Research Article

Male Greater Sage-Grouse Movements Among Leks

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ABSTRACT Movements among leks by breeding birds (i.e., interlek movements) could affect the population's genetic flow, complicate use of lek counts as a population index, and indicate a change in breeding behavior following a disturbance. We used a Bayesian multi-state mark-recapture model to assess the daily probability of male greater sage-grouse (*Centrocercus urophasianus*) interlek movements and estimate factors influencing movements among leks. We fitted 145 males with solar Argos global positioning systems platform transmitter terminals over 4 years (2011–2014) in Carbon County, Wyoming, USA. The daily probability of a male sage-grouse moving among leks ranged 0.003 (95% CI = 0.000–0.010) in 2011 to 0.010 (95% CI = 0.001–0.021) in 2013, indicating high daily lek fidelity throughout the season, although there was a 5–42% chance annually a male would move at least once to another lek throughout the season ($\bar{x}$ days analyzed/M = 55 ± 3.3 days [SE]). Interlek movement probabilities were strongly affected by day of year, peaking early in the lek season. Interlek movements were positively associated with elevation. Seasonal interlek movements occurred more frequently than previously reported, and can bias lek counts in early spring as males move from low to high elevation leks, which reinforces interlek movements as a critical component of lek ecology. © 2017 The Wildlife Society.

KEY WORDS availability bias, *Centrocercus urophasianus*, greater sage–grouse, interlek movements, lek fidelity, multi-state mark-recapture, Wyoming.

Although previously widespread in sagebrush (*Artemisia* spp.) habitats, greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) have been extirpated from 44% of their estimated historical range (Schroeder et al. 2004). Sage-grouse are a lek-forming species with range-wide declines in abundance averaging 0.83% per year since 1965, with more substantial declines in the last 10 years (Garton et al. 2011, Western Association of Fish and Wildlife Agencies [WAFWA] 2015). Although the United States Fish and Wildlife Service most recently ruled sage-grouse are not warranted for listing as threatened or endangered (U.S. Fish and Wildlife Service 2015), sage-grouse remain a species of conservation concern. Accurately monitoring abundance, demographic rates, and male lek ecology provides more precise information to managers on sage-grouse status and population trends. Leks are traditional breeding grounds where males display, and lek counts are the most commonly used long-term data set for sage-grouse population assessments, beginning as early as the 1940s (Connelly and Schroeder 2007, Johnson and Rowland 2007). Population trends are evaluated using lek count data as an index and lek counts are influenced by a male's visitation rates and detection of males on leks, along with demographic rates (e.g., reproduction, survival, emigration, and immigration; Blomberg et al. 2013, WAFWA 2015, Fremgen et al. 2016).

Lek counts may not be a useful index to population size, if males move among leks at unknown times and frequencies, resulting in males being undetected or double counted during lek counts (Anderson 2001, Gibson et al. 2014). Counting males during a survey requires males be available for detection at the lek, and the observer detects the males present on the lek (Alldredge et al. 2007, Diefenbach et al. 2007, Kéry and Schmidt 2008, Blomberg et al. 2013, Schmidt et al. 2013). Population growth and temporary absences from leks, including interlek movements (i.e., movements among leks), explain 98% of the annual variation in lek counts (Blomberg et al. 2013), so understanding interlek movements contributes to understanding the relationship between lek counts and population abundance. Previous research assessed interlek movements as the number of leks a male visited throughout the lek season

(Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985, Schroeder and Robb 2003), or more recently as the annual probability a male may move to a different lek than where he was originally captured (Gibson et al. 2014). However, evaluating the circumstances influencing interlek movements at a daily scale is useful because factors like precipitation and wind occur over short time periods, and may directly influence probabilities of interlek movements more strongly than factors that remain constant throughout a season. Managers could then predict daily interlek movement probabilities under certain conditions and avoid lek counts when interlek movements are likely to result in a non-representative availability for detection.

In addition to potentially improving the reliability of lek counts, understanding interlek movements could expand knowledge of reproduction in lek-forming species. Sage-grouse are long-lived with low reproduction relative to other gallinaceous lek-forming birds, and population growth is sensitive to breeding success (Taylor et al. 2012). Interlek movements are an important aspect of lek-breeding ecology that may influence reproductive success and gene flow because males that move frequently may not establish territories or attract females (Beck and Braun 1978, Vehrencamp et al. 1989) and few males on a lek mate (Jenni and Hartzler 1978, Emmons and Braun 1984, Gibson and Bradbury 1985). Interlek movements are reportedly uncommon in sage-grouse because males have high fidelity to leks (Campbell 1972, Dunn and Braun 1985, Schroeder and Braun 1992, Schroeder and Robb 2003, Walsh et al. 2010), but even infrequent interlek movements could affect reproductive success at a lek (Sedinger 2007).

