Journal of Wildlife Management 75(2):311–318; 2011; DOI: 10.1002/jwmg.42

Research Article

Sharp-Tailed Grouse Lek Attendance and Fidelity in Upper Michigan

THOMAS D. DRUMMER,[1] *Department of Mathematical Sciences, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, USA*

R. GREGORY CORACEIII, *U.S. Fish and Wildlife Service, Seney National Wildlife Refuge, Seney, MI 49883, USA*

STEPHEN J. SJOGREN, *U.S. Forest Service, Hiawatha National Forest, St. Ignace, MI 49781, USA*

ABSTRACT To assess and improve existing monitoring protocols for sharp-tailed grouse (*Tympanuchus phasianellus*) in the eastern Upper Peninsula of Michigan, we used data from 58 radio-collared grouse (46 M, 12 F) monitored within 3 openland landscape types: a xeric, conifer-dominated site, a wetland-dominated site, and a site dominated by low-intensity agriculture. We used lek counts and radio telemetry to determine lek attendance rates, factors affecting lek attendance rates, lek fidelity, and inter-sexual variation in these parameters. Our analysis indicated lek attendance varied with respect to sex of bird, day of year, time after sunrise, and wind speed. Peak male lek attendance rates exceeded those of females by up to 40%, and peak lekking activity for both males and females occurred during the second and third weeks of April. Male lekking activity occurred earlier and was sustained longer than that of females. Lekking activity was negatively related to time of day and wind speed. We observed strong lek fidelity as radio-collared birds attended a primary lek 94% of the time, indicating a low probability of multiple counting of individual birds. We also proposed a method to adjust lek count data for the probability that birds are on a lek during lek counts. Our proposed method can be used by researchers and managers to improve estimates of the number of birds attending a lek by reducing the negative bias associated with observed counts.

KEY WORDS lek attendance, lek fidelity, sharp-tailed grouse, upper Michigan.

Throughout much of their range, populations of sharp-tailed grouse (*Tympanuchus phasianellus*) are experiencing long-term declines (Gregg and Niemuth 2000, Samson et al. 2003, Silvy and Hagen 2004). Although conserving and restoring habitat for this species has been the objective of numerous research projects and management efforts, more study of the efficacy of sharp-tailed grouse monitoring efforts is needed, as habitat management is often evaluated based on population estimates derived from monitoring. In Michigan, at the eastern periphery for sharp-tailed grouse in the United States, the distribution and population size of sharp-tailed grouse fluctuated greatly over the past century (Ammann 1957, Brewer et al. 1991, Connelly et al. 1998, Silvy and Hagen 2004). Pre-European patterns of suitable cover types and disturbance regimes suggest a potentially broad distribution in the state (Peterle 1954, Ammann 1957, Brewer et al. 1991, Monfils 2007). The first official documentation of sharp-tailed grouse occurred on Isle Royale in 1904 (Barrows 1912). Subsequently, as lands were opened by logging and agricultural development during the early 20th century, the number of birds increased and a legal hunting season was established (Ammann 1957, Losey et al. 2007).

By the 1930s, the sharp-tailed grouse was a popular game species and received considerable management attention (Ammann 1957, Losey et al. 2007). Concomitantly, the Michigan Department of Natural Resources and Environment (MDNRE) began conducting lek (dancing ground) surveys in 1937. Although these surveys were halted during World War II, they resumed in 1946 and continue today (Maples and Soulliere 1996). However, in the interim, considerable change in the regional landscape occurred and sharp-tailed grouse habitat was reduced in extent and distribution due to vegetative succession, fire suppression, disadvantageously placed plantations, and intensified agriculture. In response to an apparent decline in sharp-tailed grouse abundance, MDNRE prohibited the hunting of sharp-tailed grouse in 1996. However, renewed efforts at managing habitat in the eastern Upper Peninsula (UP) and a recently proposed reopening of a hunting season have stimulated the need for improvement of the sharp-tailed grouse monitoring program.

Using MDNRE protocols, past efforts to monitor sharp-tailed grouse in the UP consisted of identifying occupied areas and leks and determining the mean number of birds flushed at known leks. For each count observers recorded the number of males (dancing birds) and females (non-dancing birds) and general weather conditions. Observers were instructed not to conduct counts during periods of heavy rain or high winds. However, these lek searches and surveys were not conducted using rigorous statistical protocols.

Other researchers have suggested that due to problems with the conversion of lek count data into abundance estimates, these data were best used as an abundance index (Applegate 2000). As with all abundance indices, users must assume that there is a correlation between the index and the true

Received: 5 August 2009; Accepted: 29 July 2010

[1]*E-mail: tdrummer@mtu.edu*

abundance, but this assumption can be difficult to validate (Thompson et al. 1998). Moreover, use of the mean number of birds per lek as an abundance index is problematical because that statistic does not reflect possible fluctuations in the number of leks. Research in northeastern Colorado indicated that about 23% of greater prairie chicken (*Tympanuchus cupido*) leks disappeared between years (Schroeder and Braun 1992).

