Research Article

Male Greater Sage-Grouse Detectability on Leks

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ABSTRACT It is unlikely all male sage-grouse are detected during lek counts, which could complicate the use of lek counts as an index to population abundance. Understanding factors that influence detection probabilities will allow managers to more accurately estimate the number of males present on leks. We fitted 410 males with global positioning system and very high frequency transmitters, and uniquely identifiable leg-bands over 4 years in Carbon County, Wyoming. We counted male sage-grouse using commonly used lek-count protocols and evaluated variables associated with our ability to detect marked males using sightability surveys on 22 leks. We evaluated detection probabilities of male sage-grouse based on factors related to bird characteristics such as age or posture, lek and group size, lek characteristics such as vegetation cover or aspect, light conditions, weather, and observer. We then applied the detection probabilities to more accurately estimate male counts on leks. Detection probabilities were generally high ($\bar{x} = 0.87$) but varied among leks from 0.77 to 0.93. Male sage-grouse detection declined with increasing sagebrush height and bare ground and increased with more snow cover. Detection probabilities were also lower when observers counted from a higher elevation than the lek. Our sightability models predicted detection well and can be used to accurately estimate male abundance on leks from lek counts, which is especially useful where accurate abundance estimates are required or inference about population status is based on only 1 count. Further, it is important to consider lek attendance as a component of counts on leks because it affects availability of male sage-grouse for detection during lek counts. Detection can be maximized by conducting lek counts from 30 minutes before sunrise to 30 minutes after sunrise, although current protocols recommend lek counts can be performed up to 1 hour after sunrise. Detection can also be maximized by conducting lek counts ≥2 days after snowfall, which maximizes attendance and detection. © 2015 The Wildlife Society.

KEY WORDS abundance, *Centrocercus urophasianus*, detectability, detection, greater sage-grouse, index, lek counts, sightability, Wyoming.

Biologists and managers must be able to accurately monitor the status and trends of species that are declining in abundance, or under consideration for listing as endangered. For many species, detectability during surveys is an important factor affecting the accuracy and reliability of monitoring programs. When detection rates differ over time and space, observed trends in abundance may be biased unless they are corrected (Johnson 2008, Kéry and Schmidt 2008, Schmidt et al. 2013). Consequently, attempts have been made to identify factors affecting detectability of large mammals (Samuel et al. 1987, Bodie et al. 1995, Rice et al. 2009, Vander Wal et al. 2011, Walsh et al. 2011), songbirds (Farnsworth et al. 2002, Alldredge et al. 2007, Diefenbach et al. 2007, Kéry and Schmidt 2008, Schmidt et al. 2013), and other species to avoid bias

in assessments of trends. Problems with detectability are a primary reason new analytical approaches, such as occupancy modeling (MacKenzie et al. 2003), have become so popular in recent years. For species such as the greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse), which was previously designated as warranted but precluded from listing as endangered under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service [USFWS] 2010), careful monitoring is necessary to aid conservation efforts.

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 abundance assessments (Connelly and Schroeder 2007, Johnson and Rowland 2007). 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). Lek locations and the timing of the breeding season are predictable because sage-grouse have high site fidelity to leks 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).

Although lek counts are used to survey male sage-grouse populations and may be useful to monitor relative abundance annually, lek counts may not provide a reliable index to population size if imperfect detection and variability in detection exist among leks or through time (Samuel et al. 1987, Anderson 2001, Johnson 2008). Lek counts may be unreliable estimates of relative abundance as well, if detection varies among survey events within a year. 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, and thus bias male abundance estimates. When detection is imperfect, detection probabilities can be used to estimate the number of males missed during a lek survey, and more accurately estimate the number of males present (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 on upland game birds (Walsh et al. 2004, Clifton and Krementz 2006, Baumgardt 2011). Sightability studies can be used with marked animals to determine factors influencing detection, including variables related to the marked animal and its immediate surroundings.

Factors that may 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 bird, and vegetative cover (Samuel et al. 1987, Vander Wal et al. 2011, Walsh et al. 2011). The physical size of the lek and group size of displaying birds on the lek may also affect an observer's ability to effectively search the area, and observers may have difficulty accurately counting males on leks with many birds (Samuel et al. 1987, Rice et al. 2009). Movement or posture of birds can increase an observer's ability to notice them (Bodie et al. 1995, Garton et al. 2007). Topography and vegetation at leks, or an observer's location in relation to the bird, could also influence detection (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 characteristics of a lek, conditions of the count, and characteristics of male sage-grouse.