Interlek movements likely vary by a bird's characteristics, lek attributes, day of year, and weather. Although previous research demonstrated adult males move among leks less frequently than yearling males (Schoenberg 1982, Emmons and Braun 1984, Dunn and Braun 1985, Schroeder and Robb 2003), many other factors motivating interlek movements remain unexplored (Gibson et al. 2014). Dominant males may move among leks infrequently, successfully establish territories, and contribute strongly to the gene pool at 1 lek (Jenni and Hartzler 1978, Gibson and Bradbury 1985). Certain leks may be more desirable display sites based on their topographic attributes (Patterson 1952) or have more sagebrush vegetation nearby, providing food and cover (Vehrencamp et al. 1989, Barnett and Crawford 1994, Connelly et al. 2000, Gregg 2006, Gregg et al. 2008). Males may prefer to move to larger leks (Lank and Smith 1992, Alonso et al. 2004) or smaller leks (Westcott 1997). Precipitation and high winds decrease lek attendance (Bradbury et al. 1989) and bird activity levels (Robbins 1981), so males may be less likely to move among leks during poor weather conditions. Male sage-grouse might move among leks more often in the beginning or end of the lek season (Emmons and Braun 1984, Wegge and Larsen 1987).

Interlek movements have been documented at coarse temporal scales, but daily probabilities would contribute to understanding breeding behavior, and improve the reliability

between lek counts and population abundance. Our objectives were to estimate the daily probability of sage-grouse interlek movement and identify factors that influence movement rates, including bird and lek characteristics timing within the breeding season and weather.

STUDY AREA

This study was conducted on the Overland Trail Ranch (OTR), a 1,295-km^2 checkerboard of private and public land (Bureau of Land Management, Wyoming Office of State Lands and Investments) south of Rawlins, Wyoming, USA. The OTR is the future site for a proposed 1,000-turbine wind energy development and is a basin with rocky ridges to the north and northeast, and foothills to the south and southwest, with elevations ranging from 1,890 m to 2,590 m. The climate was semiarid with long, cold winters and short, hot summers. Highest temperatures were in July ($\bar{x}$ max. $= 31\,°C$) and lowest temperatures occurred in December and January ($\bar{x}$ max. $= -1\,°C$; Western Regional Climate Center [WRCC] 2008). Annual precipitation was 19–26 cm in the basin, mostly falling April–October, with more precipitation in the foothills and ridges (WRCC 2008). Vegetation consisted primarily of sagebrush (*Artemisia* spp.) with short grasses. Mountain big sagebrush (*A. tridentata* ssp. *vaseyana*) dominated higher precipitation zones and elevations, Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*) was common in lower precipitation zones and elevations, with silver sagebrush (*A. cana*) in lowlands and black sagebrush (*A. nova*) in rocky, exposed soils (Thatcher 1959, Chapman et al. 2004). Several potential local predators and nest predators include golden eagles (*Aquila chrysaetos*), coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), great-horned owls (*Bubo virginianus*), red foxes (*Vulpes vulpes*), and common ravens (*Corvus corax*; Hartzler 1974, Hansen et al. 2016).

METHODS

Trapping and Marking

We monitored 58 leks on and around the OTR, with 20–33 active leks each spring (2011–2014). We trapped male sage-grouse near known, active leks in spring. High site fidelity by dominant males captured near leks in spring could bias results towards fewer interlek movements (Walsh et al. 2004), so we also captured 21% of males in autumn habitats, not associated with leks, during September and October.

We captured male sage-grouse using spotlighting and hoop-netting techniques (Giesen et al. 1982, Wakkinen et al. 1992) facilitated by all-terrain vehicles at roosting sites. We weighed captured males and classified them as a juvenile (hatched earlier in the year), yearling (first breeding season, captured in spring), or adult (at least second breeding season) based on primary wing feather characteristics (Eng 1955, Crunden 1963, Braun and Schroeder 2015). Trapping and handling procedures were approved through the University of Missouri Institutional Animal Care and Use Committee (protocol no. 6750) and Wyoming Game and Fish Department Chapter 33 Permit (permit no. 752).

