effect of ordinal date and elevation	$\beta_0 + \beta_1(J)^2 + \beta_2(E)$	$\beta_1 < 0, \beta_{(10)}^2 < 0, \beta_2 < 0$
	ψ_{PPT}	Negative effect of precipitation on that day	$\beta_0 + \beta_1(PPT)$	$\beta_1 < 0$
	ψ_{PPTP}	Negative effect of precipitation the previous day	$\beta_0 + \beta_1(PPTP)$	$\beta_1 < 0$
	ψ_{WIND}	Negative effect of wind on that day	$\beta_0 + \beta_1(WIND)$	$\beta_1 < 0$
	ψ_{WINDP}	Negative effect of wind the previous day	$\beta_0 + \beta_1(WINDP)$	$\beta_1 < 0$
Global model	$\psi_{O + A + SLO + E + PPT + PPTP + WIND + WINDP\ B + C + T + F + M + VC + J + ASP}$	Negative effects of bird age, average lek attendance, slope, elevation, precipitation on that day, precipitation the previous day, wind on that day, and wind the previous day. Positive effects of blinds at lek, counting a lek, or trapping at a lek, maximum female count, maximum male count, bird weight, and percent sage within 603 m of the lek. Quadratic effect of ordinal date and aspect.	$\beta_0 + \beta_1(O_{juvenile}) + \beta_2(O_{adult}) + \beta_3(SLO) + \beta_4(E) + \beta_5(PPT) + \beta_6(PPTP) + \beta_7(WIND) + \beta_8(WINDP) + \beta_9(B) + \beta_{10}(C) + \beta_{11}(T) + \beta_{12}(F) + + \beta_{13}(M) + \beta_{14}(VC) + \beta_{15}(J)^2 + \beta_{16}(ASP)^2$	$\beta_1 > \beta_2, \beta_3 < 0, \beta_4 < 0, \beta_5 < 0, \beta_6 < 0, \beta_7 < 0, \beta_8 < 0, \beta_9 > 0, \beta_{10} > 0, \beta_{11} > 0, \beta_{12} > 0, \beta_{13} > 0, \beta_{14} > 0, \beta_{15} > 0, \beta_{(15)}^2 < 0, \beta_{16} > 0, \beta_{(16)}^2 < 0$

APPENDIX D

Appendix D. A priori models representing predictions about male greater sage-grouse detectability in Carbon County, Wyoming, 2012 – 2014.

Prediction	**Model**	**Written Model**	**Model Structure**	**Expected Result(s)**
Null	$\hat{y}_0$	Null (sightability is random)	β_0	$\beta_0 = 0$
Vegetation	$\hat{y}_{SAGECC}$	Negative effect of sage canopy cover	$\beta_0 + \beta_1(SAGE\_CC)$	$\beta_1 < 0$
	$\hat{y}_{GRFBCC}$	Negative effect of herbaceous (grass and forb) cover	$\beta_0 + \beta_1(GRFB\_CC)$	$\beta_1 < 0$
	$\hat{y}_{SAGEHT}$	Negative effect of sage height	$\beta_0 + \beta_1(SAGE\_HT)$	$\beta_1 < 0$
	$\hat{y}_{GRFBHT}$	Negative effect of herbaceous height	$\beta_0 + \beta_1(GRFB\_HT)$	$\beta_1 < 0$
	$\hat{y}_{SAGECC + GRFBCC}$	Negative effects of sage canopy cover and herbaceous canopy cover	$\beta_0 + \beta_1(SAGE\_CC) + \beta_2(GRFB\_CC)$	$\beta_1 < 0, \beta_2 < 0$
	$\hat{y}_{SAGECC + VOR}$	Negative effects of sage canopy cover and visual obstruction	$\beta_0 + \beta_1(SAGE\_CC) + \beta_2(VOR)$	$\beta_1 < 0, \beta_2 < 0$