This research was part of a larger, long-term study using a before–after, control-impact design to assess relationships between wind energy development and sage-grouse ecology in Carbon County, Wyoming. We estimated detection probabilities on leks in the pre-construction phase of a wind energy development. Our objectives were to 1) evaluate how bird characteristics and activity, lek size, lek characteristics, vegetation, light conditions, and observer affected detection probabilities, 2) apply estimated detection probabilities to lek count data for an accurate estimate of male abundance on leks, and 3) determine optimal conditions for lek counts to maximize detectability of male sage-grouse on leks.

STUDY AREA

The wind energy development was proposed on The Overland Trail Ranch (OTR), an approximately 1,295-km^2 mix of private and public land (Bureau of Land Management and Wyoming Office of State Lands and Investments) south of Rawlins, Wyoming. The OTR is a sagebrush steppe basin with foothills to the south and southwest and rocky ridges to the north and northeast with elevation ranging from 1,890 m to 2,590 m.

The climate is semiarid, with long, cold winters and short, hot summers (Bailey 1995). Highest temperatures are in July ($\bar{x}$ max. $= 31°$ C) and lowest temperatures in December and January ($\bar{x}$ max. $= -1°$ C; Western Regional Climate Center [WRCC] 2008). Annual precipitation is typically between 19 cm and 26 cm, with most precipitation occurring between April and October (WRCC 2008).

Vegetation in our study area was classified as intermountain semidesert province (Bailey 1995). Vegetation predominantly consisted of sagebrush 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 wyomingensis*) dominated lower elevations and mountain big sagebrush (*A. t. vaseyana*) dominated higher elevations, with silver sagebrush (*A. cana*) in lowlands and black sagebrush (*A. nova*) in rocky, exposed soils (Thatcher 1959, Chapman et al. 2004, Connelly et al. 2004, Welch 2005).

METHODS

Trapping and Marking

We trapped birds and distributed transmitters among active leks on and around the OTR. To avoid bias for dominant males roosting near leks (Walsh et al. 2004), we captured male sage-grouse in late fall and early spring to supplement the number of marked individuals and account for overwinter mortality. We captured male sage-grouse using spotlighting and hoop-netting techniques (Giesen et al. 1982, Wakkinen et al. 1992) facilitated by all-terrain vehicles. We weighed captured males and classified them based upon primary wing feather characteristics (Eng 1955, Crunden 1963) as adults (≥ 2 years old) or yearlings (1–1.5 years old). Each bird received uniquely identifiable colored leg band combinations to facilitate resighting on leks (Walsh 2002; National Band and Tag Company, Newport, KY).

We deployed 20 transmitters in 2011, 20 in 2012, and 10 in 2013 using 30-g solar-powered platform transmitter terminal (PTT-100) global positioning system (GPS) transmitters (accuracy ± 18 m, Microwave Telemetry, Columbia, MD). The GPS–PTT transmitters had ultra high frequency (UHF) tracking. We marked an additional 50 males in

2011 with very high frequency (VHF) transmitters and attempted to maintain a sample size of 50 males with VHF transmitters every year by replacing expired transmitters and tagging new birds. Adult and yearling males tagged in spring with VHF transmitters usually 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) or 15-g Telonics (LB-35, Telonics, Mesa, AZ) transmitters. All GPS-PTT and VHF transmitters were <2% of grouse body weight and were attached using the Rappole and Tipton (1991) method. Trapping and handling procedures were approved through the University of Missouri Institutional Animal Care and Use Committee (Protocol #6750) and Wyoming Game and Fish Department (WGFD) Chapter 33 Permit (Permit #752).

Sightability Surveys

We monitored 58 leks throughout the study area (Fig. 1). Twenty-four to 33 leks were active each year of the study (2012–2014). We completed 2.65 ± 0.06 ($\bar{x} \pm$ SE) sightability surveys per lek on 20–22 active leks each spring (surveys per lek from 2012 to 2014 range $= 1$–11). Sightability surveys began 2 April 2012, 28 March 2013, and 19 March 2014 and continued until most leks were inactive or 3 lek counts were completed on each lek (22 May each year). We set up ground blinds at an observation point

Figure 1. The Overland Trail Ranch in Carbon County, Wyoming, with all active greater sage-grouse leks in the study area. Active leks had ≥1 male from 2012 to 2014. Symbol size represents relative lek size based on 2013 count data. Because leks were active and inactive different years, we had 34 active leks total throughout the study.

roughly 20–150 m from displaying males 1 week prior to lek counts to allow sage-grouse to habituate to its presence.