We attempted to maintain a sample of 20 males in 2011, 40 males in 2012, and 50 males in 2013 and 2014 marked with rump-mounted (Rappole and Tipton 1991) 30-g solar powered platform transmitter terminal (PTT-100) global positioning system (GPS) transmitters (Microwave Telemetry, Columbia, MD, USA). To maintain sample sizes, we captured new males to replace mortalities, which occurred more frequently in spring relative to autumn. During spring, GPS-PTT transmitters recorded locations every hour from 0400 to 0900, and 3 more locations throughout the day on 5 schedules to ensure locations were during different periods in the 24-hour cycle. All transmitters were equipped with a mortality sensor, and we confirmed mortalities based on the presence of primary wing and tail feathers, bones, or bite marks on transmitters and leg loops. If no sign of mortality was present, we assumed a transmitter attachment failure occurred. If transmitters temporarily failed to collect data, we attempted to locate the bird and censored the male from analysis until we confirmed the male was alive.

Mapping Lek Boundaries to Determine Attendance and Lek Associations

To determine which leks males with GPS-PTT transmitters attended and were associated with, we mapped perimeters of known, active leks. During lek counts at these known active leks, we recorded locations of birds, including females, and displaying and non-displaying males, on the lek edges (Connelly et al. 2003), and mapped leks by keeping observed bird locations and concentrations of cecal tar, droppings, and feathers on or inside the boundary. We added a 40-m buffer in a geographic information system (ArcMap 10.0; Environmental Systems Research Institute, Redlands, CA, USA) to accommodate males on the boundary periphery that were likely attending each lek. We additionally used GPS-PTT data to locate unknown leks, which we confirmed by visiting the site ≥3 times per year for ≥2 years. We determined 3 sites to be previously unknown leks, which were 2.30–8.35 km from the closest known leks and had >30 adult and yearling males displaying annually for at least 3 weeks each year.

We considered males to have attended a lek on days when ≥1 GPS location was within buffered lek boundaries. Males did not attend leks every day, so when a male did not attend a lek, we considered the male to be associated with the closest lek (measured by Euclidean distance). We assigned males lek associations only to leks they attended at least once during the breeding season, and an interlek movement occurred the day of year a male was closer to a different lek than associated with the previous day. Occasionally (0.12% of all days) a male attended 2 leks in 1 day, so we assigned the male to the lek association that differed from the lek that was attended most recently. The lek season started the first day marked males attended a lek, and ended when marked males no longer attended leks. We included data immediately after we captured a male because many males attended leks within 1–2 mornings after being captured, and results were similar if we excluded the first 3 days after capture.

Multi-State Mark-Recapture Estimates

We tested the influences of bird characteristics, lek characteristics, weather, and day of year on interlek movement probabilities. Bird characteristics included a seasonal attendance rate and age modeled as a dummy variable (1 for adults, 0 for yearlings). Males that were captured as yearlings or juveniles and tracked multiple years were graduated to the adult age class when appropriate. Seasonal lek attendance was the proportion of days a male attended any lek during the breeding season. Lek characteristics included a lek's average slope, average aspect, average elevation, and proportion of sagebrush vegetation within 603 m of lek boundaries; 603 m was the median distance from the lek to males with GPS-PTT transmitters during spring 2011–2013. We calculated average slope, aspect, and elevation within each lek's boundaries using the Geospatial Modeling Environment (GME; Beyer 2012) and a 10-m resolution digital elevation model. We used the GME and a 30-m resolution land cover layer (Driese and Nibbelink 2004) reclassified as sagebrush or other to determine the proportion of sagebrush vegetation within 603 m of the lek. We considered lek size by testing area (m^2) and the maximum number of males and females counted annually during lek counts. We assessed environmental conditions including day of year (i.e., days since 1 Jan each year), and precipitation and wind on the day a movement between leks occurred and the day preceding movement. We recorded daily precipitation and average wind speed at sunrise from the National Oceanic and Atmospheric Administration weather station in Rawlins, Wyoming, USA. To incorporate annual variability, we included 3 dummy variables to designate years 2011–2014.

We used a Bayesian multi-state mark-recapture model (Williams et al. 2002, Lebreton et al. 2009, Kéry and Schaub 2012) to estimate daily interlek movement probabilities. We classified birds into 3 states: Lek, Alt.Lek, or Dead. Males were initially within the Lek state. Birds that moved to a different lek association transitioned to Alt.Lek, where they remained until moving to a different lek association and transitioning back to Lek, or dying and transitioning to Dead. We used a transition matrix to describe the probability of transitioning from the state at time $t–1$ to the state at time t during 1-day time steps:

	Lek_t	$Alt.Lek_t$	$Dead_t$
Lek_{t-1}	$(1-\psi_{it})\phi$	$(\psi_{it})\phi$	$1-\phi$
$Alt.Lek_{t-1}$	$(\psi_{it})\phi$	$(1-\psi_{it})\phi$	$1-\phi$
$Dead_{t-1}$	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 individuals and tested our model set 3 times: allowing ϕ to vary across years, allowing ϕ to vary across years and day of year, and with ϕ held constant across time. Models fit best with ϕ held constant across time and individuals, so all inference was drawn from models with a constant ϕ.