	$\hat{y}_{GRFBCC + SAGEHT}$	Negative effects of herbaceous canopy cover and sage height	$\beta_0 + \beta_1(\mathit{GRFB\_CC}) + \beta_2(SAGE\_HT)$	$\beta_1 < 0, \beta_2 < 0$
	$\hat{y}_{SAGEHT + GRFBHT}$	Negative effects of sage height and herbaceous height	$\beta_0 + \beta_1(SAGE\_HT) + \beta_2(GRFB\_HT)$	$\beta_1 < 0, \beta_2 < 0$
	$\hat{y}_{GRFBCC + OSHRUHT}$	Negative effects of herbaceous canopy cover and other shrub height	$\beta_0 + \beta_1(GRFB\_CC) + \beta_2(OSHRU\_HT)$	$\beta_1 < 0, \beta_2 < 0$
	$\hat{y}_{SAGEHT + SNOW}$	Negative effects of sage height, positive effect of snow cover	$\beta_0 + \beta_1(SAGE\_HT) + \beta_2(SNOW)$	$\beta_1 < 0, \beta_2 > 0$
	$\hat{y}_{SAGEHT + BARE}$	Negative effects of sage height, positive effect of bare ground	$\beta_0 + \beta_1(SAGE\_HT) + \beta_2(BARE)$	$\beta_1 < 0, \beta_2 > 0$
	$\hat{y}_{SAGECC + GRFBCC + OSHRUCC}$	Negative effects of sage canopy cover, herbaceous canopy cover, and other shrub canopy cover	$\beta_0 + \beta_1(SAGE\_CC) + \beta_2(GRFB\_CC) + \beta_3(OSHRU\_CC)$	$\beta_1 < 0, \beta_2 < 0, \beta_3 < 0$

	$\hat{y}_{SAGECC + GRFBCC + VOR}$	Negative effects of sage canopy cover, herbaceous canopy cover, and visual obstruction	$\beta_0 + \beta_1(SAGE\_CC) + \beta_2(GRFB\_CC) + \beta_3(VOR)$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 < 0$
	$\hat{y}_{SAGECC + GRFBHT + VOR}$	Negative effects of sage canopy cover, herbaceous height, and visual obstruction	$\beta_0 + \beta_1(SAGE\_CC) + \beta_2(GRFB\_HT) + \beta_3(VOR)$	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 < 0$
Lek characteristics	$\hat{y}_{MALE\_PL}$	Negative effect of lek count of birds present on the lek when the male was identified	$\beta_0 + \beta_1(MALE\_PL)$	$\beta_1 < 0$, $\beta_{(1)}^2 > 0$
	$\hat{y}_{LEK\_AREA}$	Negative effect of lek area	$\beta_0 + \beta_1(LEK\_AREA)$	$\beta_1 < 0$
	$\hat{y}_{GROUP}$	Positive effect of group size (birds within 5 m)	$\beta_0 + \beta_1(GROUP)$	$\beta_1 > 0$
	$\hat{y}_{MALE\_PL + LEK\_AREA}$	Negative effects of lek count when male was identified, and lek area	$\beta_0 + \beta_1(MALE\_PL) + \beta_3(LEK\_AREA)$	$\beta_1 < 0$, $\beta_{(1)}^2 > 0$, $\beta_2 < 0$
	$\hat{y}_{GROUP + LEK\_AREA}$	Positive effect of group size, negative effect of lek area	$\beta_0 + \beta_1(GROUP) + \beta_2(LEK\_AREA)$	$\beta_1 > 0$, $\beta_2 < 0$
	$\hat{y}_{MALE\_PL + GROUP}$	Negative effect of lek count when male was identified, positive effect of group size	$\beta_0 + \beta_1(MALE\_PL) + \beta_2(GROUP)$	$\beta_1 < 0$, $\beta_{(1)}^2 > 0$, $\beta_2 > 0$