We used a protocol with 2 observers to conduct sightability surveys. One observer (observer 1) recorded numbers of displaying males on leks and noted the occurrence and location of marked birds on the lek, facilitated by telemetry. Observer 1 was in a blind on the lek perimeter, able to observe marked birds and use telemetry to locate unseen marked birds. Observer 1 entered the blind 2 hours before sunrise and counted sage-grouse at 15-minute intervals starting as soon as light was sufficient, approximately 30 minutes before sunrise, until all birds left the lek (usually before 1000 hours). Between counts, observer 1 used telemetry equipment to scan UHF and VHF radio frequencies and detect unseen radio-marked birds on the lek. Once a male was visually confirmed to be present on the lek, observer 1 would note the marked male's location. Once a bird was detected by observer 1, it was not considered again.

A second observer (observer 2) independently recorded numbers of displaying males and the occurrence and location of marked individuals with no prior knowledge of marked individuals on the lek. Observer 2 counted sage-grouse on foot, using WGFD protocols for lek surveys simultaneously with observer 1. Observer 2 conducted lek counts from a location approximately 50–200 m from the lek boundary, and the location was independently chosen by observer 2 on the observation morning to imitate a WGFD observer's location choice during conventional lek counts. Observer 2 recorded male and female birds on the lek, color band identities, locations, and associated covariates for marked males. Observer 2 noted time spent surveying for marked individuals and total time observers were present at the lek.

Once the survey was complete, observers immediately compared data. We considered grouse that observer 2 located to be detected. We considered grouse that observer 1 noted, but observer 2 failed to detect as undetected. We used covariates recorded by observer 2 when the marked male was detected by observer 2, and covariates recorded by observer 1 when the marked male was not detected by observer 2.

For lek counts, we recorded date, observer location (Universal Transverse Mercator), time, wind speed, and sky condition. We recorded sky conditions as a code including clear or a 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 or standing without strutting, or strutting), time the bird was observed, group size (no. grouse within 5 m of the marked bird), number of males present on the lek at the time of detection, and time spent searching for the marked male (i.e., sampling intensity). We determined marked bird locations using a compass and rangefinder (accuracy ± 1 m from 5 m to 686 m away, Leupold RX-750, Beaverton, OR) to determine an azimuth and distance from a known location of the observer.

After grouse left the lek, we recorded microsite vegetation measurements on the day of the sightability survey at the location where the grouse was detected. We established 2,
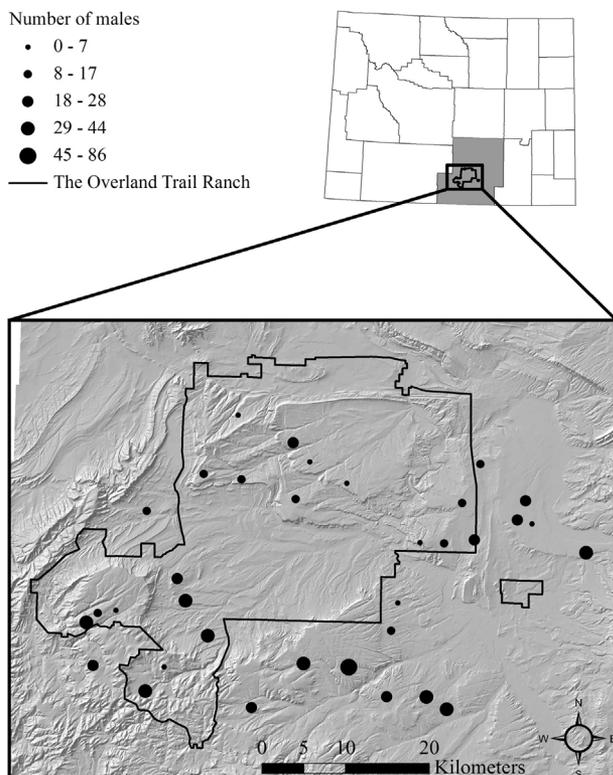
10-m perpendicular bisecting transects in cardinal directions that were centered over the sage-grouse's location. We measured visual obstruction (VOR) using a modified Robel pole with 1.27-cm increments (Robel et al. 1970, Benkobi et al. 2000) at the plot center and every meter up to 5 m from the plot 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 quadrat placed parallel to the transect (Daubenmire 1959, Hanley 1978) at 1-m intervals out to 5 m along each transect and plot center ($n = 24$). Observers estimated canopy cover classes (1 = 0–5%, 2 = 5–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–95%, 6 = 95–100%) for sagebrush, other non-sagebrush shrubs, grasses and forbs, snow, and bare ground in each quadrat (Daubenmire 1959). We measured natural droop height (cm) of 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 and vegetation height measurements for each sage-grouse location, and recoded canopy cover classes to the midpoints of the intervals and calculated average percent coverage for all cover classes at each sage-grouse location.