We modeled daily interlek movements as a function of bird characteristics, lek characteristics, and environmental conditions in 23 models with biologically meaningful combinations of variables, with male sage-grouse identity included as a random effect in all models:

$$\text{logit}(\psi_{it}) = \beta_1 + \beta_2\, x_{2\ i,t-1} + \beta_3\, x_{3\ i,t-1\ \dots} + \beta_k\, x_{k\ i,t-1} + r_i$$

where β_1 is the intercept coefficient, $\beta_2 \dots \beta_k$ are parameter coefficients, $x_{2\ i,t-1} \dots x_{k\ i,t-1}$ are covariate matrices, and r_i is a random effect for individual male sage-grouse identity. When 2 variables in a model were correlated ($P < 0.05$ for Pearson correlations), we retained only the most biologically relevant variable. We evaluated 18 *a priori* models and 5 *post hoc* models; *post hoc* models included interactions among variables, and a model testing the season in which a male was captured. We assumed vague normal (i.e., $\mu = 0$, $\sigma_2 = 100$) prior distributions for covariate parameters and a uniform $(0,1)$ prior distribution for ϕ. We included year as an additive effect in each model.

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

$$\text{state}_t \sim \text{categorical}(M_{t-1})$$

where M_{t-1} is the row of the transition matrix associated with the sage-grouse's state at time $t-1$. We imputed missing states and covariates when transmitters temporarily failed to collect locations by drawing from the covariate's prior distribution. Seventy-one percent of male sage-grouse capture histories had no missing data. We imputed data for 311 days (3.2% of the 9,641 days analyzed) for the remaining 29% of capture histories with ≥ 1 day missing (1.8 ± 0.6 [$\bar{x} \pm \text{SE}$], days imputed per male, $2.8 \pm 0.8\%$ of the days analyzed per male). We exponentiated the predicted daily probability of an interlek movement to a seasonal probability of movement, using the average number of days a male was included in analysis each year. We also exponentiated the upper and lower bounds of the 95% credible interval for predicted daily interlek movement rates to calculate a 95% credible interval for seasonal interlek movement rates. We could not test barriers to interlek movements with our models, such as distances among leks or elevation changes. Therefore, we calculated the distance from each lek to its closest neighboring lek, found the distance of each interlek movement, and compared distances among leks and distances of interlek movements using a *t*-test assuming unequal variances. We also calculated the average elevation gain for all interlek movements.

Model Building and Selection Process

We used the Deviance Information Criterion (DIC) to select the most parsimonious model (Spiegelhalter et al. 2003) and based inference on the top model, if no other models were within 2 DIC units of the top model (ΔDIC). We calculated normalized model weights (w_i) for DIC using the same procedure as for Akaike's Information Criterion model selection (Burnham and Anderson 2002, Ward 2008). We assessed goodness of fit for the top model by examining standardized residual plots and comparing the number of time steps a male was in each state for observed and simulated data (Dupuis and Schwarz 2007). Because a standardized residual of 0 indicates perfect prediction, we considered models to fit well if >66% of standardized residuals were between -5 and 5. We calculated a Bayesian *P*-value as the probability a test statistic calculated from observed data was greater than the test statistic calculated from simulated data, and established Bayesian *P*-values >0.05 and <0.95 would indicate adequate fit; 0.5 represents excellent fit and indicates the simulated data is similar to observed data (Gelman et al. 1996, King and Brooks 2002). We calculated Pearson residuals for the number of time steps each male was in state Alt.Lek in observed and simulated data sets. We also examined all predictors not included in the top model to better understand novel factors associated with interlek movements. We estimated interlek movement rates for these novel factors across the range of their data, calculated the magnitude of the difference in interlek movement rates across the range of the data, and reported the stronger associations as interlek movement trends.

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 parameters. We ran each chain for 40,000 iterations and discarded the first 20,000 iterations as burn-in, and kept every twentieth 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/chain).

Table 1. Trapping effort and data collected from solar-powered platform transmitter terminal global positioning system transmitters (GPS-PTT) attached to male greater sage–grouse each year (2011–2014) in Carbon County, Wyoming, USA.

