REPRODUCTIVE CHRONOLOGY OF GREATER PRAIRIE-CHICKENS IN KANSAS

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ABSTRACT

We conducted a 3-year study of the breeding chronology of Greater Prairie-chickens (*Typanuchus cupido*) to determine seasonal patterns of lek attendance and clutch initiation, and the duration of egg-laying and incubation for birds at three sites in the Flint Hills and Smoky Hills of eastern Kansas. Timing of lek attendance did not differ among study sites. Males attended leks from 2 March – 19 May, females were observed at leks from 20 March – 16 April, and peak attendance in both sexes was 9-10 April. Mean date of clutch initiation of first and renesting attempts was 26 April and 24 May, respectively, with active nests documented from 1 April – 8 July. Females delayed initiation of first nests at the most southerly study site, possibly because of a lack of suitable nesting cover in the early season. Egg laying rates >1 egg/day suggested that intraspecific nest parasitism occurred in 6-15% of sampled nests. The probability of renesting after failure was high (>50%) and declined with date of nest failure but not stage of loss. Females renested quickly and started egg-laying 7.8 d after nest failure on average. We modeled the relationship between egg buoyancy and embryo age for 68 nests of known age. Regression analyses showed that float angle and buoyancy of prairie-chicken eggs were accurate indicators (r^2 = 0.56 and 0.86, respectively) of nest age in days and had good predictive power (± 2 – 4 days). Hatching dates ranged from 18 May – 8 July, brood-rearing extended from 18 May – 22 July, and juveniles were independent by 7 September at 60 d of age. Our research results will be useful to wildlife biologists planning surveying or trapping activities, researchers conducting studies of nesting and brood ecology, and land managers concerned with minimizing the impacts of prescribed burning, cutting for hay or other types of rangeland management.

Key Words: clutch initiation, egg floatation, incubation, lek attendance, prairie grouse, reproduction, *Tympanuchus cupido*.

INTRODUCTION

The timing of reproductive events of grassland birds is important; especially for short-lived species whose population dynamics are sensitive to variation in reproductive success (Wisdom and Mills 1997). For prairie grouse, such as Greater Prairie-chickens (*Tympanuchus cupido*; hereafter 'prairie-chickens'), productivity may be determined by seasonal variation in the ability of females to locate mates at mating arenas or leks, and the environmental conditions at nesting and brood-rearing habitats. For example, timing of breeding and clutch initiation should be late enough to ensure that suitable vegetative cover exists for concealment of first nesting attempts, but early enough to ensure that renesting attempts can occur if needed and that juveniles are independent before inclement winter conditions (Horak 1985, Svedarsky et al. 2003). Thus, appropriate timing of reproductive events is critical for maximizing fitness of prairie-chickens.

Reproductive chronology of prairie-chickens also has implications for population monitoring, research and management. Knowledge of the timing of reproductive events is necessary for wildlife biologists planning population surveys of leks or females with broods, researchers studying nesting and brood ecology, and land managers scheduling burning, grazing or haying activities. Knowledge of reproductive chronology is particularly important for species with broad geographic ranges but regional variation in rates of population decline, such as the prairie-chicken (Rodgers 2008). More than 98% of the tallgrass prairie ecosystem, the native habitat of prairie-chickens, has been lost, and >90% of what remains occurs within the borders of Kansas (Knapp and Seastedt 1998). Kansas is home to the largest contiguous populations of prairie-chickens and is considered to be the core of the remaining extant range (Schroeder and Robb 1993). Reproductive chronology has been described for isolated populations in Minnesota

(Svedarsky 1983, 1988) and Wisconsin (Hamerstrom and Hamerstrom 1973), but relatively little is known about the timing of reproductive events of prairie-chickens breeding in Kansas (Robel 1970, Horak 1985). Given large latitudinal differences in climate and photoperiod and recent changes in range management practices in Kansas (With et al. 2008), a modern investigation of the chronology of reproductive events is needed.

Researchers working with prairie-chickens would benefit from development of accurate methods for determination of the stage of incubation for newly discovered nests. Precise estimates of incubation stage are needed for predicting the timing of nest initiation or hatching, and to determine the durations of laying, incubation and brood-rearing for calculations of productivity. Estimates of nest age are also required to assess the influence of temporal variation in nest survival, and to model daily nest survival as a function of individual- or time-specific covariates (Dinsmore et al. 2002). Field biologists estimating stage of incubation for nests of upland gamebirds have usually relied on an egg floatation technique developed for captive Ring-neck Pheasants (*Phasianus colchicus*) and Gray Partridges (*Perdix perdix*; Westerskov 1950). It is unknown whether egg flotation can be used to accurately assess age of prairie grouse nests under field conditions.