To assess and improve monitoring protocols for sharp-tailed grouse in the eastern UP of Michigan, we studied 2 aspects of using lek count data to monitor abundance: lek attendance rates and lek fidelity. Lek attendance rate refers to the probability that a bird is on a lek when lek counts are conducted, and lek fidelity refers to the likelihood that a bird attends only 1 lek. Lek attendance <100% would imply that some birds are uncounted, and lek fidelity <100% would imply that birds attend >1 lek and could be counted multiple times, with bias resulting in either case. Previous studies suggest that lek attendance probability varies seasonally and with time of day. In a study of radio-collared male sage grouse (*Centrocercus urophasianus*) in Colorado, researchers observed seasonal patterns in lek attendance probabilities, with peak lek attendance rates >90% (Emmons and Braun 1984). Counts of male sage grouse in Montana varied with respect to time of day and day of year, but without radio-collared birds the actual lek attendance probability could not be estimated (Jenni and Hartzler 1978). In Colorado, lek attendance rates of radio-collared male greater prairie chickens varied seasonally and peaked at 95% (Schroeder and Braun 1992). An evaluation of lek counts as an index for the abundance of sage grouse concluded that lek counts should be adjusted for the probability that birds visit leks (Walsh et al. 2004). This is the same approach used with sightability models which are used to adjust counts from aerial surveys for sighting probability (Steinhorst and Samuels 1989). Our objectives were 1) to construct a lek attendance model for adjusting lek counts for the probability of birds being on a lek and 2) to estimate fidelity of birds to a primary lek.

STUDY AREA

Sjogren and Robinson (1997) found that sharp-tailed grouse in the eastern UP occupied an annual home range of approximately 641 ha, usually comprised of xeric, conifer-dominated openings, large clear-cuts, low-intensity managed agricultural lands, or open wetlands. Consequently, we conducted our study among 3 sites of the eastern UP of Michigan that represented the 3 major openland ecosystem types used by sharp-tailed grouse. The Raco plains (RACO) was a xeric, conifer-dominated site managed by the United States Forest Service, Hiawatha National Forest. Seney National Wildlife Refuge (SNWR) was an open wetland-dominated site managed by the United States Fish and Wildlife Service, and AGLANDS was a low-intensity managed agriculture site that was predominately privately owned (Fig. 1). Row crops, a common openland type elsewhere in Michigan, was not a major constituent of the agricultural lands, but rather these areas were dominated by low-intensity managed hayfields (Corace et al. 2009). Many (if not most) sharp-tailed grouse in the eastern UP inhabit these sites and adjacent areas (S.J. Sjogren, U. S. Forest Service,

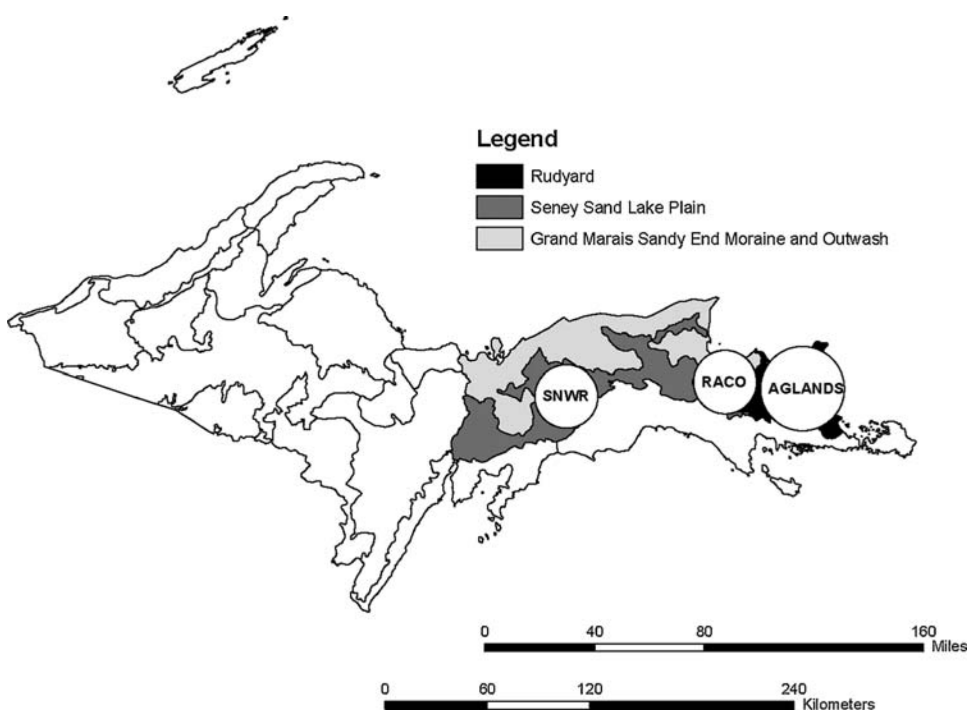

Figure 1. Sharp-tailed grouse study sites in the eastern Upper Peninsula of Michigan and their associated ecoregions (Albert 1995). RACO refers to the Raco Plains in Hiawatha National Forest; SNWR refers to Seney National Wildlife Refuge; AGLANDS refers to the agricultural area in Chippewa and Mackinaw counties.

unpublished report). Although openland is found on only about 10% (235,000 ha) of the land area of the primarily forested eastern UP, these 3 openland types accounted for up to 26% of the study sites (Corace 2007).