	2011	2012	2013	2014
GPS-PTT transmitters deployed	35	37	52	21
Active transmitters in spring[a]	21	36	58	54
No. GPS locations in spring/M ($\bar{x} \pm \text{SD}$)	151 ± 81	237 ± 146	382 ± 234	604 ± 367
No. days a M was used in analysis ($\bar{x} \pm \text{SD}$)	20 ± 10	31 ± 20	52 ± 29	88 ± 52
No. leks with a GPS-PTT transmitter M	17	21	25	28
Observed transitions[b]	3	23	89	99

[a] Some transmitters were redeployed in a single season after male mortalities.
[b] Observed transitions are an interlek movement by any GPS-PTT transmitter male from attending one lek to attending another lek.
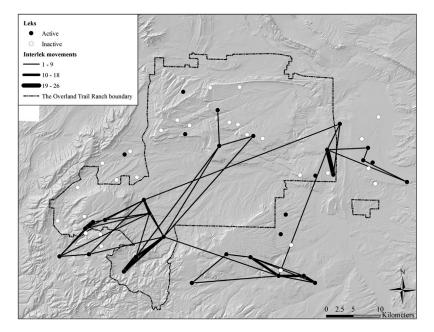
Figure 1. Interlek movements among leks in and around the overland trail ranch in Carbon County, Wyoming, USA, 2011–2014. The map shows active and inactive leks, and lines between leks designate the number of interlek movements by any male. If no interlek movement occurred between 2 leks, the leks are not connected by lines.

RESULTS

Annually, we deployed 31 ± 4 GPS-PTT transmitters and used 42 ± 9 (min. = 21, max. = 58) birds in analysis each spring (Table 1). Throughout the study, there were 4 ± 0.5 (min. = 1, max. = 11) males tagged with GPS transmitters per lek ($n = 28$ leks), which averaged $19 \pm 3\%$ of each lek's highest male count during 2011–2014. We recorded 214 interlek movements during 2011–2014 (Fig. 1) among 43 lek pairs (5 ± 1 interlek movement per lek pair with ≥ 1 interlek movement, min. = 1, max. = 26); 113 males never moved among leks and 56 (33%) males moved at least once. For males that moved among leks, 13 (23%) moved to a new lek only once, 22 (39%) moved between 2 leks ≤ 10 times, and 21 (38%) males moved among ≥ 3 leks ≤ 19 times.

The mean distance among closest neighboring leks (4.30 ± 0.38 km, min. = 1.46 km, max. = 8.61 km, median = 4.37 km) was less than the mean distance of interlek movements (5.95 ± 0.34 km, min. = 1.46 km, max. = 38.38 km, median = 4.38 km, $P_{85} = 0.002$, $t = 1.988$). Of 214 observed interlek movements by any male throughout 2011–2014, 50% of movements were to the closest lek, and an additional 28% were to the second closest lek. The average elevation gain during an interlek movement was 14 ± 9 m (min. = 286 m elevation loss, max. = 286 m elevation gain, median = 23 m elevation gain).

The daily interlek movement probability predicted from the top model (Table 2), which included year, day of year as a quadratic term, and elevation, was 0.003 (95% CI = 0.000–0.010) in 2011, and males were approximately 3.5 times more likely to move during 2013 (0.010 [95% CI = 0.001–0.021]) than 2011. Daily interlek movement probabilities in 2012 (0.006 [95% CI = 0.000–0.018]) and 2014 (0.006 [95% CI = 0.001–0.013]) were intermediate to 2011 and 2013. The

Table 2. Models describing factors influencing male greater sage–grouse daily interlek movement probabilities in and around The Overland Trail Ranch in Carbon County, Wyoming, USA, 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). Additionally, all models included 3 dummy variables to designate years as covariates, which are only shown in models including year variables as main effects in an interaction.

Model	DIC	ΔDIC	w_i
Date[a], date², elevation	2,337.9	0.0	0.710
Date, date²	2,340.8	2.9	0.167
Date, date², date × year 2012, date × year 2013, date × year 2014, date² × year 2012, date² × year 2013, date² × year 2014 (year 2012, year 2013, year 2014)	2,342.6	4.7	0.068
Capture season	2,343.6	5.7	0.041
Precipitation the day of movement	2,347.7	9.8	0.005
Date	2,348.0	10.1	0.005
Wind the day of movement	2,351.0	13.1	0.001
Age	2,351.7	13.8	0.001
Slope	2,352.0	14.1	0.001
Seasonal attendance rate	2,353.0	15.1	0.000
Elevation, date, date², elevation × date, elevation × date²	2,353.2	15.3	0.000
Precipitation the day before movement	2,353.3	15.4	0.000
Lek area	2,354.1	16.2	0.000
Elevation	2,354.4	16.5	0.000
Wind the day before movement	2,354.6	16.7	0.000
Lek area, elevation	2,354.6	16.7	0.000
Date, date × year 2012, date × year 2013, date × year 2014 (year 2012, year 2013, year 2014)	2,355.5	17.6	0.000
% sagebrush within 603 m of the lek, lek area	2,357.3	19.4	0.000
% sagebrush within 603 m of the lek	2,357.5	19.6	0.000
Elevation, date, elevation × date	2,358.6	20.7	0.000
Aspect	2,361.0	23.1	0.000
Max. F count	2,364.3	26.4	0.000
Max. M count	2,369.6	31.7	0.000

[a] Date = day of year.

