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Weather conditions and date influence male Sage Grouse attendance rates at leks

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For lek-breeding birds, lek attendance can be correlated with mating success. Variability in lek attendance could confound interpretation of male reproductive effort and complicate the use of lek counts as an index to monitor abundance. We assessed the daily probability of male Sage Grouse *Centrocercus urophasianus* lek attendance and explored implications of attendance on lek counts. We fitted 145 males with global positioning system (GPS) transmitters over 4 years in Carbon County, Wyoming. We evaluated influences of lek size and topography, date, weather, and bird characteristics such as age on daily morning lek attendance. The daily probability of attendance ranged considerably each year, from 0.120 ($\bar{x}$, 95% CI 0.051–0.259) in 2012 to 0.917 (95% CI 0.844–0.957) in 2013 with peak attendance dates ranging from 8 April (2012) to 11 May (2011). Attendance decreased with increasing precipitation on the observation day. Only 44–79% of lek counts occurred on days without precipitation and with high attendance (i.e. within 0.1 probability of peak predicted attendance). Although lek counts and population abundance, predicted using attendance rates, followed a similar trend, the relationship was not significantly correlated. We provide empirical evidence supporting current lek-count protocols: managers should avoid counting leks on days with precipitation because attendance is reduced. Although managers sometimes only complete one to two lek counts per year on active leks, completing at least three lek counts as recommended in protocols increases chances for higher male counts and improves the relationship between counts and abundance. Attendance varies annually, making it challenging to use lek counts to assess regional population trends over short time periods unless attendance is accounted for.

Keywords: *Centrocercus urophasianus*, daily attendance, lek attendance, population index, precipitation, Sage Grouse.

Grouse and other lek-breeding gallinaceous birds are threatened with extinction at a higher rate relative to other bird families (Bennett & Owens 1997) and therefore gallinaceous bird population status and trends should be accurately monitored to inform conservation and endangered species listing decisions. Leks (i.e. sites where males competitively display and females come to select a mate) are typically counted annually as an index of abundance to estimate population trends of lek-breeding species such as *Tympanuchus* spp. and

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Centrocercus spp. (Cannon & Knopf 1981, Johnson & Rowland 2007, Western Association of Fish and Wildlife Agencies [WAFWA] 2015). Lek counts are used to survey abundance because males on leks are relatively visible concentrations of cryptic and dispersed species, and leks can be inexpensively surveyed at the same locations annually (Patterson 1952, Dalke *et al.* 1963, Beck & Braun 1980, Walsh *et al.* 2004, Sedinger 2007). Additionally, lek counts are often the oldest and most complete population trend datasets for lek-breeding birds (Connelly & Schroeder 2007, Johnson & Rowland 2007). However, males do not attend leks every day throughout the breeding season, so the entire male population is not counted during lek counts (Johnson & Rowland 2007). Counting a male on a specific lek is conditional on the male being associated with the known lek and attending the lek during the count, as well as the observer's ability to detect the male when present (Alldredge *et al.* 2007, Diefenbach *et al.* 2007, Kéry & Schmidt 2008, Blomberg *et al.* 2013, Fremgen *et al.* 2016). By understanding factors affecting lek attendance (i.e. the probability an individual will visit a lek) and how attendance relates to counts, managers can improve lek-count protocols to maximize availability for detection for more accurate population trend indices.

Lek attendance has historically been expressed as an average attendance rate across long time scales. For example, Dunn and Braun (1985) averaged the highest count across 10-day periods, standardized by the season's highest count. Emmons and Braun (1984) calculated attendance as the percentage of days a given bird was observed on the lek out of the days the lek was observed. Daily attendance represents the probability an individual will attend a lek on a given day and can be used to evaluate correlations between male count data and population abundance as counts fluctuate throughout the season (Walsh *et al.* 2004, Baumgardt 2011). However, abundance estimates could be biased if factors affecting lek attendance vary spatially or temporally and are not considered when using lek counts as an index to abundance (Johnson 2008). *N*-mixture models are a robust way to improve estimates of population trends by explaining variation in detection and abundance during lek counts but are not as useful for estimating total male population size (McCaffery *et al.* 2016). Understanding how lek attendance contributes to detection may improve estimates of total male population size, which is useful for endangered species listing decisions.

Lek attendance may vary by bird age and impacts breeding success (Gibson & Bradbury 1985). Adult male Sage Grouse *Centrocercus urophasianus* have higher lek attendance and attend leks earlier in spring compared with yearlings; larger adult males achieve dominant positions with more mating opportunities and few males on the lek mate (Emmons & Braun 1984, Gibson & Bradbury 1985, Jenni & Hartzler 1978, but see also Bird *et al.* 2013). Walsh *et al.* (2004) estimated that adult male Sage Grouse attend leks 42–58% of days and yearlings attend leks 19–30% of days during the breeding season.

Weather conditions and lek characteristics could also influence attendance. Breeding season timing is largely related to elevation and snow cover (Morton 1978, Schroeder *et al.* 1999, Connelly *et al.* 2004, Green 2006) and daily weather may affect lek attendance. Precipitation and high winds can reduce male Sage Grouse counts immediately and for several subsequent days (Bradbury *et al.* 1989, Boyko *et al.* 2004). Connelly *et al.* (2003) recommend only carrying out lek counts when there is no precipitation, winds are < 15 km/h and there are clear skies. Patterson (1952) hypothesized leks have characteristics, such as spatial area, number of males or slope, that may make them preferable display sites and encourage regular attendance. For example, steeper slopes may be advantageous during territorial fights or males may prefer aspects that promote light conditions as the sun rises that improve their display or the contrast in their plumage (Endler & Théry 1996, Heindl & Winkler 2003, Sicsú *et al.* 2013). Males may prefer to display at smaller leks to avoid disturbances during copulations (Alatalo *et al.* 1996).