In this paper, we describe the reproductive chronology of Greater Prairie-chickens at three study sites in two ecological regions of Kansas. We present data on the timing of lek attendance and clutch initiation, the duration of laying and incubation, renesting propensity, and the timing of brood-rearing and fledging. We develop a regression model to predict the stage of incubation for prairie-chicken nests from egg floatation angles and egg buoyancy. Last, we discuss the ecological and management implications of regional variation in the seasonal breeding chronology of prairie-chickens in Kansas.

STUDY SITES

Greater Prairie-chickens are closely associated with native grasslands, and occur throughout the Flint Hills ecoregion of eastern Kansas. However, prairie-chickens can tolerate moderate amounts of cultivated agriculture (<40% of total area), and populations also occur in the more developed Smoky Hill ecoregion. Our field study occurred at three sites in eastern Kansas; two sites in the Flint Hills and one site in the Smoky Hills (Fig. 1). The three study sites differed in landscape composition and pattern, as well as rangeland management practices (Table 1). Study area 1 was located in the southern Flint Hills. The majority of the site is burned annually in the spring, and managed with intensive early stocking (IESB, 1 head/0.8 ha for 90 days; Smith and Owensby 1978, With et al. 2008). Study area 2 was located in the north-central Flint Hills. Annual spring burning is common and lands are managed with a mixture of IESB and season-long stock grazing (SLSB; 1 head/1.6 ha for 180 days). Study area 3 was in the Smoky Hills and is more fragmented by agricultural land uses (Table 1). Cultivated crops include sorghum, corn, wheat, and soybeans. Native grass pastures at study area 3 are burned infrequently at fire return intervals >1 year, are grazed at low intensity (1 head / > 2 ha for 90 days), and cattle stocking occurs later in the season than at the other two study sites.

METHODS

LEK ATTENDANCE

During the spring period of lekking (February – May), counts of birds at leks were conducted with two methods: birds were flushed from untrapped leks between 0600 and 0930 hrs, and prairie-chickens were observed from blinds while birds were trapped at leks. For both methods, the maximum number of males, females, and prairie-chickens of unknown sex was recorded. Multiple flush counts were conducted for each lek within a year but not on consecutive days. To assess whether survey method affected lek attendance, we used analysis of variance (ANOVA) to compare counts of prairie-chickens when leks were flushed or trapped, and among our three study sites. A Tukey-Kramer HSD was used to compare lek counts among sites at the $\alpha = 0.05$ level.

We calculated the date of peak lek attendance for males and females at each study site by weighting the Julian date of lek observation by the average number of birds attending leks:

$$\text{Day of Peak of Lek Attendance} = \frac{\sum \left(D_i \frac{A_i}{\overline{A}_{1-N}} \right)}{N},$$

where D_i is the Julian day i of lek observation, A_i is the mean lek attendance for day i, $\overline{A}_{1-N}$ is the mean lek attendance for all days of observation, and N is the total number of observation days. We compared timing of peak lek attendance among study sites with ANOVA. Female lek attendance data were log-transformed to meet the assumptions of ANOVA (Sokal and Rohlf 2000).

INCUBATION AND EGG DEVELOPMENT

We captured prairie-chickens with walk-in traps and drop-nets at leks during March – May of 2006-08 (Schroeder and Braun 1991, Silvy et al. 1990). Captured birds were sexed by plumage characteristics and size (Henderson et al. 1967). Females were fitted with 11-g necklace-style VHF radio transmitters with an expected battery life of 12 months (Model RI-2B, Holohil Systems Ltd., Ontario, Canada). We located females ≥3 times/week during the breeding and brood-rearing seasons (March – August), and daily once females began nesting. Once a female had localized in an area for three consecutive days, we used a portable radio receiver and handheld Yagi antenna to locate and flush the bird. Nest sites were visited ≤ 2 times in early incubation to determine clutch size and stage of incubation. Nests were not visited again until females had departed and were located away from the nest for ≥2 consecutive days. Once a female departed, we classified nest fate as either successful because ≥1 eggs successfully hatched chicks, or failed because the clutch was depredated, abandoned or destroyed for other reasons. Date of hatching was the last day the female was triangulated by telemetry to be incubating at a successful nest.

To estimate duration of incubation, we subtracted the Julian date of known clutch completion from the Julian date of hatch. We assessed the influence of study site, nesting attempt, clutch size, and day of nest initiation on duration of incubation using stepwise regression. Alpha (α) levels of 0.05 and 0.1 were specified for entry and removal of factors from the model.