	$\hat{y}_{MALE\_PL + LEK\_AREA + GROUP}$	Negative effect of lek count when male was identified and lek area, positive effect of group size	$\beta_0 + \beta_1(MALE\_PL) + \beta_3(LEK\_AREA) + \beta_4(GROUP)$	$\beta_1 < 0$, $\beta_{(1)}^2 > 0$, $\beta_2 < 0$, $\beta_3 > 0$
Bird characteristics and activity	$\hat{y}_{ACTIVITY}$	Positive effect of grouse activity	$\beta_0 + \beta_1(ACTIVITY_{SIT}) + \beta_2(ACTVITY_{FORAGE}) + \beta_3(ACTIVITY_{STRUT})$	$\beta_1 < \beta_2 < \beta_3$
	$\hat{y}_{ACTIVITY + ATTEND}$	Positive effects of activity and individual male attendance	$\beta_0 + \beta_1(ACTIVITY_{SIT}) + \beta_2(ACTVITY_{FORAGE}) + \beta_3(ACTIVITY_{STRUT}) + \beta_4(ATTEND)$	$\beta_1 < \beta_2 < \beta_3$, $\beta_4 > 0$

	$\hat{y}_{ACTIVITY + AGE}$	Positive effects of activity and age	$\beta_0 + \beta_1(\mathrm{ACTIVITY}_{\mathrm{SIT}}) + \beta_2(\mathrm{ACTVITY}_{\mathrm{FORAGE}}) + \beta_3(\mathrm{ACTIVITY}_{\mathrm{STRUT}}) + \beta_4(\mathrm{AGE}_{\mathrm{YEARLING}}) + \beta_5(\mathrm{AGE}_{\mathrm{ADULT}})$	$\beta_1 < \beta_2 < \beta_3$, $\beta_4 < \beta_5$
Environmental characteristics	$\hat{y}_{SLOPE}$	Positive effect of slope	$\beta_0 + \beta_1(\mathrm{SLOPE})$	$\beta_1 > 0$
	$\hat{y}_{ASPECT}$	Quadratic effect of aspect	$\beta_0 + \beta_1(\mathrm{ASPECT})^2$	$\beta_1 > 0$, $\beta_{(1)}{}^2 < 0$
	$\hat{y}_{PSAGE}$	Negative effect of percent sage within 50 m of the marked male	$\beta_0 + \beta_1(\mathrm{PSAGE})$	$\beta_1 < 0$
	$\hat{y}_{SLOPE + ASPECT}$	Positive effect of slope, quadratic effect of aspect	$\beta_0 + \beta_1(\mathrm{SLOPE}) + \beta_2(\mathrm{ASPECT})^2$	$\beta_1 > 0$, $\beta_2 > 0$, $\beta_{(2)}{}^2 < 0$
	$\hat{y}_{SLOPE + ELEV}$	Positive effect of slope, quadratic effect of elevation	$\beta_0 + \beta_1(\mathrm{SLOPE}) + \beta_2(\mathrm{ELEV})^2$	$\beta_1 > 0$, $\beta_2 > 0$, $\beta_{(2)}{}^2 < 0$
	$\hat{y}_{ASPECT + PSAGE}$	Quadratic effect of aspect, negative effect of vegetation classification	$\beta_0 + \beta_1(\mathrm{ASPECT})^2 + \beta_2(\mathrm{PSAGE})$	$\beta_1 > 0$, $\beta_{(1)}{}^2 < 0$, $\beta_2 < 0$
Light conditions	$\hat{y}_{SKY}$	Negative effect of sky conditions	$\beta_0 + \beta_1(\mathrm{SKY}_{\mathrm{CLEAR}}) + \beta_2(\mathrm{SKY}_{\mathrm{CLOUDY}}) + \beta_3(\mathrm{SKY}_{\mathrm{PPT}})$	$\beta_1 > \beta_2 > \beta_3$
	$\hat{y}_{TIME30BS}$	Positive effect of time after sunrise (standardized to 30 minutes before sunrise)	$\beta_0 + \beta_1(\mathrm{TIME30BS})$	$\beta_1 > 0$