Sage Grouse populations are estimated to have declined an average of 0.83% annually range-wide since 1965 (WAFWA 2015) and their current range is < 60% of their pre-European settlement distribution (Schroeder *et al.* 2004). As a declining lek-breeding bird, daily lek attendance rates can help managers better interpret fluctuations in lek count data due to annual or spatial variation in male Sage Grouse attendance, and daily attendance can improve lek-count protocols. We investigated daily male Sage Grouse attendance rates and the factors associated with variability in attendance, including weather, lek size and topography, bird characteristics, and day of year. Our objectives were: (1) to estimate attendance rates of male Sage Grouse in south-central Wyoming in 2011–2014; (2) to determine factors affecting attendance; and (3) to assess the relationship between lek counts and attendance rates. We predicted that attendance would be influenced by weather, characteristics of male Sage Grouse and the topography of the lek, and that attendance would influence the relationship between lek counts and abundance. We predicted precipitation and high winds would negatively influence attendance on the observation day and several preceding days and we predicted male lek attendance would peak in mid-April annually. Additionally, we predicted adult males would have a higher probability of attendance than yearling males and males would have higher attendance at larger leks with more sagebrush cover in the vicinity.

METHODS

Study area

Our study was conducted on the Overland Trail Ranch (OTR), a 1295-km^2 checkerboard of public (Bureau of Land Management, Wyoming Office of State Lands and Investments) and private land south of Rawlins, Wyoming. The OTR is in a sagebrush steppe basin with rocky ridges to the north and northeast and foothills and mesas to the south and southwest. Elevations range from 1890 to 2590 m above sea level. The climate is semi-arid, 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 in April–October, with an average annual precipitation of 26 cm in the basin (WRCC 2008) and more precipitation at higher elevations. Precipitation varied annually in January through June: 2011 had ~ 40% more precipitation than the historical average; 2012 had < 50% of average precipitation; 2013 had half of the average precipitation but high snowpack; 2014 had nearly average precipitation (National Climatic Data Center 2014).

The vegetation in the study area is primarily rolling sagebrush steppe, with Wyoming Big Sagebrush (*Artemisia tridentata wyomingensis*) at lower elevations, Mountain Big Sagebrush (*A. tridentata vaseyana*) at higher elevations, Black Sagebrush (*A. nova*) in rocky, exposed soils and Silver Sagebrush (*A. cana*) in areas with shallow drainage (Thatcher 1959, Bailey 1995, Chapman *et al.* 2004).

Trapping and marking

We captured 145 male Sage Grouse throughout 2011–2014 using spotlighting and hoop-netting (Giesen *et al.* 1982, Wakkinen *et al.* 1992) within ~ 2 km of active leks (n = 20–33 active leks per year) in spring (79% of all males captured). We also trapped from September to the end of October in frequently used autumn habitats not associated with leks (21% of all males captured) to reduce the potential bias of capturing an artificially high proportion of males more likely to attend leks (Walsh *et al.* 2004). Active leks have at least two males displaying for ≥ 2 of the last 5–10 years (Connelly & Schroeder 2007). We weighed and classified each captured bird as a yearling (entering first breeding season) or adult (entered two or more breeding seasons) based upon primary wing feather characteristics (Eng 1955, Crunden 1963, Braun & Schroeder 2015). 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).

We deployed 50 rump-mounted (Rappole & Tipton 1991), 30-g solar-powered platform transmitter terminal (PTT-100) Global Positioning System (GPS) transmitters (horizontal accuracy ± 18 m, Microwave Telemetry, Columbia, MD, USA) on males in a phased-in approach. Each year we replaced mortalities to maintain our sample sizes (at least 20 males in 2011, 40 males in 2012, 50 males each in 2013 and 2014). High overwinter and summer survival and low spring survival increased the number of males trapped in spring relative to autumn to maintain sample sizes. From 1 March to 14 June, GPS-PTT transmitters recorded locations every hour from 04:00 to 09:00 h and collected three additional locations at staggered times.

Lek attendance estimates

We defined the lek season as starting on 1 March and ending on 15 June and we restricted our analysis to GPS locations recorded from 45 min before sunrise to 90 min after sunrise, when most lek counts were completed. To avoid misclassifying males as not attending a lek and underestimating attendance, we used male location data to locate leks that were previously unknown to management agencies ($n = 3$ leks found). Previously unknown leks were confirmed as active leks when two or more adult males attended the site during three or more counts for ≥ 2 years.

We mapped lek perimeters to determine the location of a GPS-PTT-tagged male in relation to known active leks. Because lek perimeters shift over time (Bergerud & Gratson 1988), we mapped perimeters separately each year except in 2011, when we were unable to map boundaries and therefore used the 2012 boundaries. We mapped perimeters including any known satellite leks after observing the lek multiple times during counts. During lek counts, observers used a compass and rangefinder to record locations of Sage Grouse on the lek edges. We mapped the boundary, keeping observed bird locations and concentrations of caecal droppings, faecal droppings and feathers on or inside the boundary. We added a 40-m buffer in ArcMap 10.0 (Environmental Systems Research Institute, Redlands, CA, USA) to ensure all males that were probably attending the lek, some of which recorded GPS locations near the observed periphery, were included within lek boundaries.

We considered males to be attending a lek when their GPS locations were within buffered lek boundaries and not to be attending when locations were outside buffered lek boundaries. Because all males observed on a lek are counted regardless of whether they are displaying or not (T. Christiansen pers. comm.), we did not differentiate male activity. We summarized daily attendance as a binary response for each male daily, where the male was considered to be attending a lek any day the male had a GPS location within the lek boundary. Given our high GPS location data accuracy ($\pm$ 18 m), we did not censor location data from our analysis except for obvious outliers such as single locations far outside our study area.

Covariates for lek attendance models

To assess influences of landscape features on attendance, we calculated covariates using ArcMap including elevation, slope and aspect of the lek, and surrounding sagebrush cover. We calculated average slope, aspect and elevation within lek boundaries using a 10-m resolution digital elevation model (DEM) and the Geospatial Modelling Environment (GME; Beyer 2015). Additionally, we reclassified a 30-m-resolution land cover layer (Driese & Nibbelink 2004) as sagebrush or other cover to determine the proportion of sagebrush vegetation within 603 m of the lek; 603 m represents the median distance from a lek boundary for all male locations on the study site in spring 2011–2013.