NEST AND BROOD CHRONOLOGY

First nests were defined as the first nest discovered for an individual female within a breeding season, whereas renests were nesting attempts by radio-marked females where the first nest was known to have failed. If the clutch size increased between visits, the date of clutch initiation was determined by backdating by the number of eggs from the first visit assuming 1 egg laid per day (Svedarsky 1988). If clutch size did not change between successive visits, the date of clutch initiation was determined by backdating from the hatch date assuming an incubation period of 24 days (Schroeder and Robb 1993), or from the stage of incubation determined by egg floatation (see below). We used stepwise regression to model Julian dates of clutch initiation as a function of study year, study site, and nesting attempt. Alpha (α) levels of 0.05 and 0.1 were specified for entry and removal of factors from the model. We then fitted a linear model with the resulting significant predictor variables and assessed model fit.

We used logistic regression to evaluate the relationship between the probability of renesting versus study site, clutch size of the first nest, day of incubation when the initial attempt failed, and the Julian date of nest failure. Date of failure was considered to be the midpoint between the last day the nest was known to be active and the day it was identified as failed. The average interval ($\pm$SD) between the last day a nest was known to be active and the day it was determined to have failed was 4 ± 4 days. We excluded females that were unavailable to renest because they died while incubating first nests, could not be located after first nests failed, or lost their transmitters within two weeks of failure of the first nest. We also excluded 10 nests for which explanatory data were missing. We fit 13 *a priori* models to data from 82 failed first nest attempts. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) for model selection, and models where $\Delta AIC_c \leq 2$ were considered to be equally parsimonious (Burnham and Anderson 1998).

We located radio-marked hens with broods daily via triangulation. Date of hatching was assumed to be the last day the female was located by telemetry at the nest site. Brood flushes were conducted at 14-d post-hatching to estimate pre-fledge brood survival. Prairie-chickens fledge at 14-d old and are considered to be independent of their mothers at 60-d post hatch (Schroeder and Robb 1993). Therefore, age at fledging and date of independence were estimated for successful broods and compared to that of all hatched broods. Sample sizes of successful broods were too small to conduct statistical analyses and descriptive statistics are presented.

EGG FLOATATION

To evaluate the relationship between egg buoyancy and stage of incubation, we restricted our analysis to nests of known age. Known-age nests included nests discovered during egg-laying and nests that successfully hatched. We collected the clutch from the nestbowl and retreated to a distance of >100 m to float the eggs in a small, clear container of lukewarm water. Eggs were individually placed on the bottom of the container to ensure they were not being held by surface tension of the water. If an egg touched the bottom of the container, the angle between the bottom of the container and the center axis of the egg was measured. If the eggs floated freely in the water, the distance between the top of the egg and the surface of the water was measured. Sample sizes of successful nests of known-age were small, and we pooled float data from all sites and years to calculate float curves. Only one mean float measurement was included for each nest but we included two nests laid by the same female in different years. We accepted a low level of pseudoreplication to increase sample size.

We used regression to evaluate the relationship between float angle and the age of the clutch in days (after Liebezeit et al. 2007). We converted egg angles to proportions (P = angle/90) before transforming them to the logit scale. Values of 0 and 1 cannot be logit transformed, and we set angles of 0° and 90° to 1° and 89°, respectively, before transformation. Proportional angles were transformed to logits by:

$$\text{logit } P = \ln [P / 1\text{-}P].$$

We then used linear regression to assess the relationship between the logit-transformed proportional float angles and days of incubation. For nests where eggs floated above the bottom of the cup, linear regression was used to predict the day of incubation from float height; measured as the distance between the surface of the water and the top of the egg (in mm). The predictive ability of regression equations was assessed by subtracting the nest age in days of incubation from the predicted age for each nest on a given day. The absolute mean deviation ± SE was considered as the statistic of model error. Deviations were plotted against embryo age to illustrate model precision. All statistical analyses were conducted using Program SAS (ver. 9.1, SAS Institute Inc., Cary, NC).

RESULTS

Lek Attendance

During 2006-08, we conducted 673 lek surveys at our three study sites from 2 March – 19 May. We conducted 408 lek observations from blinds during trapping activities and 265 flush counts where no traps were deployed. A random sample of 265 trapped lek observations were selected and compared to flush counts. The maximum number of prairie-chickens observed was greater during lek observations of trapped leks (10.9 $\pm$ 0.4 birds per day) than flush counts (7.2 $\pm$ 0.4; $F_{1,522} = 56.8$, $P < 0.001$). Similarly, female lek attendance was greater for observations conducted during trapping (1.3 $\pm$ 0.9 birds per day) than during flush counts (0.4 $\pm$ 0.1; $F_{1,367} = 30.7$, $P < 0.001$).