The climate of the eastern UP was strongly influenced by the Great Lakes. Temperatures were moderated by Lake Huron, Lake Michigan, and Lake Superior. Lake effect snow and rain were common with precipitation evenly distributed within the year. A detailed description of the climate, bedrock geology, landforms, soils, and presettlement and present day vegetation of the eastern UP was provided by Albert (1995).

METHODS

Capture and Telemetry Relocation

To capture birds we used a combination of mist nets and baited 1.0-m × 1.5-m × 0.5-m rectangular-shaped walk in traps consisting of metal wire and nylon netting fastened to a plywood base (Kutz 1945). At one end of each trap we cut a funneled opening for bird entry. We trapped at AGLANDS site primarily off leks near bird feeding sites, and ease of access meant that trapping began earliest at this site. Trapping started between 14 February and 13 April and continued until 7 May. We had limited trapping success with walk-in traps at RACO and SNWR and instead used mist nets. We captured most birds at these sites <100 m from leks. We attempted to age birds based on condition of feathers (Henderson et al. 1967), but decided that age data were not reliable. We fitted birds with avian necklace collars that weighed 16 g and had an expected lifetime >500 days (Advanced Telemetry Systems, Isanti, MN).

We located radio-collared birds via telemetry 3–4 times per week during the lekking season (Apr–May) of 2005–2007, avoiding extreme weather conditions (e.g., consistent rain, wind speeds >30 km/hr). We started telemetry relocation as soon as we collared birds and continued until mid-May when past experiences have shown lekking activity ends. Around the perimeter of each trapping or netting location we established fixed locations using Global Positioning System (GPS) units. Observers estimated the azimuth of the location of the bird with a compass based on the strength of signal, and recorded date, time, wind speed, and wind direction. Observers determined if the bird being monitored was or was not on a known lek based on visual observation, but this determination was not always possible for several reasons, including distance to the lek and obstructed views of the lek. If presence or absence on a lek could not be determined, we did not use that observation in the telemetry data analysis. In some cases radio-collared birds could be seen and their location determined without error. In other cases, for birds with ≥3 telemetry points, we estimated bird locations and the 95% error ellipse with maximum likelihood estimation of Von Mise distribution parameters (Lenth 1981). We used estimated locations primarily for home range mapping and as a check of the accuracy of observers in classifying birds as being on or off leks, but we did not reclassify lek status based on an estimated location. If we had doubts as to the accuracy of the lek status we dropped that data point, but this occurred rarely (<1% of observations).

Lek Counts Data and Analysis

Using existing MDNRE protocols we conducted lek counts at leks near capture sites within each of the 3 study areas in conjunction with the collection of telemetry data. We used the lek count data to assess patterns of lek attendance, for illustration of the adjusted counts method, and to collect data for planning future surveys. Each lek count consisted of a 15-min visit during which the observer recorded date, time of day, wind speed and direction, and the number of dancing birds (assumed to be males). At the end of the 15-min period the observer approached the lek and flushed and counted all birds. While visiting the lek, the observer also inspected birds with a spotting scope and via telemetry to document presence of radio-collared birds. We conducted all lek counts between sunrise and 1,000 hr and concluded them by 15 May, per MDNRE guidelines.

We conducted lek counts at 28 spatially explicit leks among the 3 study sites. Monitored leks within sites were clustered (<8 km apart) because we concentrated trapping in small areas within each year. At SNWR we monitored the same 4 leks each year. At the RACO and AGLANDS sites we changed some leks between years so as to maximize the generalizability of the data. At AGLANDS we monitored 14 different leks over 3 yr, with 5 leks monitored in >1 yr. We monitored 10 leks at RACO; 4 in 2005, 3 in 2006, and 4 in 2007, with 1 lek monitored in 2 yr. We attempted to conduct multiple counts at each lek each year, but in 5 instances we only conducted 1 lek count within a year. In all other cases each lek had >2 lek counts, with 70% of leks counted ≥4 times in a year. We conducted 124 lek counts in 2005, 78 in 2006, and 75 in 2007.

We used regression analysis of the lek count data to build a descriptive model of lek attendance patterns with respect to day of year, time of day, and wind speed. We pooled data across sites and years and used the total number of flushed birds as the dependent variable. Based on our experience and MDNRE protocols, we restricted our analysis to lek counts conducted after 1 April, within 3 hr of sunrise, and when wind speeds were <30 km/hr. We first checked for correlations among the independent variables to assess possible collinearity. We fit a negative binomial regression model that included polynomial terms for day of year, time after sunrise, and wind speed, as well as cross products between these terms. We also included a term to account for variability between leks. We used the negative binomial model to allow for possible over-dispersion (Myers et al. 2002). We ranked models based on Akaike's Information Criteria (AIC) value (Burnham and Anderson 2002). We assessed model adequacy using Pearson residual plots and the Pearson chi-square goodness-of-fit statistic (Myers et al. 2002).

Lek Attendance Model

We pooled telemetry data across all study sites and years and used data points on individual birds temporally separated by ≥24 hr. We only used those estimated locations with an error polygon size <1.0 ha. The dependent variable was the binary variable indicating if a bird was on or off a lek and explanatory variables were sex of the bird, day of year, time after sunrise, and wind speed. In the model selection process we included polynomial terms for day of year, time after sunrise, and wind speed, as well as cross products between these terms. We also included cross products between gender and all other explanatory variables.