We recorded precipitation and average wind speed at sunrise daily from the National Oceanic and Atmospheric Administration weather station in Rawlins, Wyoming. We calculated average wind speed and average precipitation for the previous 1, 4, 6, 8, 10 and 12 days to assess lag effects of weather (Bradbury *et al.* 1989).

We also included bird characteristics, including age (yearling was the reference class), an interaction between age and day of year (number of days since 1 January each year) and capture season (whether the bird was captured in spring or autumn). We did not include body condition or mass in our analyses because although those metrics were measured at capture, they vary throughout the year (Vehrencamp *et al.* 1989) and have not been important in previous analyses (Blomberg *et al.* 2013).

Model building and selection process

We constructed *a priori* models for daily attendance, which included influences of weather, day of year, lek size and topography, and bird characteristics (Tables S1–S4). We included day of year in all *a priori* models because this was expected to strongly influence lek attendance (Jenni & Hartzler 1978, Walsh *et al.* 2004).

Prior to fitting models, we used the corrected Akaike information criterion (AIC_C; Burnham & Anderson 2002) to determine the best structural form of each variable (Franklin *et al.* 2000, Washburn *et al.* 2004) by ranking univariate models with linear, quadratic and pseudothreshold forms of each variable. We used the quadratic term $(x–x)^2$ to avoid multicollinearity between the linear effect and quadratic term in the polynomial equation (Bonnot *et al.* 2011). Pseudo-threshold forms were represented as $\log_e(x + 0.05)$ with 0.05 added to avoid the natural logarithm of zero. We selected the linear form for simplicity if it was within 2 AIC_C points of the highest ranked nonlinear form and confidence intervals for the quadratic term overlapped 0, or if the Pearson χ^2/df of the linear form was closer to one or equal to the Pearson χ^2/df for the pseudo-threshold form. If one form was strongly supported in one year (> 8 AIC_C points from the next best model) and was < 2 AIC_C points from the top form in another year, we used the strongly supported form in both years.

We also evaluated data to see whether they could be combined across years by comparing AIC_C scores for models, including year as an additive categorical covariate to the same models without year. Model convergence was poor with data pooled across years with year as a categorical covariate, so we analysed data separately by year. We also tested average weather conditions over the previous 1, 4, 6, 8, 10 and 12 days to assess the most influential time scales for the long-term effects of weather on attendance. We modelled each lag effect of weather in a model with date using their appropriate structural forms and compared model ranks. To keep the model set smaller, we used only the same two most influential time scales across all years in further analysis. We selected the covariance matrix structure in SAS (SAS Institute, Cary, NC, USA) to best reduce the Pearson χ^2 of the global model divided by degrees of freedom (χ^2/df) while still producing standard error estimates for all parameters. We used an unstructured covariance matrix in 2011 and 2012, and the variance component covariance matrix for 2013 and 2014.

We used logistic regression (PROC GLIMMIX, SAS 9.3) with bird and lek identity as random effects to assess how bird characteristics, weather, day of year, and lek topography and size influenced daily attendance. We fitted the *a priori* models to the data each year and averaged parameter estimates for all models with an Akaike weight (w_i) $\geq$ 1/8 the weight of the top model (Burnham & Anderson 2002). We calculated average daily attendance annually by calculating the inverse logit of a regression including the average value of each covariate across the range of data we observed and the averaged top model parameter estimates, weighted by their model rank; average attendance represents attendance near the middle of the breeding season under average conditions. We additionally calculated attendance during recommended weather conditions for lek counts and defined recommended conditions as no precipitation for any day or lag effect, wind speeds of 16 km/h on the day of the count or the previous day and the lowest observed average wind speed for wind lag effects (Connelly *et al.* 2003). Although Connelly *et al.* (2003) recommended little to no wind during lek counts, our study area had high wind speeds in spring (14 ± 12 km/h, $\bar{x}$± sd, min. = 0 km/h, max. = 52 km/h), so we calculated attendance with 16 km/h (10 miles/h) wind speeds, which is the upper limit of acceptable wind speeds during lek counts according to WGFD protocols. We calculated attendance during recommended conditions for each day within 3 weeks of the predicted peak in daily attendance, when most lek counts are completed (Johnson & Rowland 2007) and averaged the predicted attendance under recommended conditions across all days.

Model fit and validation

We evaluated goodness-of-fit using Pearson χ^2/df, McFadden's pseudo-R^2 (McFadden 1974), 10-fold cross-validation (Boyce *et al.* 2002) and Spearman-rank correlation. We calculated McFadden's pseudo-R^2 as 1 − (LL_1/LL_0), where LL_1 is the log likelihood of the top model and LL_0 is the log likelihood of the null model (no covariates); McFadden's pseudo-R^2 is interpreted as the proportion of variability explained by the model, where a pseudo-R^2 > 0.2 represents excellent fit (McFadden 1974, 1978). The 10-fold cross-validation evaluated the predictive ability of the best supported model (Boyce *et al.* 2002) and we calculated the average difference between observed attendance and the predicted probability of attendance. We calculated Spearman-rank correlation coefficients, interpreted similarly to Pearson correlations, by dividing the observed attending locations into 10 bins based on their predicted probability of attendance and found the correlation between the predicted probability of attendance and the frequency of observed attendance in each bin.

Lek attendance and lek counts

Once fieldwork was completed in 2014, we evaluated lek counts and attendance to determine whether counts were completed when male lek attendance was high when following a typical WGFD biologist's lek count protocol. We monitored 58 leks on or near the OTR, of which 20–33 were active. We attempted to count active leks at least three times each spring; all other leks were inactive or abandoned and were checked at least once each spring. Lek counts were usually separated by 1 week and completed from 0.5 h before sunrise to 1 h after sunrise (Jenni & Hartzler 1978, Emmons & Braun 1984, Connelly *et al.* 2003). Every day, we recorded the number of lek counts that occurred on any of the 58 leks in the study area. We calculated attendance with observed weather as the inverse logit of a regression using observed date and weather variables identified as important in model selection and averaged model parameter estimates weighted by model probability. Attendance with observed weather was not calculated until after lek counts were completed so lek count timing was not biased by daily attendance results. Each year, we defined 'high lek attendance' as predicted attendance with observed weather within a 0.1 probability of the maximum estimated attendance with observed weather probability. We created a 'highest attendance interval' starting with the first day and ending with the last day throughout spring that attendance with observed weather probabilities was considered high lek attendance.