The peak of male lek attendance was 9 April across all years and study sites in Kansas, with males present on leks during the entire 79-d observation period (2 March - 19 May; Fig. 2). Peak female attendance at leks was 10 April when data were pooled across years and sites, with 95% of female lek visitations occurring during a 28-d period between 20 March – 16 April (Fig. 2). Timing of peak lek attendance did not differ among study sites for males ($F_{2,174} = 0.38$, $P = 0.68$) or females ($F_{2,174} = 0.32$, $P = 0.73$), but the duration of female lek attendance appeared to be a shorter period at study area 1 (Fig. 2). A total of 13 copulations were observed during the 3-year study during the 37-d period from 3 April – 9 May.

Timing of Clutch Initiation and Renesting

During 2006-08, we located 231 nests of 155 females. A total of 167 nests were first nests, 61 nests were renests, and three nests were third nesting attempts. Mean date of clutch initiation for first nests at all sites was 28 April (range = 1 April – 7 June; n = 167). Several apparent first nests were initiated after the mean date of second nest initiation and could have been renesting attempts if a clutch was destroyed before observers located the first nest (n = 5). If we excluded these nests, the mean date of clutch initiation for first nests was 26 April (range = 1 April – 22 May; n = 162). Mean date of nest initiation for known renesting attempts was 24 May (range = 29 April – 4 July; n = 64). Stepwise regression revealed that nesting attempt and the interaction between study site and nesting attempt were significant predictors of date of nest initiation ($r^2 = 0.45$, $P < 0.01$). Study year and site alone did not improve model fit and were removed from the model. Mean date of clutch initiation for first nests was 7 days later at study area 1 than the two northerly study sites ($F_{1,167} = 3.4$, $P = 0.03$), but timing of renests was similar among all three study sites (Fig. 3). Mean date of hatching was 6 June for first nests (range = 18 May – 21 June) and 26 June for renests (7 June – 8 July, Fig. 4). Date of hatching was similar among study sites ($F_{2,40} = 2.0$, $P = 0.15$) and years ($F_{2,21} = 0.23$, $P = 0.79$). However, mean date of hatching for successful first nests was 7 days later than what would be predicted if all initiated clutches had been successful, suggesting higher survival among nests initiated later in the season. There was no difference between actual and predicted dates of hatching for renesting attempts.

The probability of a prairie-chicken initiating a renesting attempt was influenced by the date of failure for the first nest (Fail Day) and the stage of incubation at failure (First Nest Age). An additive model with these two factors was the minimum AIC_c model, and models that included fail date had 98% of the relative support of the data. However, the regression coefficient for First Nest Age ($\beta = -0.002$) was not significantly different than zero (95% CI = -0.06 to 0.06) and was considered spurious. Females losing first nests late in the season had a lower probability of renesting ($\beta_{\text{Fail Day}} = -0.11$, 95% CI = -0.17 to -0.05; Fig. 5), and the odds of a female attempting a renest decreased by 11% per day during the nesting season. Prairie-chickens renested quickly and the average interval between failure of the first nest and initiation of a renesting attempt was 7.8 $\pm$ 1.1 days (range = 0 – 27 days, n = 45).

The fledging period of prairie-chickens at all study sites ranged across a 53-d period from 31 May – 22 July (mean day of fledge = 30 June). Timing of fledging was similar for broods that successfully fledged and days predicted for unsuccessful broods (difference = 2 days). Prairie-chicken chicks at study area 3 tended to fledge earlier than the other two sites but the difference was not significant ($F_{2,40} = 2.1$, $P = 0.13$). Dates of independence for prairie-chicken young at 60 days of age would be predicted to occur from 16 July – 7 September.