Table 3. Parameter estimates for the models predicting male greater sage–grouse interlek movement probabilities 2011–2014 in and around the Overland Trail Ranch in Carbon County, Wyoming, USA. Included are the standard deviation for the estimate (SD), and lower and upper credible interval limits (LCI, UCI). Parameter estimates for random effects of individual grouse are not shown.

Predictor	Estimate	SD	LCI	UCI
Elevation, date, and date^2				
Intercept	−5.285	0.778	−6.786	−3.865
Year 2012	0.545	0.775	−0.935	2.080
Year 2013	0.902	0.759	−0.524	2.366
Year 2014	0.409	0.770	−1.028	1.902
Date[a]	−0.562	0.205	−0.986	−0.178
Date^2	−0.566	0.152	−0.874	−0.279
Elevation	0.046	0.082	−0.123	0.179

[a] Date = day of year.

average seasonal probability of moving to a new lek was lowest during 2011 (0.051 [95% CI = 0.006–0.178]) and 2012 (0.173 [95% CI = 0.013–0.421]) and increased each year subsequently (0.406 [95% CI = 0.047–0.692] in 2013, and 0.423 [95% CI = 0.081–0.686] in 2014). Daily survival was 0.995 (95% CI = 0993–0.996), which extrapolates to a 0.631 (95% CI = 0.524–0.692) survival rate from 1 March through 31 May.

Day of year strongly influenced interlek movements (Table 3). In 2011 daily interlek movement rates declined throughout spring, although we did not extrapolate predicted movement rates earlier than males were first captured, in late April (Fig. 2). In 2012–2014, interlek movements peaked on 6 March, which is early in the lek season. Males were 1.9–8.5 times more likely to move towards a high elevation lek (2,354 m, $\bar{x}$ + SD) than a low elevation lek (2,143 m, $\bar{x}$ − SD; Fig. 3). Extreme residuals indicated the model slightly over-predicted interlek movements and mortality, and under-predicted the number of time steps a male was in state Lek, but model fit was good (71% of residuals between −5 and 5; Fig. S1, available online in Supporting Information). The model estimated the number of days a male would be in state Alt.Lek adequately (Bayesian $P = 0.910$; Fig. S2, available online in Supporting Information).

Although no other models were competitive, other factors indicated interlek movement trends and provided novel information. There was a trend for males to move towards a larger lek, including leks with higher male counts, higher female counts, and larger areas. Males were 1.1 times more likely to move to a lek with 40 females than a lek with 0 females, 1.1 times more likely to move to a lek with 40 males than 0 males, and 1.1 times more likely to move to a larger lek ($\sim$268,000 m^2) than a smaller lek ($\sim$6,000 m^2). Sage-grouse were 1.2–1.3 times more likely to move among leks on days with no wind than days with winds 50–60 km/hour, and 1.7 times more likely to move on days with 0.5 cm precipitation than with no precipitation (Fig. 4). Although credible intervals for adult and yearling interlek movement rates overlapped substantially, adult males were 1.6–1.7 times more likely to move among leks than yearling males (Fig. 5). Because credible intervals largely overlapped, there was no substantial difference in the probability of an interlek movement for males that were captured in spring or fall.
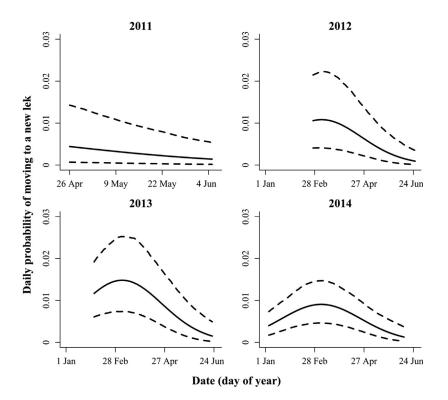