We calculated lek attendance rates, surrounding sagebrush cover, and elevation differences from observer to grouse as additional covariates. We calculated a seasonal lek attendance rate for each male sage-grouse by dividing the number of days the bird attended a lek by the number of days he was available to attend the lek throughout the season (Walsh et al. 2004, Fremgen 2014). We used ArcMap 10.0 (Environmental Systems Research Institute, Redlands, CA) with a 30 × 30-m categorical land cover layer based on Landsat ETM+ data (Driese and Nibbelink 2004), which we reclassified as sagebrush or other cover to calculate the percent of sagebrush within 50 m of the marked male. The 50-m radius provided a larger-scale representation of surrounding sagebrush cover on the lek, whereas the 5-m microsite vegetation measurements characterized sagebrush cover surrounding the male. We used a 30 × 30-m digital elevation model (DEM) to determine elevation for observation points and marked males, and we subtracted the elevation of the marked male's location from observer 2's elevation to model effects of the observer's position in relation to the lek. After the lek season ended, observers mapped leks using known locations of marked and unmarked birds noted during lek counts, and sign such as feathers, cecal tar, and droppings (Fremgen 2014). We calculated lek area (m^2) in ArcMap 10.0 using mapped lek perimeters.

Sightability Model Data Analysis

We created a priori models related to observer characteristics, lek size, vegetation characteristics, environmental conditions, and bird characteristics. We created models using biologically reasonable combinations of variables (Fremgen 2014: appendix D). We tested for correlation among covariates using PROC CORR in SAS 9.3 (SAS Institute, Cary, NC) and eliminated 1 variable of the pair when they were correlated ($r > 0.8$); we kept the variable 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; because year did not influence detection, we analyzed data pooled across years.

We modeled sightability of male sage-grouse using covariates for birds that were and were not detected using logistic regression in a generalized linear mixed model with observers modeled as a random effect using PROC GLIMMIX in SAS 9.3. We used second-order small sample size Akaike's Information Criterion (AIC$_c$; Burnham and Anderson 2002) to identify the most parsimonious model. Our model selection process involved 2 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 structural forms of each variable using AIC$_c$ to rank linear, quadratic, and pseudothreshold forms with the quadratic term centered on its mean to avoid multi-collinearity between linear and quadratic terms in the polynomial (Bonnot et al. 2011). For simplicity we selected linear structural forms unless a nonlinear form was >2 ΔAIC$_c$ units less than the linear form for that variable. We fit our a priori model set and averaged parameter estimates for all models with an Akaike weight (w_i) >12.5% the weight of the top model (Burnham and Anderson 2002). We did not consider interactions among variables because it would be complex for our many categorical variables. Initially, 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 recorded early in the morning. We removed models including those variables from analysis.

We evaluated goodness-of-fit using the Pearson χ^2 statistic divided by degrees of freedom (Pearson χ^2/DF). We evaluated the predictive ability of the most-supported model using 10-fold cross validation (Boyce et al. 2002) by dividing data into 10 random subsets and removing 1 subset for testing data, and refitting the model set using the remaining 9 subsets as training data. We estimated detection probabilities for testing sets based on 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 by dividing our observations of detected males into 10 equal size bins based on the range of predicted probability of detection, and calculated the Spearman-rank correlation between the predicted probability and frequency of observed detections in each bin.