EGG-LAYING AND INCUBATION

On average, prairie-chickens laid 1 egg every 1.1 $\pm$ 0.3 days. In 10 of 67 cases (15%), the estimated rates of egg-laying were >1 egg/day (range = 1.1 – 2.0). To be conservative, we adjusted clutch initiation dates by the maximum error of our floatation technique (see below), and found that the laying rates of 6 of 10 nests still exceeded 1 egg per day. Thus, 6-15% of prairie-chicken clutches in our study showed evidence of intraspecific nest parasitism by other female prairie-chickens. Prairie-chickens incubated nests for 25.0 $\pm$ 2.5 days on average (range = 22 - 29 days, n = 38). Stepwise regression indicated that incubation duration was not affected by study site ($F_{2,34} = 0.5$, $P = 0.63$), date of nest initiation ($r^2 = 0.07$, $P = 0.11$, df = 1, n = 35), or nesting attempt ($F_{1,35} = 3.4$, $P = 0.08$). Duration of incubation was positively related to clutch size but most of the variation was unexplained ($r^2 = 0.12$, $P = 0.03$, df = 1, n = 35):

$$\textit{Duration of Incubation} = 20.9 + 0.32\ (\textit{Clutch Size})$$

First nests initiated earlier in the season contained more eggs (12.4 $\pm$ 2.3 eggs) than renests (10.5 $\pm$ 2.4 eggs), and duration of incubation tended to be shorter at the end of the breeding season.

USE OF EGG FLOTATION TO ESTIMATE CLUTCH AGE

We collected float data from 68 clutches of known age. Mean float angle was estimated for eggs of 62 clutches found early in incubation. Average float height between the top of the egg and the water surface was measured for six clutches where eggs were floated above the cup bottom. Logit-transformed egg angle was a significant predictor of embryo age in early incubation (< 14-d old; $r^2 = 0.56$, $P < 0.001$; Fig. 6):

$$\textit{Day of Incubation} = 3.25 + 1.19\ (\textit{logit } P).$$

The mean deviation (± SE) between actual embryo age and predicted embryo age was 0.001 ± 0.24 days and the 90th percentile of the predicted error for the early-mid incubation period was <9% (± 2 days). Model error was greater for clutches floated during mid-incubation (10-14 days) and was ± 4 days from predicted values. For clutches floated late in incubation (>14 d), linear regression analysis revealed a significant relationship between egg buoyancy and stage of incubation ($r^2 = 0.86$, $P = 0.007$; Fig. 6):

$$\textit{Day of Incubation} = 12.0 + 0.73\ (\textit{Float Height})$$

Mean deviation of model predictions for the late incubation period was ± 1 day.

DISCUSSION

Greater Prairie-chickens breeding in Kansas showed no differences in timing of lek attendance but a difference of about a week in the timing of clutch initiation among sites in the Flint Hills and Smoky Hills ecoregions. Compared to populations of prairie-chickens in the northern extent of the range (Hamerstrom and Hamerstrom 1973, Svedarsky 1983; 1988), the seasonal timing of lek attendance and clutch initiation was earlier in Kansas, the duration of the nesting and brood-rearing periods was longer, and rates of renesting were higher. Duration of incubation and age at fledging were similar for all populations, but egg-laying rates >1 egg per day indicate that intraspecific nest parasitism may be more common in Kansas than elsewhere. Last, float angle and buoyancy of prairie-chicken eggs were useful for estimating stage of incubation and promise to be a useful tool for field studies of upland gamebirds.

TIMING OF LEK ATTENDANCE AND NESTING

Lek attendance by prairie-chickens in Kansas was highest during the second week of April, with no annual variation in seasonal timing. Timing of lek attendance was earlier in Kansas than at northern study sites in Wisconsin and Minnesota (Hamerstrom and Hamerstrom 1973, Svedarsky 1988); a latitudinal trend reported for other species of prairie grouse (Connelly et al. 1998, Schroeder et al. 1999). Earlier breeding phenology at lower latitudes may be due to differences in photoperiod or local cues based on availability of resources (Schoech and Hahn 2008). Male attendance at leks was stable throughout March to May, although males were most active in display behaviors when females visited in mid-April (Nooker and Sandercock 2008). We did not observe seasonal declines in male lek attendance as previously described for birds in Kansas (Robel 1970), and our results were more consistent with the stable lek attendance reported for other populations (Hamerstrom and Hamerstrom 1973, Svedarsky 1983).

Trapping activity at leks did not negatively influence lek attendance. Contrary to our expectations, counts of birds were higher when leks were trapped than in routine flush counts. The difference was likely due to methodological differences in our survey techniques rather than attraction of birds to traps. Lek attendance was the maximum count of birds observed from a blind during a 2-3 hour morning observation period if a lek was trapped, but was a single count of the birds flushed by an approaching observer if the lek was not trapped. Lek surveys have been previously criticized as indices of density because not all birds in the population attend leks

(Applegate 2000, Clifton and Krementz 2006). Our results indicate that use of flush counts may be an additional source of bias if the number of birds attending leks is underestimated.