We calculated Pearson correlations annually during the lek season and highest attendance interval for attendance with observed weather, number of lek counts and precipitation. To determine under what conditions lek counts were performed, we calculated the proportion of lek counts completed during the highest attendance interval. Not all days in the highest attendance interval had attendance with observed weather high enough to be considered high lek attendance. Therefore within the highest attendance interval, we calculated the proportion of days and lek counts with attendance with observed weather less than high lek attendance. Finally, we calculated the proportion of days with precipitation for all days with lek counts in the highest attendance interval. We only included days and lek counts when males had transmitters because some lek counts in 2011 occurred before males were radiotagged.

Additionally, we evaluated the relationship between lek count data and male abundance. We estimated male abundance for each lek that had one or more lek count annually while male Sage Grouse had GPS-PTT transmitters. For each lek count, we found the predicted attendance probability from observed weather and the top model parameter estimates. We used bootstrap methods to estimate the mean and variance for an estimate of male abundance per lek, based on the highest male count per lek. If multiple counts recorded the same number of males, we selected the highest male count with the highest predicted attendance on the date of the lek count for our regional population estimate. We divided the highest male count by the predicted daily attendance, sampled from the 95% confidence limits of the predicted daily attendance, for 1000 iterations. We summed all of the highest male counts per lek and summed all of the estimated male abundances per lek and compared results across years.

RESULTS

Trapping and marking

We analysed data from 24–58 males annually during spring (Table 1). The GPS-PTT transmitters recorded 45 ± 30 locations per male within the

Table 1. Summary of trapping effort and data collected from male Sage Grouse fitted with solar-powered platform transmitter terminal Global Positioning System transmitters (GPS-PTT) in Carbon County, Wyoming, 2011–2014.

Data collected	2011	2012	2013	2014
GPS-PTT transmitters deployed (new males trapped)	28	37	38	21
Active transmitters in spring, total	24	36	58	53
Active transmitters in spring, yearling males	4	7	4	4
All GPS locations in spring per male ($\bar{x}$)	23	37	51	87
All GPS locations in spring per male (sd)	15	22	45	61
No. of leks attended	17	18	24	29
Boundary points used to map lek perimeters	221	221	337	288

The number of leks attended increased as the study progressed because (1) we discovered three new leks, (2) leks became active that were previously inactive, and (3) males moved to a new lek from one of the sample leks at which they were trapped. There were fewer GPS locations per male in 2011 because males were captured later in spring and no males had been captured in autumn 2010.

Table 2. Top models describing factors influencing male Sage Grouse daily lek attendance in and around the Overland Trail Ranch in Carbon County, Wyoming, 2011–2014.

Year	Model	−2 LL[a]	K[b]	n[c]	ΔAIC$_C$[d]	w_i[e]
2011	Date, Date^2, Wind_d[f], Wind_p, Wind_p^2, Precip_p	471.6	9	562	0.000	0.451
	Date, Date^2, Precip_p, Precip_d	476.2	7	562	0.446	0.361
	Date, Date^2, Precip_d, Wind_p4, Wind_p4^2	475.6	8	562	1.911	0.174
2012	Date, Date^2, Age, Age × Date, Age × Date^2	776.4	8	1341	0.000	1.000
2013	Date, Date^2, Precip_d, Precip_d^2, Wind_p12, Wind_p12^2	2514.6	9	2626	0.000	1.000
2014	Date, Date^2, Precip_d, Precip_d^2, Wind_d, Precip_p4, Precip_p4^2	2621.7	10	3225	0.000	0.835

[a]−2 log likelihood. [b]No. of parameters. [c]No. of observations. [d]Change in AIC$_C$ units from the top model (top model AIC$_C$ = 489.9 in 2011, = 792.5 in 2012, = 2532.7 in 2013, and = 2641.8 in 2014). [e]Akaike weight. [f]Weather variables for precipitation are 'Precip' and average wind as 'Wind.' A '_d' ending denotes weather on the observation day, '_p' denotes weather the previous day, '_px' denotes weather averaged over x previous days. A superscript 2 designates the quadratic term for the variable.

timeframe of our analysis ($\bar{x} \pm$ sd, n = 7754 total locations, n = 3629 locations within lek boundaries). The first males were caught in spring 2011 and some lek counts occurred prior to trapping males, leading to less data being collected in 2011. In addition, because all males captured in 2011 were captured in spring and often near leks, results from this year may be biased.

Daily attendance

There was low model selection uncertainty among daily attendance models (Table 2, Tables S1–S4). For all years except 2012, top models included day of year, precipitation on the observation day and additional weather variables. In 2012, the top model included day of year, age and interactions between those variables. The daily attendance probability under average conditions was lowest in 2012 ($\bar{x} = 0.120$, 95% CI 0.051–0.259 for adults, n = 1341 days), nearly three times higher in 2011 ($\bar{x} = 0.326$, 95% CI 0.171–0.532, n = 562 days) and about seven to eight times higher in 2014 ($\bar{x} = 0.850$, 95% CI 0.734–0.920, n = 3225 days) and 2013 ($\bar{x} = 0.917$, 95% CI 0.844–0.957, n = 2626 days). Daily attendance under recommended lek count conditions was lowest in 2011 ($\bar{x} = 0.294$, 95% CI 0.076–0.652) and three times higher in 2013 ($\bar{x} = 0.958$, 95% CI 0.913–0.980) and 2014 ($\bar{x} = 0.897$, 95% CI 0.817–0.944). Although top models in 2012 did not include weather conditions, attendance within 3 weeks of the peak in attendance averaged 0.603 (95% CI 0.370–0.797) for adults. Day of year was the most important predictor for daily attendance (Table S5, Fig. 1). Attendance peaked over a month earlier in 2012 (8 April) than in 2011 (11 May). The dates of peak attendance in 2013 and 2014 were between the dates of the two earlier years (18 April 2013, 9 April 2014). The predictive ability of the models was good, with high Spearman rank correlation coefficients in 2013 (P_{10} = 0.005) and 2014 (P_{10} = < 0.001; Table S6).