Because the data were repeated observations of individual birds that we could not consider independent, we fit longitudinal logistic regression models. These models require specification of a dependence structure among repeated observations on individuals while assuming independence among individuals. Because the response variable was binary, linear correlation measures used for continuous responses were not appropriate measures of dependence. We therefore used the natural logarithm of the odds ratio of lek attendance between successive observations of an individual as the measure of dependence (Fitzmaurice et al. 2004). The odds ratio equaled $P_{11}\,P_{01}/P_{10}\,P_{00}$ where P denotes the probability of being on a lek, the first subscript denotes current lek status ($1 =$ on lek, $0 =$ off lek), and the second subscript denotes previous lek status. A positive value of this parameter indicates that a bird was more likely to be on a lek if it was previously on a lek, and a negative value indicates a bird was less likely to be on a lek if it was previously on a lek. We fit models that varied the odds ratio by gender of the bird as well as models with the same odds ratio for males and females.

Standard information based measures such as AIC are not available for model selection because longitudinal models are fit with generalized estimating equations rather than maximum likelihood. To rank models based on model fit and correlation structure adequacy we used the quasi-likelihood information criteria (QIC, Pan 2001). Smaller values of QIC indicate a better model fit. After model selection we tested for a size effect by including the weight of the bird in the model. Due to a small sample size for females we restricted this analysis to male birds. We fit all models with SAS PROC GENMOD (SAS Institute, Inc., Cary, NC).

We used the final lek attendance model to estimate the mean number of birds attending leks we monitored. We restricted this analysis to 11 leks with $\geq$2 counts within the same year conducted under moderate conditions: wind speed <25 km/hr, within 3 hr of sunrise, and between 8 April and 30 April. We computed number of females as number of birds flushed minus the number of dancing males. We compared mean adjusted and mean observed counts to assess the effect of adjusting counts.

Lek Fidelity

Birds visiting multiple leks could result in multiple counting of individuals and bias an abundance estimate, with lower levels of lek fidelity presumably resulting in greater bias. To estimate lek fidelity we used data from both lek counts and telemetry location trials and regarded individual birds as the sampling unit. For each collared bird within each year we determined which leks each bird was located on and defined the primary lek as the lek on which we most often found the bird. For birds with >1 location in a year, we defined lek fidelity as the proportion of locations we found the bird on its primary lek. We assessed lek fidelity annually because although we observed some birds in >1 yr, whether or not a bird switched leks between years would be immaterial to an annual abundance estimate. To estimate overall lek fidelity we pooled data across birds, sites, and years and used the ratio estimator $\hat{R} = \sum_{i=1}^{n} x_i \big/ \sum_{i=1}^{n} y_i$ where x_i denotes the number of observations of the ith bird on its primary lek and y_i denotes the total number of observations of the ith bird on leks. We estimated sampling variances using the ratio estimator variance (Cochran 1977). Sample size for each estimate was the number of birds observed. We estimated overall fidelity for males and females combined and separately although the sample size for female birds was small. We estimated year and site-specific fidelity to assess temporal and spatial variability.

RESULTS

Capture and Telemetry Relocation

We captured 99 birds (76 M, 23 F). We captured 19 birds in February, all at AGLANDS. We captured 17 birds in March, some at each study site, and we captured the remaining birds after 1 April. We did not observe some collared birds due to collar failure, emigration, or predation, so those birds yielded little or no data. We observed mortality for 8 females and 16 males.

We obtained 737 telemetry observations of radio-collared birds, but our effective sample size was $n = 424$ from 58 birds. In 143 of the 737 telemetry observations the location estimation algorithm did not converge and location estimation was not possible, usually when the bird was at a greater distance from the lek than was typical or when the bird was moving. We could not determine lek status of the bird for 133 other observations for unknown reasons and we dropped 37 observations due to failure to record $\geq$1 variables, most often wind speed. Thus our total usable sample size was $n = 424$, consisting of $n = 186$ at RACO, $n = 51$ at SNWR, and $n = 187$ at AGLANDS. In these observations, we located the collared bird on a lek 69% of the time. We obtained only 49 observations of females from 12 birds, and the remainder of the observations came from 46 male birds. Data were sparse during the first 2 weeks of April ($n = 46$), with female data especially sparse during that period. Some observations occurred well after sunrise but 75% of observations occurred within 3 hr after sunrise. Nearly all (98%) observations occurred at wind speeds <25 km/hr. We sighted the bird on a lek in 99% of observations in which we classified birds as being on a lek.

Lek Count Data and Analysis

In the regression analysis we used 277 lek counts from 28 leks pooled over the 3 study sites and years. Number of counts per lek varied, ranging from 1 to 24, and the number of birds flushed varied among leks ($P < 0.001$). There was little collinearity among independent variables, as no correlation exceeded 0.14 in magnitude. Based on the AIC ranking, the

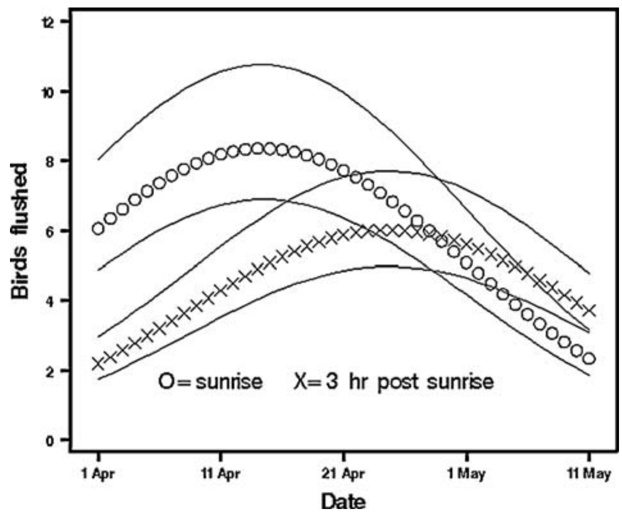

Figure 2. Predicted mean lek count (±SE) by date from negative binomial regression model fit to 277 lek counts of sharp-tailed grouse from 28 leks counted during 2005–2007 in the eastern Upper Peninsula of Michigan.