We used averaged model parameter estimates, weighted by model probability, to calculate detection probabilities at each lek using characteristics of the lek observed during the lek count with the highest male count, and we estimated an average detection probability by averaging characteristics

across leks. Once we calculated the detection probability ($\hat{y}$) for each lek, we used it to obtain an accurate estimate of males present on the lek from count data. The estimated number of males on the lek ($\widehat{N}$) was:

$$\widehat{N} = \sum_1^t \frac{l_i}{\hat{y}_i}$$

where l_i is the maximum number of birds counted on lek i throughout the season by any observer, and $\hat{y}_i$ is the detection probability on lek i. We calculated variance for the corrected abundance using bootstrap methods. At each active lek, we sampled from the estimated detection probability and used the male high count to calculate abundance for 1,000 iterations. We summed the estimated numbers of males at each lek for the corrected male abundance at all leks. Male sage-grouse move among leks, but the probability that a male would move to a new lek and be double counted during lek counts was low because lek counts were completed near the peak of attendance, when interlek movements are less likely (Fremgen 2014). Therefore, lek counts are not likely to overestimate total male abundance from double counting males if counts are completed at an appropriate time of year, near the peak of male attendance.

RESULTS

We deployed an average of 85 ± 27 ($\bar{x} \pm$ SE) transmitters each year (37 ± 9 GPS-PTT transmitters and 48 ± 19 VHF transmitters) to assist with lek counts and sightability survey effort (Table 1). From 2012 to 2014, we detected 222 marked birds; 44 birds were not detected by observer 2 but present on the lek. Most of the marked male sage-grouse were recorded as detected between 30 minutes before sunrise to 1 hour after sunrise (Fig. 2). Only 12 (5%) marked individuals were detected >1 hour after sunrise.

The top sightability model included sagebrush height and snow cover, which were the most important factors for detection, but we model-averaged parameter estimates across the top 3 models because of model uncertainty (Table 2). Detection of marked males increased with greater snow cover and lower sagebrush height (Fig. 3). Although detection also had a negative relationship with bare ground and elevation difference between observer and the observed grouse, the
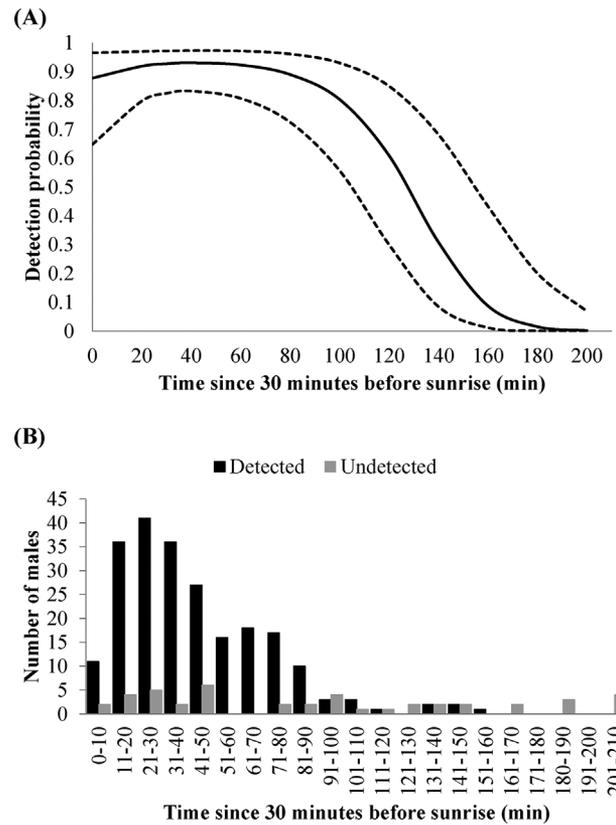
Figure 2. Detection of greater-sage grouse across time (since 30 min before sunrise) during sightability surveys in Carbon County, Wyoming from 2012 to 2014 including A) the probability of detection (with 95% CI) predicted from logistic regression with a random effect for observer identity, modeled across the range of times we observed and B) counts of males that were detected or undetected through different time intervals. We calculated time since 30 minutes before sunrise for males that were not detected by observer 2 (undetected) as time spent searching the lek without finding the marked male. Time since 30 minutes before sunrise was initially the top model, and the effect is shown in panel A, but we removed the variable from model selection because it was highly correlated with the rate at which we recorded marked males.

effects were not as strong, with little change in predicted detection across the range of data we observed (Table 3; Fig. 3).