Precipitation on the observation day and previous day was associated with lower daily probabilities of males attending a lek. Males were at least 1.7 times more likely to attend leks on days with no precipitation than on days with 0.5 cm precipitation in 2011, 2013 and 2014 (Fig. 2). Males in 2011 were three times less likely to attend leks when there was 0.5 cm precipitation the previous day than no precipitation the previous day. In 2014, attendance declined slightly with an increase in average precipitation the previous 4 days, but the difference was not substantial over the range of data we observed.

Average wind on the observation day, previous day, previous 4 days and previous 12 days were included in top models but usually did not have strong effects on attendance. In 2011, attendance was highest with ~ 21 km/h average wind the previous 4 days but did not change over the range of data observed in 2013. Average wind the previous 12 days was lowest at 15 km/h in 2013. Males were 1.3 times more likely to attend leks on calm days than on days with 52 km/h wind in 2013 and 1.2 times more likely to attend leks on calm days than on days with 37 km/h wind in 2011. Males were also 1.8 times more likely to attend leks the day after winds reached 37 km/h than the day after a calm day.

In 2012, adult attendance peaked on 9 April, whereas yearling attendance increased throughout

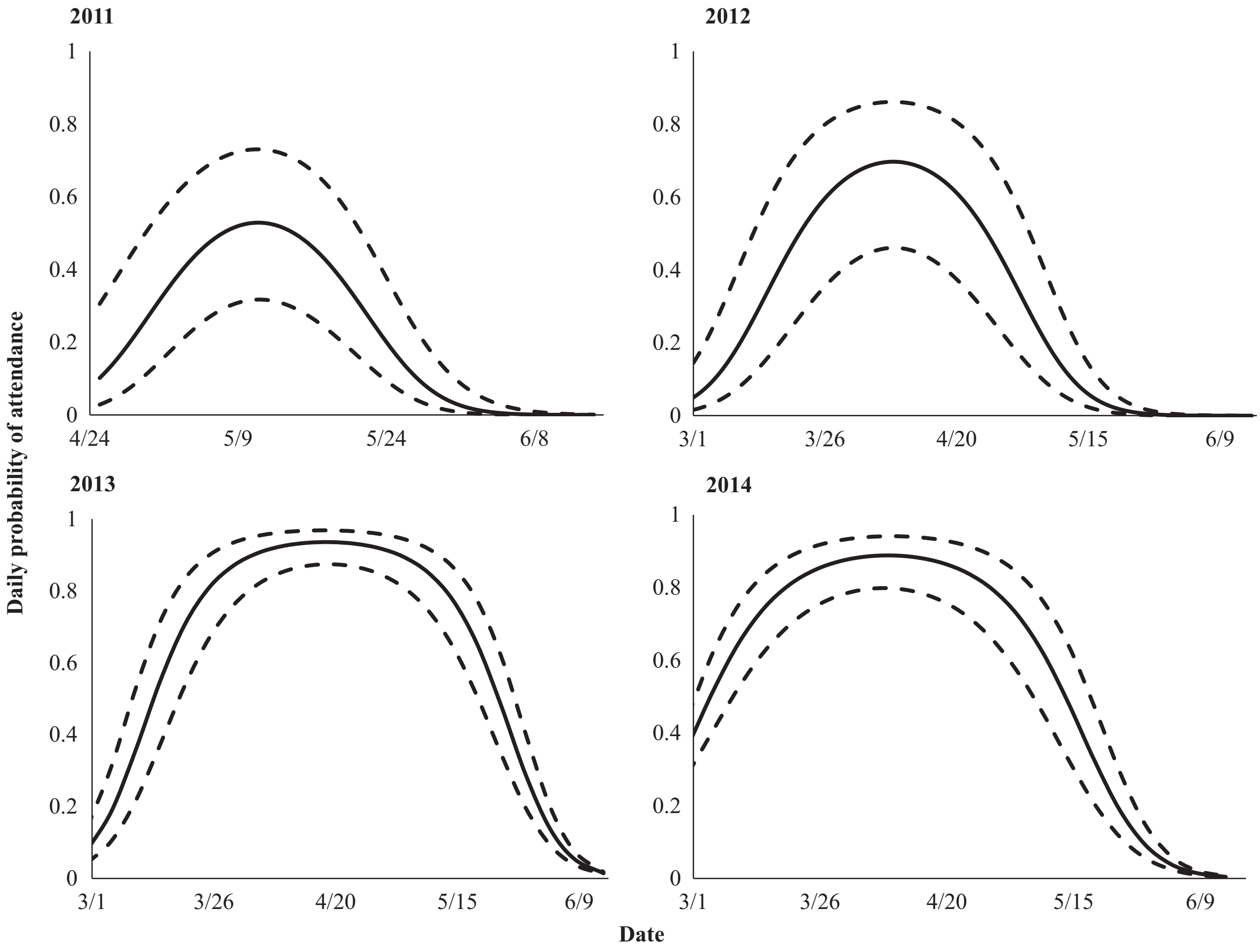

Figure 1. Influence of date on daily lek attendance by male Sage Grouse in Carbon County, Wyoming, 2011–2014.

the season, and the peak of adult attendance was 12 times higher than the peak of yearling attendance (Fig. 3). Capture season was not included in the top models. Daily attendance rates overlapped for males captured in autumn and males captured in spring in all years except 2013, and there was no consistent pattern for higher or lower attendance for males captured in spring. Parameter estimates and their standard errors for the capture season effects were 2.62 ± 1.11 in 2012, -2.117 ± 0.62 in 2013, and 0.90 ± 0.58 in 2014, with autumn as the reference capture season.