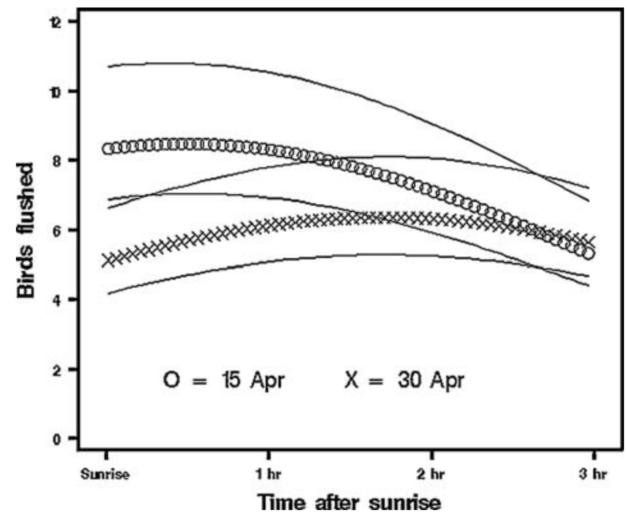

Figure 3. Predicted mean lek count (±SE) by time after sunrise from negative binomial regression model fit to 277 lek counts of sharp-tailed grouse from 28 leks counted during 2005–2007 in the eastern Upper Peninsula of Michigan.

best approximating model for the mean count was

$$\log(\text{count}) = \beta_0 + \beta_1\text{Date} + \beta_2\text{Date}^2 + \beta_3\text{Time} + \beta_4\text{Time}^2 + \beta_5\text{Date} \times \text{Time}$$

where Date denotes day of year and Time denotes time after sunrise. Residual plots did not indicate any model inadequacy, and the Pearson statistic ($\chi^2_{244} = 243.8$, $P = 0.49$) indicated an adequate fit. Whenever Wind was included in the model the AIC value worsened so we dropped the Wind term. The second best model (ΔAIC = 8.56) was similar to the best model but did not include the cross-product term Date × Time. The third best model (ΔAIC = 11.99) included only Date, Date^2, and Time. We also added higher order interaction terms Date × Time^2 and Date^2 × Time^2 to our selected model but these did not improve the AIC value.

Counts at sunrise peaked mid-April but counts conducted later in the day tended to peak later in the lekking period (Fig. 2). Fixing the Date and varying Time indicated that lek counts decreased after sunrise in mid-April, but late April lek counts increased slightly after sunrise (Fig. 3).

Lek Attendance Model

Correlations among variables were minimal: the strongest correlation ($r = 0.30$) was between day of year and time after sunrise. There was little difference in QIC values for the top 5 ranked models (Table 1). We selected the logit scale model

$$\beta_0 + \beta_1 G + \beta_2\text{Date} + \beta_3\text{Date}^2 + \beta_4 G \times \text{Date} + \beta_5\text{Wind} + \beta_6\text{Time} + \beta_7\text{Time}^2$$

where G is the binary gender variable, Date denotes day of year, Time denotes time after sunrise, and Wind denotes wind speed. We selected the second ranked model because the confidence interval for the Gender × Wind coefficient in the first ranked model overlapped zero. For this model the estimated log(odds ratio) parameter for females was 2.06 (SE = 0.51, $P < 0.001$) and for males 0.54 (SE = 0.26, $P = 0.03$). Positive values indicate that a bird that previously visited a lek was likely to continue to visit leks. Magnitudes of these estimates appear to indicate that this response was stronger in females than males. When we fit models forcing these parameters to be equal for males and females the increase in QIC values was negligible (ΔQIC < 0.10), so we could not conclude that male and female responses were different. From the final model, probability of lek attendance for males exceeded 80% starting about 10 April (depending on weather) and remained high into early May, whereas female lek attendance peaked mid-April but declined quickly thereafter (Fig. 4). Male lek attendance probability was constant from sunrise to 3 hr postsunrise, whereas lek attendance probability for females increased slightly after sunrise before declining (Fig. 5). Probability of lek attendance declined with increased wind speed for both males and females (Fig. 6). We found no evidence of a size effect in male birds ($P > 0.05$).

Applying the final lek attendance model to the lek count data resulted in a substantial increase in (adjusted) mean birds per lek. Mean number of birds observed per lek was 9.0 and mean adjusted count was 16.6. Most of this increase was

Table 1. Differences in quasi-likelihood values (ΔQIC) for the 6 best-fitting longitudinal logistic regression models of sharp-tailed grouse lek attendance as a function of gender (G), time after sunrise (T), day of year (D), and wind speed (W) based on 424 locations of 58 radio-collared birds in the eastern Upper Peninsula of Michigan, (2005–2007). Models included gender-specific dependence structure.