The model-averaged probability of bird detection across all leks was generally high (0.87 [95% CL: 0.78, 0.93]), but the model-predicted, lek-specific detection probabilities varied

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 Apr	28 Mar	19 Mar
End date of sightability surveys	22 May	22 May	22 May
No. leks counted	49	56	58
No. occupied leks	24	29	33
High count of males on occupied leks ($\bar{x} \pm$ SE)	20 ± 3.09	17 ± 2.35	23 ± 3.03
Range of number of males on an occupied lek	1–63	1–48	1–86
Lek high counts (total for leks with sightability surveys)	408	428	540
No. sightability surveys completed	48	56	60
Leks with sightability surveys	20	20	22
No. observations of marked males	33	112	121
No. marked males that were detected by observer 2 (without telemetry equipment)	23 (70%)	99 (88%)	100 (83%)
No. unique marked males observed	28	67	67

Table 2. Top 3 sightability models, ranked by second order Akaike's Information Criterion (AIC$_c$) predicting male sage-grouse detectability in Carbon County, Wyoming, 2012–2014. All other models had a model weight (w_i) <12.5% of the top model.

Model[a]	−2 LL[b]	K[c]	AIC$_c$	ΔAIC$_c$	w_i[d]
ln(sagebrush height + 0.05) + snow cover	221.8	4	229.9	0.0	0.420
ln(elevation difference + 0.05)	226.9	3	233.0	3.1	0.089
ln(sagebrush height + 0.05) + *ln*(bare ground + 0.05)	225.1	4	233.3	3.3	0.079
Null model	233.0	2	237.0	49.2	0.000

[a] Parameters with +0.05 indicate we added 0.05 to linear structural forms to make values non-zero before natural logarithm transformation into the pseudo-threshold structural form. Elevation difference is between the observer and the grouse detected (i.e., observer elevation − grouse elevation).
[b] LL, log likelihood.
[c] No. parameters in model.
[d] Model weight.
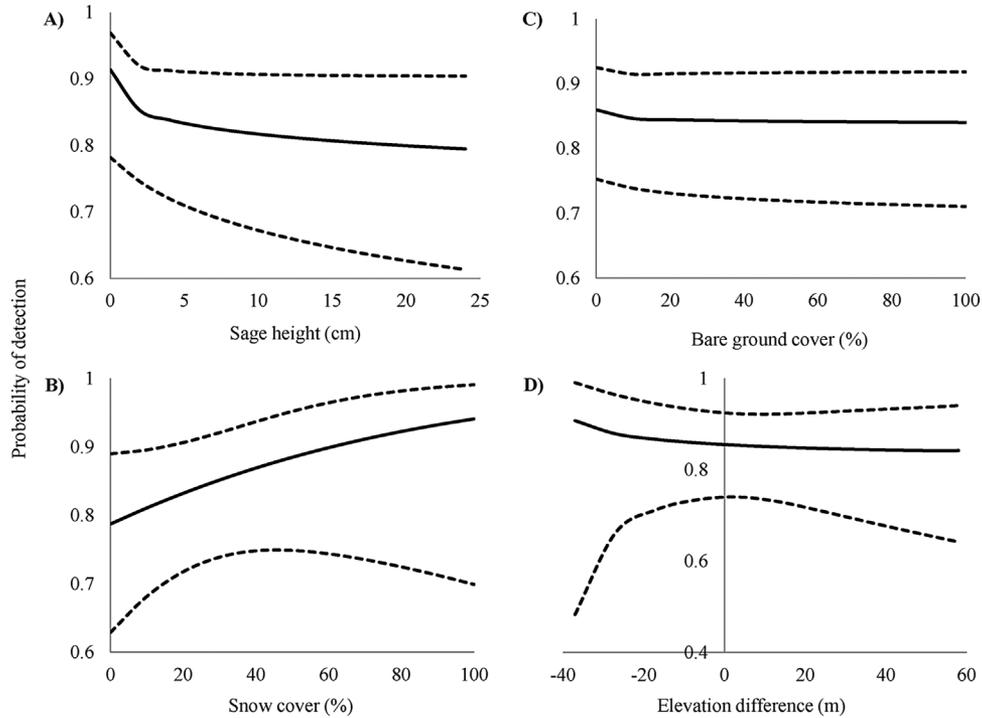
Figure 3. Variables included in the model-averaged top models for male greater sage-grouse detectability in Carbon County, Wyoming from 2012 to 2014. Variables are graphed across the range observed throughout the study, and include 95% upper and lower confidence limits as dotted lines. Detection was influenced by A) sagebrush height, B) snow cover, C) bare ground cover, and D) elevation difference between the observer and the bird (i.e., observer elevation − grouse elevation).