Lek attendance and lek counts

The daily probability of attendance considered 'high lek attendance' (i.e. within a 0.1 probability of the maximum predicted daily attendance) was lowest in 2011 (0.55–0.65) and higher in later years (0.60–0.70 in 2012, 0.86–0.96 in 2013, 0.84–0.94 in 2014); the low values in 2011 may be due to the different sampling strategy that year. Highest attendance intervals ranged from 11 days in 2011 to 56 days in 2013 (25 days in 2012, 46 days in 2014). During the highest attendance interval, precipitation was strongly negatively correlated with predicted attendance, but the association was weaker or weakly positive when extended to the entire lek season (Table S7). More than 75% of lek counts were completed during the highest attendance interval for first and second observations at leks in 2013 and 2014, and for first observations in 2012 (Table 3). Annually, > 70% of the days in the highest attendance interval had predicted attendance < 0.1 of the peak predicted attendance and lek counts were often completed on those days (Table 4). Additionally, there was often precipitation during the highest attendance

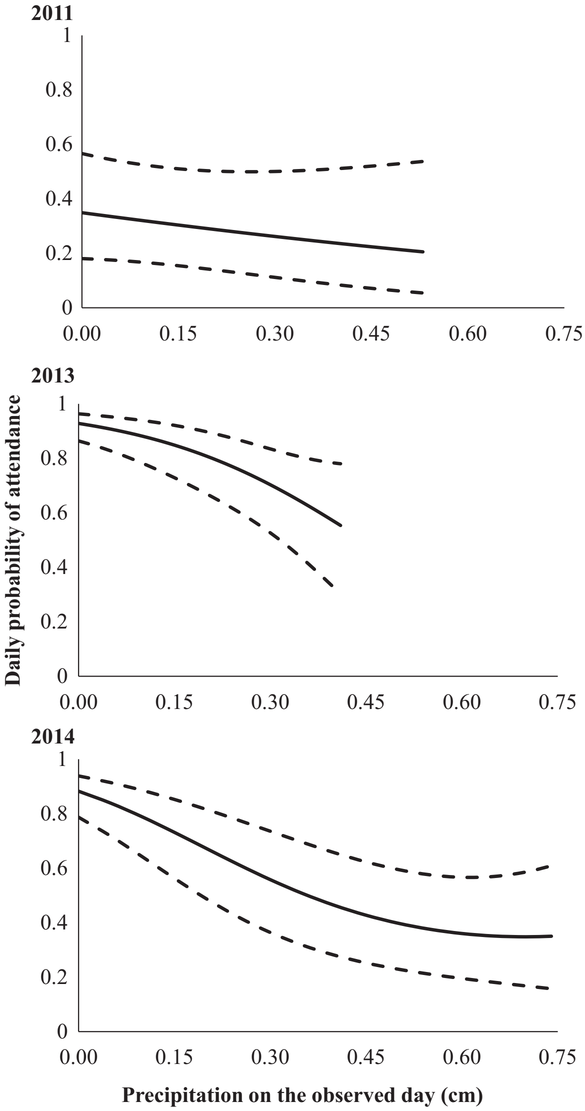

Figure 2. Influence of precipitation on daily lek attendance by male Sage Grouse in Carbon County, Wyoming, in 2011 and 2013–2014.

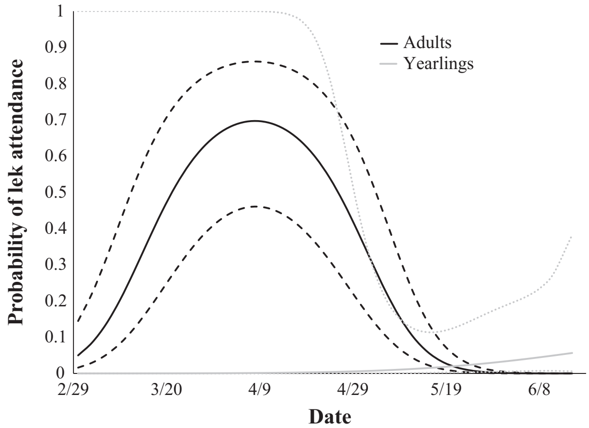

Figure 3. Influence of age on daily lek attendance by male Sage Grouse in Carbon County, Wyoming, in 2012.

interval. Therefore, only 44–79% of lek counts during the highest attendance interval occurred on days with no precipitation and with predicted attendance within a 0.1 probability of the peak attendance probability.

Estimated male abundances were 1.1–3.8 times higher than male lek counts every year. In 2011, the total number of males counted on leks was 427, but incorporating daily attendance rates corrected counts by 383% for an estimate of 1635 males (95% CI 0–4926). In 2012, we counted 392 males on leks and estimated 671 males (95% CI 385–957) in the study area (171% of count). In 2013, we counted 339 males on leks and estimated 380 males (95% CI 370–390) in the study area (112% of count), and in 2014 we counted 442 males on leks and estimated male abundance as 534 (95% CI 516–552, 121% of count). Although high counts and estimated abundance of males followed a similar pattern over time for 2012–2014 (Fig. 4), the relationship was not significant (r = 0.543, P_4 = 0.228).

DISCUSSION

Lek counts are used to estimate population trends for lek-breeding gallinaceous birds, thereby informing management decisions (Connelly *et al.* 2003, WAFWA 2015). However, imperfect lek attendance creates an availability bias in detection where some males are not present on the lek to be counted during lek counts (e.g. Western Capercaillie *Tetrao urogallus*, Jacob *et al.* 2010). When detection varies spatially or temporally, the variability must be accounted for before an index can be related to population abundance (Johnson 2008, WAFWA 2015), especially for short-term regional datasets. We found substantial year-to-year variation in peak attendance and seasonal timing of daily attendance probabilities. The predicted maximum daily attendance was 86% in 2013 and male counts were similar to male population estimates, whereas maximum predicted attendance in 2012 was 60%; lek counts in 2012 may reflect a male abundance substantially lower than the breeding population.

Table 3. Proportion of lek counts performed during the highest lek attendance interval for male Sage Grouse in Carbon County, Wyoming, 2011–2014.