Model rank	Variables	ΔQIC
1	$G, D, D^2, G \times D, W, T, T^2, G \times W$	0.00
2	$G, D, D^2, G \times D, W, T, T^2$	0.59
3	$G, D, D^2, G \times D, W, T, T^2, T \times D$	0.71
4	$G, D, D^2, G \times D, W, T, T^2, G \times W, G \times T$	1.30
5	$G, D, D^2, G \times T, W, T, T^2$	1.56
6	$G, D, D^2, G \times D, T, T^2$	6.48

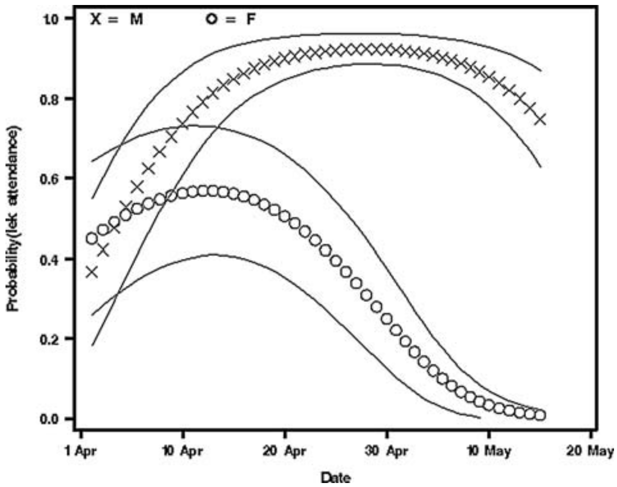

Figure 4. Predicted probability (±SE) of lek attendance by date for male and female sharp-tailed grouse from longitudinal logistic regression model fit to 424 observations of 58 radio-collared birds grouse in the eastern Upper Peninsula of Michigan. We fixed wind speed at 0.0 km/hr.

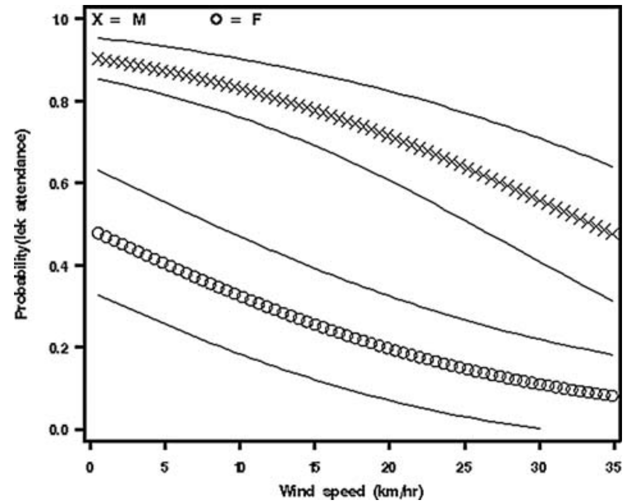

Figure 6. Predicted probability (±SE) of lek attendance by wind speed for male and female sharp-tailed grouse from longitudinal logistic regression model fit to 424 observations of 58 radio-collared birds in the eastern Upper Peninsula of Michigan. We fixed time of day to sunrise and date at 20 April.

due to adjusted counts of females. Mean number of males observed per lek was 4.8 with a mean adjusted count of 5.5. For females respective means were 4.2 and 11.1. The number of counts per lek ranged from 2 to 6 ($\bar{x} = 3.8$).

Lek Fidelity

We observed strong fidelity to a primary lek at all sites and in all years. Based on 796 sightings of birds on leks, overall estimated lek fidelity for males was 0.95 (SE = 0.02, $n = 67$ birds). The sample size exceeded the number of collared birds because we observed some birds in >1 yr. For females estimated lek fidelity was 0.81 (SE = 0.10, $n = 10$ birds), although this estimate was based on only 55 observations of birds on leks. For males and females pooled, lek fidelity was 0.94 (SE = 0.02, $n = 77$). We observed lowest lek fidelity by site at RACO ($\hat{R} = 0.90$, SE = 0.03, $n = 23$), compared to 0.98 at SNWR (SE = 0.02, $n = 22$) and 0.96 at AGLANDS (SE = 0.02, $n = 32$). There was some inter-annual variation with lowest lek fidelity of 0.86 in 2005 (SE = 0.04, $n = 21$) compared with lek fidelity of 0.97 in both 2006 (SE = 0.02, $n = 34$) and 2007 (SE = 0.02, $n = 22$). Standard errors for estimates were small due to the large positive correlation ($r > 0.9$ in all cases) between x_i and y_i in the ratio estimates. We did not observe any birds on >2 leks. On 2 occasions we observed a male bird visiting 2 leks on the same day.