from 0.77 (95% CL: 0.58, 0.89) to 0.93 (95% CL: 0.73, 0.98). The Pearson χ^2/DF statistic indicated adequate model fit for the top 3 models, ranging from 0.81 ($\chi^2_{266} = 216.15$) to 0.83 ($\chi^2_{266} = 220.05$). The difference between observed detection and predicted detection probabilities averaged 0.27 ± 0.28 ($\bar{x} \pm$ SE) and the Spearman rank correlation coefficient indicated the model predicted well ($\rho_{10} = 0.96$, $P \leq 0.001$).

Table 3. Model-averaged parameter estimates with unconditional standard errors (SE), odds ratios, and 95% confidence intervals (LCL, UCL) for detection probabilities of male greater sage-grouse on leks in Carbon County, Wyoming, 2012–2014.

Parameter[a]	Estimate	SE	Odds ratio	LCL	UCL
ln(bare ground + 0.05)	−0.0202	0.0375	0.9800	−0.0937	0.0533
ln(elevation difference + 0.05)	−0.2174	0.3967	0.8046	−0.9949	0.5600
Intercept	2.3693	1.6479	10.6902	−0.8606	5.5993
ln(sagebrush height + 0.05)	−0.1639	0.1145	0.8488	−0.3883	0.0605
Snow cover	0.0146	0.0112	1.0147	−0.0074	0.0366

[a] Parameters with +0.05 indicate we added 0.05 to linear structural forms to make values non-zero before natural logarithm transformation into the pseudo-threshold structural form. Elevation difference = observer elevation − grouse elevation.

Detection probabilities and associated male population estimates varied throughout the study area. When accounting for undetected males during lek counts on leks with sightability surveys, abundance in 2012 differed by 17% between the raw count (408) and estimated (478 ± 6.31, $\bar{x} \pm$ SD) number of males; the male population in 2013 differed by 18% between raw (428) and estimated (503 ± 5.79) abundance; and the male abundance in 2014 differed by 19% between raw (540) and estimated (644 ± 6.75) number of male sage-grouse. Counts were corrected by as much as 14 males on a relatively large lek with tall and dense sagebrush where the detection probability was 0.79.

DISCUSSION

Detection probabilities for male sage-grouse on leks in Carbon County, Wyoming were generally high and the most important factors affecting detection were sagebrush height and snow cover, although bare ground and the elevation difference between the observer and sage-grouse were also included in supported models. Our hypothesis that vegetation cover inhibits detection of male sage-grouse on leks was corroborated by the most strongly supported model. Vegetation is consistently an important variable influencing detection of wildlife during surveys because 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). Less bare ground and shorter sagebrush predicted higher detection probabilities for male sage-grouse. However, bare ground may have been a spurious variable because it had wide confidence intervals, and although bare ground was never included in a priori models with snow cover because they were negatively correlated, they were in the same model after model averaging (Cade 2015). Higher snow cover increased our ability to observe male sage-grouse on leks. Most snowfall during our study occurred as several heavy storms, creating a white background on the lek that contrasted the male's dark plumage, making them more easily visible. Samuel et al. (1987) also reported snow cover increased contrast and detection rates of animals in surveys. There was a slight trend toward low detection when observers were higher than the lek, possibly because some males were obscured in small depressions in the landscape such as drainages.

Sage-grouse behavior, lek size, topographic characteristics of the lek, light conditions, and number of birds on the lek did not affect our ability to detect marked individuals in our study. Movement by animals or posture increased an observer's ability to detect some animals (Samuel et al. 1987, Bodie et al. 1995). In our study, observers had similar resight probabilities for all sage-grouse postures, possibly because male sage-grouse can be completely obscured by vegetation irrespective of 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). However, this expectation was not supported in our data and we did not conduct lek counts during heavy precipitation (Connelly et al. 2003) that would have resulted in low-light and high-cloud cover and likely low detection

probabilities. During light precipitation, few males were present on leks and observers often located marked males within 30 minutes before or after sunrise. We also anticipated males would be difficult to detect at larger leks resulting in lower detection probabilities (Baumgardt 2011), but marked males were visible regardless of the number of birds present or the lek's physical area. High detection rates for sage-grouse on leks resulted from the relatively flat, open landscapes (Patterson 1952) with less habitat diversity and landscape diversity than areas surveyed for other wildlife.