	2011[a]	2012	2013	2014
All lek counts	0.209 (43)	0.583 (108)	0.745 (141)	0.733 (191)
1st observation	0.111 (9)	0.857 (49)	0.839 (56)	0.780 (59)
2nd observation	0.154 (13)	0.556 (27)	0.842 (38)	0.797 (64)
3rd observation	0.211 (19)	0.25 (16)	0.583 (36)	0.655 (58)
Additional observations	1.000 (2)	0.125 (16)	0.455 (11)	0.500 (10)

[a]We included fewer lek counts in 2011 than the other years because 52 additional lek counts occurred before male Sage Grouse were trapped, so they were excluded from daily lek attendance predictions. Additionally, each year we counted more leks when we discovered previously undocumented leks within our study area and increased sampling at inactive and abandoned leks. The highest lek attendance interval is the time span with the highest predicted daily lek attendance, within a 0.1 probability of the peak probability of lek attendance predicted using observed weather and averaged models. The number of lek counts is shown in parentheses.

Table 4. Proportion of lek counts that occurred under favourable conditions, including high attendance and no precipitation, for male Sage Grouse in Carbon County, Wyoming, 2011–2014.

	2011	2012	2013	2014
Per cent of days in HAI[a] with high attendance[b]	72.7	100	94.6	71.7
Per cent of lek counts during HAI occurring on days with high attendance	66.7	100	96.2	77.9
Per cent of days during the HAI with precipitation	36.4	28.0	37.5	23.9
Per cent of lek counts during the HAI with no precipitation and high attendance	44.4	79.4	61.9	75.0
Per cent of days during the HAI with no precipitation and high attendance	54.5	72.0	62.5	65.2

[a]High Attendance Interval. [b]Predicted attendance within 0.1 of the highest predicted daily attendance each year.

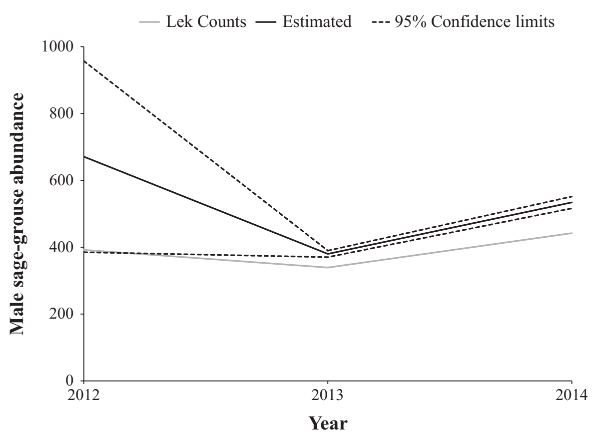

Figure 4. Male Sage Grouse abundance at study leks in Carbon County, Wyoming, in 2012–2014 from counts of males during lek counts, and male abundance estimated from male lek counts and predicted daily lek attendance.

Incorporating attendance rates into regional abundance estimates did not substantially change the population trend. For small geographical areas and short time periods, incorporating attendance rates into population abundance estimates may not be necessary and lek counts may be a suitable index for population trends (Johnson & Rowland 2007). If attendance strongly impacts counts of lek-breeding birds, incorporating availability for detection into population estimates can help alleviate the effects of attendance on lek counts (Farnsworth *et al.* 2002, Johnson 2008). For example, in years with above average precipitation it is difficult to count all leks during recommended count conditions and therefore attendance may be lower at leks during counts. Incorporating daily lek attendance into abundance estimates during wet springs can dramatically increase the estimated male abundance in comparison with lek count data, and improve the index to population abundance for short-term regional datasets. However, in years with normal precipitation, lek counts followed a similar trend to population abundance predicted by adjusting lek counts for attendance, and attendance rates can be high enough that the lek count index is nearly equal to estimated population abundance based on lek counts adjusted for imperfect lek attendance.

In addition to the availability bias from lek attendance, there is a detection bias in which some males attending the lek may not be counted; managers must maximize detection and availability simultaneously for lek-breeding species (Walsh *et al.* 2004, Fremgen *et al.* 2016). For example, Sage Grouse lek counters are encouraged to wait 2 days after a snow storm to conduct lek counts, at which time attendance has recovered and sightability is high against the snow (Bradbury *et al.* 1989, Fremgen *et al.* 2016). Ideally, both detection and availability for detection should be accounted for when lek counts are used as an index of population abundance (Diefenbach *et al.* 2007, Kéry & Schmidt 2008, Blomberg *et al.* 2013, WAFWA 2015). When estimating total populations of lek-breeding birds, other factors may influence the relationship between lek counts and population abundance, including the presence of unknown leks, unequal movement of males among leks, number of counts completed per lek and sex ratios (Cannon & Knopf 1981, Sedinger 2007, Drummer *et al.* 2011, Fedy & Aldridge 2011, WAFWA 2015). If logistical and financial constraints make it infeasible to estimate detection and attendance annually, lek counts may underestimate male abundance and should not be used to represent abundance in any given year (Applegate 2000), although lek counts may still provide an adequate assessment of population trends (Cannon & Knopf 1981, Blomberg *et al.* 2013, Dahlgren *et al.* 2016).

Peak lek attendance varied with date, which complements results from previous research on lek attendance (Jenni & Hartzler 1978, Walsh *et al.* 2004), probably from varying spring weather patterns. Elevation varied by > 500 m throughout the study area, so favourable breeding conditions occurred earliest at low elevations and later with increasing elevation (Schroeder *et al.* 1999, Green 2006). A mild winter and spring in 2012 coincided with an earlier peak in attendance than in years with average weather conditions (e.g. 2013 and 2014), demonstrating that shifts in lek season timing may be related to broad-scale weather patterns. We note that data were collected later in spring 2011 and somewhat later in spring 2012 than in other years, and we may not have adequately captured the peak in attendance during those years.