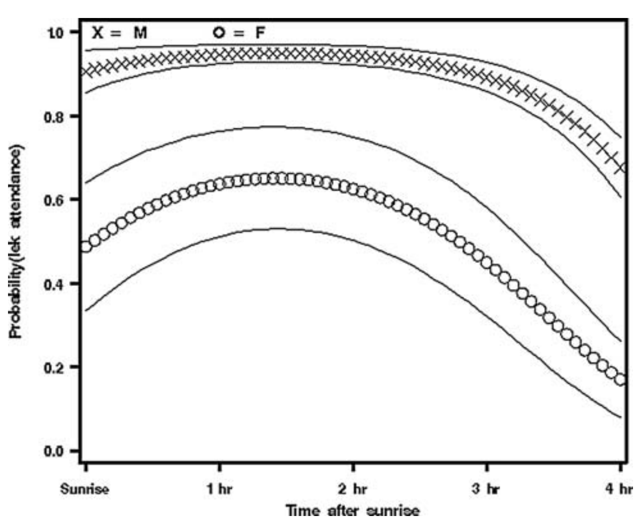

Figure 5. Predicted probability (±SE) of lek attendance by time after sunrise for male and female sharp-tailed grouse from longitudinal logistic regression model fit to 424 observations of 58 radio-collared birds in the eastern Upper Peninsula of Michigan. We fixed wind speed at 0.0 km/hr and date at 20 April.

DISCUSSION

We observed strong lek fidelity to a primary lek, so the potential effect of multiple counting of birds does not seem large, although lek fidelity could change if lek density changes. We observed one bird visiting 2 leks 12 km apart, so considerable movement is possible. For now we believe the effect of inter-lek movement can be mitigated by surveying nearby leks within a short time interval. To obtain reliable estimates of birds per lek we recommend that the lek attendance model only be applied when probability of lek attendance is high. When probability of lek attendance is small the adjustment factor is large, which tends to increase the variance of the adjusted count (Williams et al. 2001).

We pooled data across sites thereby assuming that the same lek attendance model was applicable at all 3 sites. We did not test for site (habitat) effects in lek attendance because the data were temporally unbalanced across sites, with most of the early lekking season data from the AGLANDS site. Consequently a hypothesis test comparing sites would also compare lek attendance at different stages of the lekking season and would be difficult to interpret.

A potential source of bias in estimating lek attendance was trapping birds that were more (or less) likely to attend leks than were randomly selected birds. For example, birds we captured near leks could have higher lek attendance rates than birds trapped off leks. We trapped most of the birds we captured at the AGLANDS off leks near winter feeding stations, whereas we trapped most birds at SNWR and RACO close to leks later in the lekking season. Previous research on greater prairie chickens in Colorado indicated that male birds captured prior to lekking in winter had higher lek attendance rates (97%) than birds captured later near leks (93%; Schroeder and Braun 1992). We observed a similar effect in our data, with a 5% higher lek attendance rate for birds captured in mid-February compared to birds captured mid-April. But birds captured prior to peak lekking had more opportunity to lek, and it seems counter-intuitive that birds captured near leks would have a lower lek attendance rate than birds captured off leks. We therefore discount trap location and date of capture as possible sources of bias. Also, we observed similar day of year and time of day patterns in the telemetry and lek count data which we believe increases the credibility of the telemetry data.

Other possible sources of variability in lek attendance include attributes of individual birds such as gender, age, and size of bird. We observed a strong gender effect, and application of our model requires accurate gender identification of birds, with substantial bias resulting otherwise. Our inability to age birds prevented us from testing for an age effect, and we found no evidence of a size effect in males. Even if we found individual covariates to have an effect, we could only use them in adjusted counts if they were measurable for un-collared birds on leks, which does not seem likely.

We proposed a method to estimate the number of birds attending a lek. To estimate abundance the number of leks must be known or estimated. Other researchers have investigated estimation of the number of leks. In Oklahoma aerial and ground surveys were used to determine how the cumulative number of aerial surveys affected the proportion of greater prairie chicken leks sighted (Martin and Knopf 1981). A capture–recapture type estimator with collared birds was used to estimate the number of sage grouse leks in Colorado (Walsh 2002). Use of repeated aerial surveys to estimate the number of greater and lesser prairie chicken (*Tympanuchus pallidicinctus*) leks was investigated by Schroeder et al. (1992). In all cases, a correction factor for the probability of lek detection could have been developed and used in future surveys.

MANAGEMENT IMPLICATIONS

The high lek fidelity and high lek attendance rates of male sharp-tailed grouse in our study indicate that accurate counts of lekking males may yield a useful index of male abundance if possible change in the number of leks is also considered. Application of our lek visitation model to lek counts can be used to estimate abundance if an estimate of the number of leks is available. In Upper Michigan we recommend that lek counts be conducted within 3 hr of sunrise, between 8 and 30 April, and when wind speeds are <25 km/hr. Our method required the capture and radio-collaring of birds, but it may be possible to use other identifying marks on birds that cost less than radio-collars.

ACKNOWLEDGMENTS

This work was funded by the MDNRE, the United States Forest Service Hiawatha National Forest, the United States Fish and Wildlife Service Seney National Wildlife Refuge, the Seney Natural History Association, and the UP Sustainable Forest and Wildlife Fund. Those who assisted with data collection and assimilation include E. Brosnan, K. Henslee, B. Johnson, D. McCormick, D. Munson, J. Patton, J. Patton, J. Polasik, J. Reattoir, J. Reis, S. Rouser, W. Sterling, K. Traylor, and H. Whitman. We thank the Michigan Sharp-tailed Grouse Association for their enthusiasm and encouragement. We also thank the reviewers and Associate Editor whose comments greatly improved this manuscript. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the United States Fish and Wildlife Service or the United States Forest Service.