Mean date of clutch initiation for prairie-chickens in Kansas was 28 April, which was earlier than populations in Minnesota (Svedarsky 1983) and Wisconsin (Hamerstrom and Hamerstrom 1973). Active nests were located in a 3-month period between 1 April and 4 July. Elsewhere, prairie-chicken nests have usually been found in a 2-month period between mid-April and early June (reviewed by Schroeder and Robb 1993). Thus, in additional to latitudinal differences in the onset of clutch initiation, the duration of the nesting season appears to be longer for prairie-chickens in Kansas than at northern sites. Early nesting and a longer breeding season may allow prairie chickens in Kansas to cope with nest failure with higher rates of renesting.

We observed site differences in the timing of clutch initiation, but unexpectedly, nests were initiated later at the most southerly study site in the Flint Hills. Differences in rangeland management may explain differences in timing of clutch initiation of about a week among our study sites in Kansas. Most of the native tallgrass pastures at study areas 1 and 2 were burned during March and April (>70%), whereas none of the native tallgrass pastures at study area 3 were burned during our study period. Burning improves forage quality for cattle by removing dead plant matter from the previous growing season, but may affect timing of nesting if female prairie-chickens delay egg-laying until vegetative cover is sufficient to conceal the clutch. Alternatively, differences in timing of clutch initiation could have been due to site differences in food availability. Prairie-chickens and other grouse are income breeders that require exogenous nutritional resources for egg-laying (Meijer and Drent 1999). Site differences in rangeland quality or access to subsidies from agricultural crops could have affected variation in timing through effects on nutritional status.

Egg-Laying and Incubation

The average egg-laying rate of female prairie-chickens in Kansas was 1 egg per 1.11 days, similar to published reports from other populations (Schroeder and Robb 1993). We estimated that 6-15% of the nests in our sample had egg-laying rates of >1 egg per day, with uncertainty due to the margins of error in our egg flotation technique. Given that egg-laying rates of >1 egg per day are unknown for large-bodied birds (Welty and Baptista 1988); we conclude that a subset of our nests were affected by conspecific nest parasitism by other prairie-chickens. Intraspecific nest parasitism has not been previously undocumented for prairie-chickens but might be expected for high density populations in Kansas. Unlike waterfowl, intraspecific parasitism is relatively rare among grouse and has been previously reported for only a few species (Martin 1984, Gratson 1989, Yom-Tov 2001).

Female prairie-chickens renested readily if the first nest was destroyed by predators, with some females producing up to three clutches in a single breeding season. The probability of renesting by female prairie-chickens was relatively high (>50%) and declined seasonally with the date of failure for first nesting attempts. In other species of grouse, renesting propensity is usually lower (<36%) and has been explained by other factors, including stage of loss during the nesting cycle and female age-class (Sopuck and Zwickel 1983, Robb et al. 1992, Connelly et al. 1993, Storaas et al. 2000). Prairie-chickens may have high rates of renesting because they are a relatively short-lived species that make a large investment in reproduction (Bergerud and Gratson 1988). Date of failure may have been more important than stage of loss because prairie-chickens breed at southerly latitudes and have a longer breeding season than forest and tundra grouse.

Duration of incubation for prairie-chicken nests in Kansas (25 ± 2.5 days) was similar to values reported for northern populations in Wisconsin and Minnesota (23-25 days; Hamerstrom and Hamerstrom 1973, Svedarsky 1988, Schroeder and Robb 1993). Age-specific mortality rates can influence patterns of nest attentiveness through effects on residual reproduction, leading to variation in duration of incubation for songbirds (Martin 2002). We found no regional variation in the duration of incubation in prairie-chickens, despite pronounced differences in nest survival and adult female mortality rates among our three study sites (L.B. McNew, unpubl. ms).

Egg floatation data for prairie-chicken clutches were accurate indicators of stage of incubation and had good levels of predictive power. Using data on egg angle and egg buoyancy and the regression techniques described by Liebezeit et al. (2007), we found that 90% of prairie-chicken nests could be aged to ±1-2 days if the clutch was floated early or late in incubation (<10 or >14 d). Error was greater (± 4 d) for clutches floated during mid-incubation (10-14 d), due to greater variability in egg buoyancy in a smaller sample of clutches. Our study is one of the first uses of egg floatation data to estimate stage of incubation for prairie grouse, and extends float curves developed for other species of upland gamebirds (Westerskov 1950). Use of float curves developed for pheasants and partridge consistently overestimated the age of clutches of Greater Prairie-chickens by an average of ~3 days and the magnitude of the error increased with stage of incubation. Wildlife biologists working with other species of grouse could use our regressions as a starting point, but would be prudent to calibrate the float curves by collecting egg floatation data from known-age nests to account for interspecific variation in egg size and rates of embryonic development.