Figure 2. The influence of day of year on the probability of a male greater sage-grouse moving to a new lek in Carbon County, Wyoming, USA, 2011–2014. In 2011 we did not tag males before late April. Dotted lines depict 95% credible intervals around the solid line estimate.
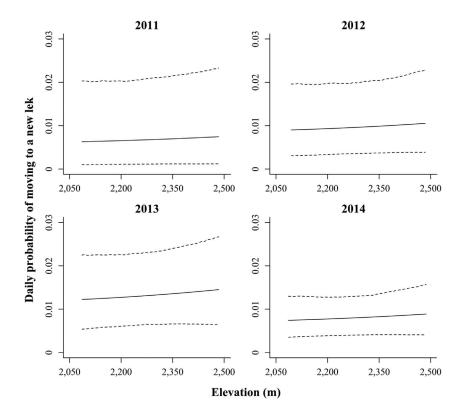
Figure 3. The influence of elevation on the probability of a male greater sage-grouse moving to a new lek in Carbon County, Wyoming, USA, 2011–2014. Dotted lines depict 95% credible intervals around the solid line estimate.
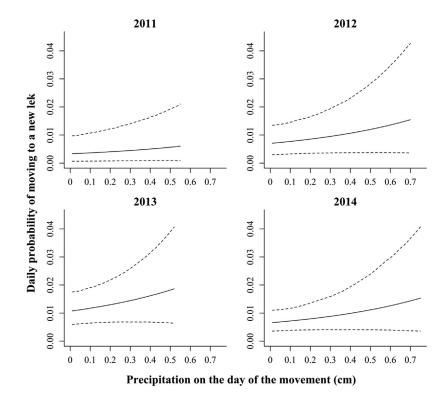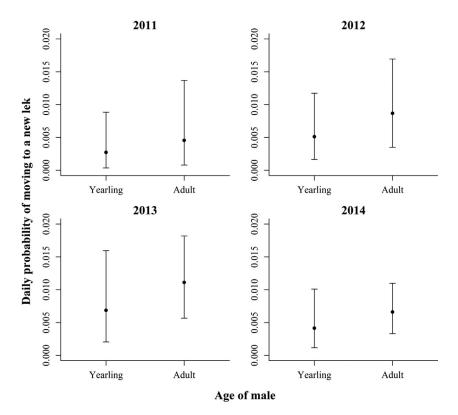

Figure 4. The influence of precipitation on the probability of a male greater sage–grouse moving to a new lek in Carbon County, Wyoming, USA, 2011–2014. Dotted lines depict 95% credible intervals around the solid line estimate.

Figure 5. The influence of male sage–grouse age on the probability of moving to a new lek in Carbon County, Wyoming, USA, 2011–2014. Dotted lines depict 95% credible intervals around the solid line estimate.

DISCUSSION

Male sage-grouse had high daily fidelity to leks with a ≤1% chance of an interlek movement. Males of lek-forming grouse species have high fidelity to leks for life (Campbell 1972, Dunn and Braun 1985, Schroeder and Braun 1992, Schroeder and Robb 2003, Walsh et al. 2010), resulting in high annual persistence of leks (Patterson 1952, Jenni and Hartzler 1978, Connelly et al. 2003). High daily lek fidelity helps males establish central territories, which are attractive to mates (Hovi et al. 1994) and males with high fidelity learn about local predators and competitors (Bergerud and Gratson 1988). Even infrequent interlek movements can be demographically impor- tant (Sedinger 2007) by affecting gene flow and influencing when males are available to breed at leks. Our models additionally calculated a daily survival rate. Extrapolating average daily survival to an annual rate indicates our study had lower survival than in other areas (Musil et al. 1993; Connelly et al. 2000, 2011; Zablan et al. 2003), but the annual survival rate was consistent with low sage-grouse survival in our study area as compared to other sites and times (Schreiber et al. 2016).

Although we observed high daily fidelity, 33% of males moved to another lek at least once during the breeding season, indicating interlek movements are more common than previously reported (Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985, Gibson et al. 2014), and reinforcing interlek movements as a critical component of lek ecology, especially for a species of conservation concern such as the greater sage-grouse. Previous research observed 15–27% of adult males on ≥2 leks

(Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985), and reported a 3% chance annually a male would move from the lek where it was captured (Gibson et al. 2014). Our estimates were likely higher because we knew where each bird was daily, whereas other studies relied on very high frequency telemetry (Wallestad and Schladweiler 1974, Emmons and Braun 1984, Dunn and Braun 1985) and resighting and recapturing banded birds (Gibson et al. 2014), which would result in substantially fewer opportunities to observe male sage-grouse interlek movements. Although we observed wide credible intervals around our seasonal interlek movement estimates (e.g., 95% CI = 0.081–0.686 for 2014), we believe the estimates are reasonable because 67% of the male-sage-grouse population never moved among leks, and 33% of males moved among leks, sometimes >10 times. The population itself had substantial variation in the frequency with which males would move among leks. Temporary absences from leks during counts, including absences due to an interlek movement, can explain 40% of the variation in annual lek counts (Blomberg et al. 2013); therefore, frequent annual interlek movements could affect the ability of managers to relate lek counts to population trends.