Male Sage Grouse attendance rates could be sensitive to sampling design if the males captured are not representative of the population. Attendance may not have been representative in 2011 and 2012 due to timing of trapping because sample sizes were low until early May. Although we attempted to minimize biases by trapping away from leks in spring and autumn, an age-related sampling bias (Jenni & Hartzler 1978) or lack of a strong age effect could potentially result if we captured primarily adult males with high attendance rates in spring on leks (but see Schroeder & Braun 1992). Our sample of yearling males may have been too small to detect strong age effects on attendance (but see also Dunn & Braun 1985, Schroeder & Braun 1992), although our small sample of yearlings probably closely approximates the age distribution in the population, given low chick survival rates in our area during the study (4.2–19.1%, Schreiber *et al.* 2016). Capturing males near leks in spring could bias lek attendance estimates high if males that roost near leks are adults that have higher attendance (Walsh *et al.* 2004). However, the season in which a male was captured did not consistently influence attendance rates (Fig. S1) and was not included in top models and there was no correlation between the distance a male was captured from a lek and his seasonal attendance rate (number of days available to attend leks divided by the number of days the male did attend a lek, $r_{170} = -0.003$, $P = 0.969$). Additionally, affixing a transmitter may cause lower lek attendance in Sage Grouse, either temporarily or annually, so our lek attendance estimates may be biased low for males captured during the breeding season (Gibson *et al.* 2013).

Weather is rarely studied in relation to lek attendance but our research supports our prediction that daily attendance was strongly negatively associated with precipitation, which provides empirical support for existing lek-count protocols (Connelly *et al.* 2003), although weather may have been less important in 2012 when there was little precipitation to influence attendance. Bradbury *et al.* (1989) also observed precipitation and wind decreased Sage Grouse lek counts immediately and through a decline in attendance for several days. The negative effects of precipitation were short-term in our study on the observation day and a decline in attendance the day after precipitation was only supported in 2011. Similarly, fewer Black Grouse *Lyrurus tetrix* males attended leks during precipitation (Baines 1996). Band-tailed Pigeon *Patagioenas fasciata monilis* counts at mineral sites are biased for up to 2 days after precipitation because pigeon attendance at mineral sites responds strongly to precipitation (Overton *et al.* 2005). Current Sage Grouse lek-count protocols and other avian survey techniques avoid counts during precipitation because behaviour and availability for detection can change during rain or snow (Robbins 1981, Connelly *et al.* 2003). For Sage Grouse, three lek counts at active leks are recommended (Connelly *et al.* 2003) and completing these maximizes opportunities for managers to record the highest male counts at leks despite lower attendance during some counts that may be due to precipitation, thus improving small regional population estimates (Fedy & Aldridge 2011).

Although wind variables had less of an influence on attendance compared with date or precipitation, our prediction that daily attendance would be lower with high average wind speeds over the preceding days (i.e. up to 43 km/h averaged across the previous 10 days) was supported. Access to finer resolution wind speed data across the study area, rather than a single weather station, would be more accurate for each lek and may have changed the trend. Consistently high wind could decrease attendance because birds might not be able to meet thermoregulatory requirements (Gessaman 1972, Sherfy & Pekins 1995) while simultaneously engaging in energetically costly displays for extended periods of time (Vehrencamp *et al.* 1989). The generally negative association between male Sage Grouse lek attendance and wind speed supports protocols avoiding avian counts during high winds (Robbins 1981, Connelly *et al.* 2003). Sharp-tailed Grouse *Tympanuchus phasianellus* lek attendance was also negatively correlated with higher wind speeds (Drummer *et al.* 2011) and Lesser Prairie Chicken *Tympanuchus pallidicinctus* lek surveys were more likely to detect attending birds when wind speeds were lower (Sadoti *et al.* 2016). High winds could also inhibit females from hearing and selecting mates or may inhibit males from keeping their tail feathers erect for their display postures, potentially making strutting displays on leks ineffective (Gibson & Bradbury 1985, Gibson 1989, 1996, Blickley & Patricelli 2012, Whalen 2015). Additionally, observers may not be able to locate new leks during high winds if the observer cannot hear strutting displays (Butler *et al.* 2010).

Age influenced attendance in 2012. Older males of lek-breeding bird species attend leks more frequently and earlier in spring than yearlings (Jenni & Hartzler 1978, Höglund & Lundberg 1987, Fiske *et al.* 1998, Walsh *et al.* 2004, Alonso *et al.* 2010). Attendance was previously examined at time scales longer than a single day, where variables consistent throughout the season such as age may have a stronger influence; generally, however, on a daily scale other factors may be more important (as occurs in 2011, 2013 and 2014) and age may have been attenuated across the length of the season.

Other predictions were not supported in top models. Males in lek-breeding species have high site-fidelity and consistently visit the same leks (Campbell 1972, Dunn & Braun 1985, Schroeder & Braun 1992, Schroeder & Robb 2003, Walsh *et al.* 2010, Fremgen *et al.* 2017), so lek characteristics may not influence attendance. Leks are flat open areas surrounded by sage (Patterson 1952), so our study area may not have had enough variation in physical characteristics of leks, such as slope or aspect, for those features to influence male Sage Grouse attendance.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. The daily probability of lek attendance for males captured in spring and autumn 2011–2014 in Carbon County, Wyoming. Bars represent 95% confidence limits.

Table S1. Top models describing factors influencing male Sage Grouse daily attendance per lek in and around the Overland Trail Ranch in southwestern Wyoming in 2011. The number of days analysed for lek attendance in spring was 562.

Table S2. Top models describing factors influencing male Sage Grouse daily attendance per lek in and around the Overland Trail Ranch in southwestern Wyoming in 2012. The number of days analysed for lek attendance in spring was 1341.

Table S3. Top models describing factors influencing male Sage Grouse daily attendance per lek in and around the Overland Trail Ranch in southwestern Wyoming in 2013. The number of days analysed for lek attendance in spring was 2626.

Table S4. Top models describing factors influencing male Sage Grouse daily attendance per lek in and around the Overland Trail Ranch in southwestern Wyoming in 2014. The number of days analysed for lek attendance in spring was 3225.

Table S5. Parameter estimates for top models predicting daily lek attendance by male Sage Grouse from 2011 to 2014 in and around the Overland Trail Ranch in Carbon County, Wyoming.

Table S6. Goodness-of-fit for top models describing male Sage Grouse daily lek attendance in and around the Overland Trail Ranch in Carbon County, Wyoming, 2011–2014.

Table S7. Pearson correlation coefficients among lek counts per day, precipitation and predicted male Sage Grouse daily lek attendance in Carbon County, Wyoming, 2011–2014.