Several factors complicate use of lek counts as a population index and should be quantified, because lek counts are the only long-term population trend data available for sage-grouse across their range. Not all leks are known and those that are known may not be a representative sample of all leks (Anderson 2001, Johnson and Rowland 2007). Further, not all leks are counted every year because of logistical constraints (Johnson and Rowland 2007), although some state agencies monitor male abundance trends using only leks that have been surveyed consistently through time (R. S. Gamo, Wyoming Game and Fish, personal observation). Often, not all males will be present on the lek during counts because date, time of day, weather, and predators affect lek attendance (Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh et al. 2004, Johnson and Rowland 2007, Fremgen 2014), and occasionally birds visit different leks (Emmons and Braun 1984, Schroeder and Robb 2003, Fremgen 2014). Most bird surveys, including lek counts, have issues with availability of birds for counting such as lek attendance or interlek movements, which should be considered in addition to detectability (Farnsworth et al. 2002, Alldredge et al. 2007, Diefenbach et al. 2007, Kéry and Schmidt 2008, Schmidt et al. 2013). Finally, despite being present, not all males are accurately counted (Walsh et al. 2004). We quantified accuracy of counts given birds were present on the lek, but other aspects of lek counts should be assessed for their influence on the validity of lek counts.

Because sage-grouse population estimates are often based on the highest count observed on a lek during a season (Walsh et al. 2004, Johnson and Rowland 2007, Garton et al. 2011), accurate estimates of abundance should maximize detection and attendance by males. Many bird species are less active during high winds and precipitation, and, therefore, not available for detection during count-based surveys (Robbins 1981). Male sage-grouse attendance rates are lower on days with precipitation and increasing wind speeds and can remain low for an additional day (Bradbury et al. 1989, Fremgen 2014). Precipitation in our study had a stronger effect on attendance than high winds, with substantial declines in attendance the day of a precipitation event and the subsequent day (Fremgen 2014). However, detection on leks increased with increasing snow cover immediately after precipitation, creating a challenge to balance maximum detection and availability. To accurately estimate population abundance, managers must identify the highest count of males available on the lek, which should be done by maximizing detectability and availability for detection and performing at least 3 lek counts on active leks (Connelly et al. 2003).

Counts are a good index to the population when detection is constant through time and space and independent of population size (Johnson 2008). In our preliminary data analysis, we found that detectability on leks did not vary annually and substantially from one lek to another. Therefore, lek counts can be a reasonable index to population abundance assuming all other components of detection listed above are also constant. Additionally, we found detectability on leks was independent of the lek size and number of males present on the lek, indicating lek counts may be adequate indices to population abundance at a larger scale.

MANAGEMENT IMPLICATIONS

If accurate estimates of male abundance on leks are desirable for small regional populations, especially if there is great variation in vegetation or snow cover among leks or surveys within a year, we recommend concurrent sightability surveys to estimate and correct for detection probabilities. If detection on leks is not accounted for, lek counts can underestimate regional abundance of males on leks by 17–19%. However, because detectability on leks is constant spatially and temporally, and independent of population size, lek counts may be an adequate index for broader scale population trends unless other components of detection vary. Current lek count protocols recommend avoiding lek counts during precipitation or high winds but do not incorporate any lag effect after precipitation (Connelly et al. 2003). We found snow cover increased detection, but we recommend waiting to perform lek counts until 2 days after snow storms in areas with severe storms to maximize availability of grouse (Fremgen 2014). Current lek count protocols recommend performing lek counts 30 minutes before sunrise to 1 hour after sunrise (Connelly et al. 2003). We found the rate of recording marked males was highest within the recommended time frame but most efficient in the first hour. We do not advocate observers performing lek counts from a lower elevation than the birds; rather we suggest counters consider visibility of birds in relation to landscape features such as drainages. Although we were able to determine variables that can be manipulated to maximize detection probabilities during lek counts, other factors contributing to detection may be beyond the control of observers. For example, detection improved with shorter sagebrush near males on the lek, but vegetation cannot be controlled during lek counts. Modeling detection probabilities based on sightability surveys are critical to accounting for these factors when estimating abundance.

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