LITERATURE CITED

Albert, D. A. 1995. Regional landscape ecosystems of Michigan, Minnesota and Wisconsin: a working map and classification. U.S. Forest Service Report NC-178. North Central Research Station, St. Paul, Minnesota, USA.

Ammann, G. A. 1957. The prairie grouse of Michigan. Michigan Department of Conservation Technical Bulletin, Lansing, Michigan, USA.

Applegate, R. D. 2000. Use and misuse of prairie chicken lek surveys. Wildlife Society Bulletin 28:457–463.

Barrows, W. B. 1912. Michigan bird life. Michigan Agricultural College, East Lansing, USA.

Brewer, R., G. A. McPeek, and R. J. Adams, Jr. 1991. The atlas of breeding birds of Michigan. Michigan State University Press, East Lansing, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. Springer Verlag, New York, New York, USA.

Cochran, W. G. 1977. Sampling techniques. Third edition. Wiley, New York, New York, USA.

Connelly, J. W., M. W. Gratson, and K. P. Reese. 1998. Sharp-tailed grouse (*Tympanuchus phasianellus*). The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

Corace, R. G. III. 2007. Using multiple spatial scales to prioritize openland bird conservation in the Midwest. Dissertation, Michigan Technological University, Houghton, USA.

Corace, R. G. III, D. J. Flaspohler, and L. M. Shartell. 2009. Geographic patterns in openland cover and hayfield mowing in the Upper Great Lakes region: implications for grassland bird conservation. Landscape Ecology 24:309–323.

Emmons, S. R., and C. E. Braun. 1984. Lek attendance of male sage grouse. Journal of Wildlife Management 48:1023–1027.

Fitzmaurice, G. M., N. M. Laird, and J. H. Ware. 2004. Applied longitudinal analysis. Wiley, New York, New York, USA.

Gregg, L. E., and N. D. Niemuth. 2000. History, status, and management of sharp-tailed grouse in Wisconsin. Passenger Pigeon 62:159–164.

Henderson, F. R., F. W. Brooks, and R. B. Dahlgren. 1967. Sexing prairie grouse by crown feather patterns. Journal of Wildlife Management 31:764–769.

Jenni, D. A., and J. E. Hartzler. 1978. Attendance at a sage grouse lek: implications for spring censuses. Journal of Wildlife Management 42:46–52.

Kutz, H. L. 1945. An improved game bird trap. Journal of Wildlife Management 9:35–38.

Lenth, R. V. 1981. On finding the source of a signal. Technometrics 23:149–154.

Losey, E. B., B. R. Deemer, and R. G. Corace, III. 2007. History of sharp-tailed grouse (*Tympanuchus phasianellus*) at Seney National Wildlife Refuge and surrounding areas, Schoolcraft County, Michigan. Passenger Pigeon 69:339–348.

Maples, T. E., and G. J. Soulliere. 1996. Status of Michigan sharp-tailed grouse in the 1990's. Michigan Department of Natural Resources, Lansing, USA.
Martin, S. A., and F. L. Knopf. 1981. Aerial surveys of greater prairie chicken leks. Wildlife Society Bulletin 9:219–221.
Monfils, M. J. 2007. Special animal abstract for *Tympanuchus phasianellus* (sharp-tailed grouse). Michigan Natural Features Inventory, Lansing, USA.
Myers, R. H., D. C. Montgomery, and G. G. Vining. 2002. Generalized linear models. Wiley, New York, New York, USA.
Pan, W. 2001. Akaike's information criterion in generalized estimating equations. Biometrics 57:120–125.
Peterle, T. 1954. The sharp-tailed grouse in the Upper Peninsula of Michigan. University of Michigan, Ann Arbor, USA.
Samson, F. B., F. L. Knopf, C. W. McCarthy, B. R. Noon, W. R. Ostlie, S. M. Rinehart, S. Larson, G. E. Plumb, G. L. Schenbeck, D. N. Svinge, and T. W. Byer. 2003. Planning for population viability on Northern Great Plains national grasslands. Wildlife Society Bulletin 31:986–999.
Schroeder, M. A., and C. E. Braun. 1992. Greater prairie chicken attendance at leks and stability of leks in Colorado. Wilson Bulletin 104:273–284.
Schroeder, M. A., K. M. Giesen, and C. E. Braun. 1992. Use of helicopters for estimating numbers of greater and lesser prairie-chicken leks in eastern Colorado. Wildlife Society Bulletin 20:106–113.
Silvy, N. J., and C. A. Hagen. 2004. Management of imperiled grouse species and their habitat. Wildlife Society Bulletin 32:2–5.
Sjogren, S. J., and W. L. Robinson. 1997. Seasonal habitat utilization and home range size of Sharp-tailed Grouse in the Hiawatha National Forest, Michigan. Michigan Birds and Natural History 4:177–189.
Steinhorst, R. K., and M. D. Samuels. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425.
Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, New York, New York, USA.
Walsh, D. P. 2002. Population estimation techniques for greater sage-grouse. Thesis, Colorado State University, Fort Collins, USA.
Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Wildlife Society Bulletin 32:56–68.
Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. Analysis and management of animal populations. Academic Press, New York, New York, USA.

Associate Editor: Daniel J. Twedt.