In summary, wildlife biologists planning lek surveys for population monitoring or live-trapping of prairie-chickens for translocations or population studies would optimize field effort in Kansas by planning field work from late March to mid-April, the period of greatest lek attendance and activity. Prairie-chickens in this study initiated nests from early April to mid-July. Rangeland management practices that remove or reduce residual vegetative cover during March and April, such as annual spring burning and intensive early stocking of cattle, have the potential to negatively impact prairie-chickens by delaying onset of clutch initiation and reducing nesting success. Similarly, lands that are managed as hay fields should not be cut until late July to avoid destroying nests or killing prairie-chicken chicks. A better understanding of the breeding chronology of prairie grouse and the duration of reproductive stages will assist management efforts and provide a foundation for intensive studies of population demography in the future.

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TABLE 1. Comparison of study sites for population studies of Greater Prairie-chickens in Kansas, 2006-08.

Study Site	Eco-region	Size (km^2)	Proportion Grassland	Proportion Cropland	Road Density (km per km^2)	Land Management[a]
1	Flint Hills	1,106	0.90	0.03	0.32	IESB
2	Flint Hills	671	0.81	0.10	0.57	IESB, SLSB
3	Smoky Hills	1,630	0.53	0.38	1.04	SLSU, RG&B

[a] Dominant land management at each study site: IESB = intensive early stocking, annual burning; SLSB = season long stock grazing, annual burning; SLSU = season long stocking, unburned; RG&B = rotational grazing and burning (after Smith and Owensby 1978, With et al. 2008).

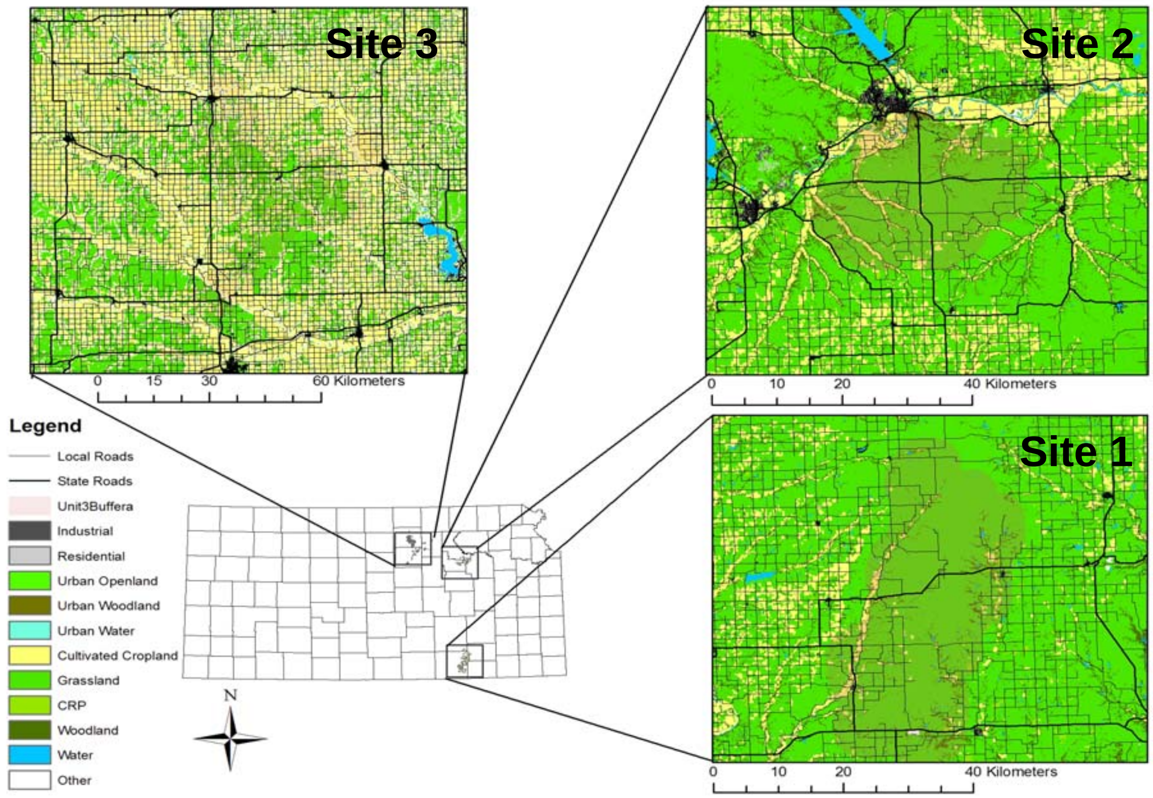

FIGURE 1. Study sites 1 to 3 for population studies of Greater Prairie-chickens in eastern Kansas, 2006-08.