Lek counts likely do not accurately reflect population abundance when males move frequently, which occurs in areas with topographic relief as snowpack melts and males move to high elevation leks early in the breeding season. Immediately following substantial precipitation, we observed inflated high counts during lek counts at low elevation leks that received less precipitation, because birds moved among leks on days with

precipitation and temporarily attended leks at lower elevations. Interlek movements were more likely early in the breeding season, potentially because males initially displayed on low elevation leks and moved to favorable high elevation leks early in the breeding season as snowpack melted and weather conditions improved (Schroeder et al. 1999, Green 2006). Observers often count high elevation leks later in spring once snow melts and the leks become accessible, possibly as males move from low to high elevation leks, which could result in males being double counted. One assumption for lek counts is that males do not move among leks, and if they do, movement rates are equal to and from each lek (Sedinger 2007), but we observed trends of unequal movement to leks at high elevations, and to larger leks. Interlek movements contribute to an availability bias, in which males are not present at leks when counted, and the availability bias should be quantified to relate lek counts to population abundance (Diefenbach et al. 2007, Kéry and Schmidt 2008, Blomberg et al. 2013, Schmidt et al. 2013, WAFWA, 2015).

Interlek movements are affected primarily by time of year and elevation, but trends indicate other factors influence movements as well, such as lek size. Male birds in lek-mating systems may prefer to move to larger leks partially as a result of conspecific attraction (Smith and Peacock 1990, Lank and Smith 1992, Alonso et al. 2004). Females may prefer larger leks because females can compare more males during a single lek visit, which results in higher female visitation and higher average male mating success for males displaying on larger leks (Alatalo et al. 1992, Lank and Smith 1992). Male sage-grouse may gather and display in areas of high female densities (i.e., hotspots) for access to more mates at the larger leks with higher female visitation, but males may experience greater competition for copulations (Beehler and Foster 1988, Bradbury et al. 1989). Males may also prefer to disperse to larger leks, which eventually can cause smaller leks to be abandoned if no males disperse to smaller leks (Alonso et al. 2004). Alternatively, males may move to larger leks with more males to display near a dominant hotshot male, which can improve subordinate male's survival and displays, and subordinates may be able to move into the dominant male's territory when the dominant male dies, potentially allowing the subordinate male to receive more copulations (Beehler and Foster 1988).

Adult males were slightly more likely to move among leks than yearling males, although all ages displayed high fidelity to leks. Heavier, dominant adult males attend leks frequently and are more likely to mate and establish successful territories on a lek than yearlings (Beck and Braun 1978, Vehrencamp et al. 1989), and are unlikely to provide gene flow among leks because they have high lek fidelity, although they strongly contribute to the reproductive success at 1 lek. Although adult males were slightly more likely to move among leks more often than yearling males, gene flow primarily occurs from dispersing yearlings (Bush et al. 2010) and frequent female interlek movements (Wallestad and Schladweiler 1974). Yearling males are usually smaller, attend leks less frequently, 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), and yearling males

move among leks more than adults (Schoenberg 1982, Emmons and Braun 1984, Schroeder and Robb 2003) except in Nevada and our study area, where there were no difference in movement rates based on age (Gibson et al. 2014). Strong lek fidelity by dominant males may explain why lek abandonment occurs slowly in oil and gas developments. Adult males return to leks for years after development until death and leks are abandoned after yearling males stop dispersing to disturbed leks (Holloran 2005, Walker et al. 2007, Holloran et al. 2010), potentially because leks near development have greater fragmentation and may have fewer attending males and females. Fragmentation from fires, agriculture, or energy development and the resulting lower sagebrush vegetation around leks may cause declines in sage-grouse populations (Smith et al. 2005, Hess and Beck 2012). Similarly, local blue grouse (*Dendragapus obscurus fuliginosus*) populations are often extirpated after their habitat is altered because adults remain in their territories until death even after the area has become unsuitable, and yearling males stop dispersing to those areas (Bendell and Elliott 1966, Zwickel and Bendell 1985). Interlek movements should be monitored for changes following disturbances, which could result in long-term declines in reproductive success at leks and lowered lek persistence.

MANAGEMENT IMPLICATIONS

Because interlek movements occur most frequently early in spring and alter availability for detection, lek counts in early March may not accurately reflect population abundance in our study area. To maximize availability for detection and minimize double-counting males, lek counts should occur later in the season around the peak of attendance (mid Apr) rather than when interlek movements are frequent (early Mar). Managers should also consider topography and recent weather events to avoid counts when males may move from high to low elevation leks. Because males have high site fidelity, it is important to assess interlek movements for many years to assess impacts from disturbance.

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