	$\hat{y}_{SKY + TIME30BS}$	Negative effect of sky conditions and positive effect of time after sunrise	$\beta_0 + \beta_1(\mathrm{SKY}_{\mathrm{CLEAR}}) + \beta_2(\mathrm{SKY}_{\mathrm{CLOUDY}}) + \beta_3(\mathrm{SKY}_{\mathrm{PPT}}) + \beta_4(\mathrm{TIME30BS})$	$\beta_1 > \beta_2 > \beta_3$, $\beta_4 < 0$
Observer	$\hat{y}_{ELEVDIFF}$	Positive effect of elevation difference (observer to lek)	$\beta_0 + \beta_1(\mathrm{ELEVDIFF})$	$\beta_1 > 0$
	$\hat{y}_{GPSVHF}$	No effect of transmitter type	$\beta_0 + \beta_1(\mathrm{GPSVHF})$	$\beta_1 = 0$
	$\hat{y}_{INTENS}$	Positive effect of sampling intensity	$\beta_0 + \beta_1(\mathrm{INTENS})$	$\beta_1 > 0$
	$\hat{y}_{INTENS + ELEVDIFF}$	Positive effect of sampling intensity and elevation difference	$\beta_0 + \beta_1(\mathrm{INTENS}) + \beta_2(\mathrm{ELEVDIFF})$	$\beta_1 > 0$, $\beta_2 > 0$

Full model	$\hat{y}$ SAGE_CC + OSHRU_CC + GRFB_CC + SAGE_HT + OSHRU_HT_ + GRFB_HT + VOR + ELEV + LEK_AREA + PSAGE + SKY+ BARE + ACTIVITY + AGE + ATTEND + GROUP + TIME30BS + ELEVDIFF + INTENS + SLOPE + ASPECT + MALE_PL + GPSVHF	Negative effects of sage canopy cover, other shrub canopy cover, herbaceous canopy cover, sage height, other shrub height, grass/forb height, visual obstruction, elevation, lek area, vegetation classification, and sky conditions. Positive effects of bare ground cover, activity, bird age, lek attendance, group size (within 5 m), time after sunrise, elevation difference (observer to lek), search intensity, and slope. Quadratic effect of aspect and males present on the lek. No effect of transmitter type.	β_0 + β_1(SAGE_CC) + β_2(OSHRU_CC) + β_3(GRFB_CC) + β_4(SAGE_HT) + β_5(OSHRU_HT) + β_6(GRFB_HT) + β_7(VOR) + β_9(ELEV) + β_{10}(LEK_AREA) + β_{11}(PSAGE) + β_{12}(SKY$_{CLEAR}$) + β_{13}(SKY$_{CLOUDY}$) + β_{14}(SKY$_{PPT}$) + β_{15}(BARE) + β_{16}(ACTIVITY$_{SIT}$) + β_{17}(ACTIVITY$_{FORAGE}$) + β_{18}(ACTIVITY$_{STRUT}$) + β_{19}(AGE$_{YEARLING}$) + β_{20}(AGE$_{ADULT}$) + β_{21}(ATTEND) + β_{22}(GROUP) + β_{23}(TIME30BS) + β_{24}(ELEVDIFF) + β_{25}(INTENS) + β_{26}(SLOPE) + β_{27}(ASPECT)^2 + β_{28}(MALE_PL)^2 + β_{29}(GPSVHF)	$\beta_1 < 0$, $\beta_2 < 0$, $\beta_3 < 0$, $\beta_4 < 0$, $\beta_5 < 0$, $\beta_6 < 0$, $\beta_7 < 0$, $\beta_8 < 0$, $\beta_9 < 0$, $\beta_{10} < 0$, $\beta_{11} < 0$, $\beta_{12} > \beta_{13} > \beta_{14}$, $\beta_{15} > 0$, $\beta_{16} < \beta_{17} < \beta_{18}$, $\beta_{19} < \beta_{20}$, $\beta_{21} > 0$, $\beta_{22} > 0$, $\beta_{23} > 0$, $\beta_{24} > 0$, $\beta_{25} > 0$, $\beta_{26} > 0$, $\beta_{27} > 0$, $\beta_{(27)}^2 < 0$, $\beta_{28} < 0$, $\beta_{(28)}^2 > 0$, $\beta_{29} = 0$