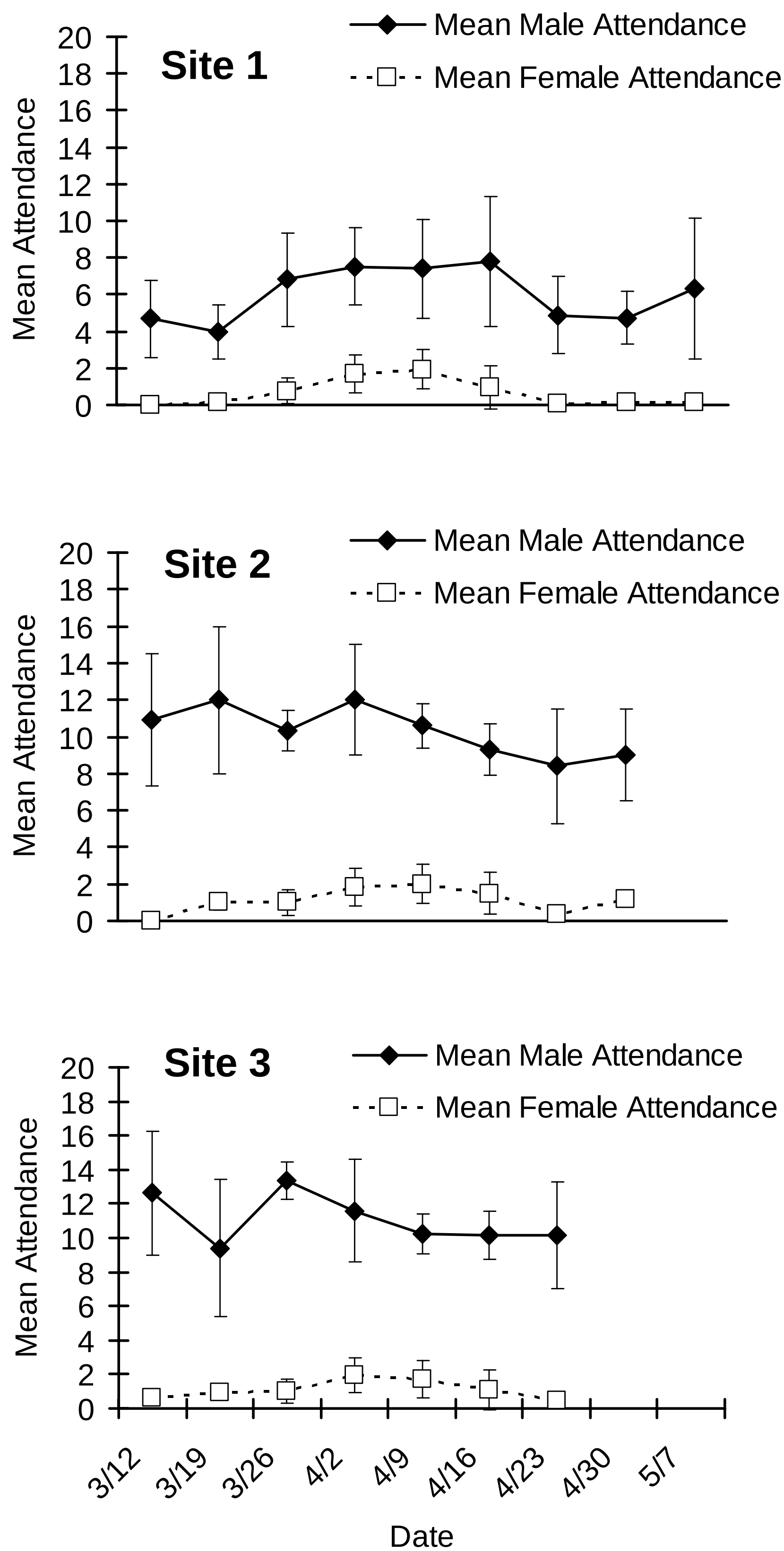

FIGURE 2. Mean daily lek attendance (birds per day ± SD) of male and female Greater Prairie-chickens at study sites 1 to 3 in eastern Kansas, 2006-08.

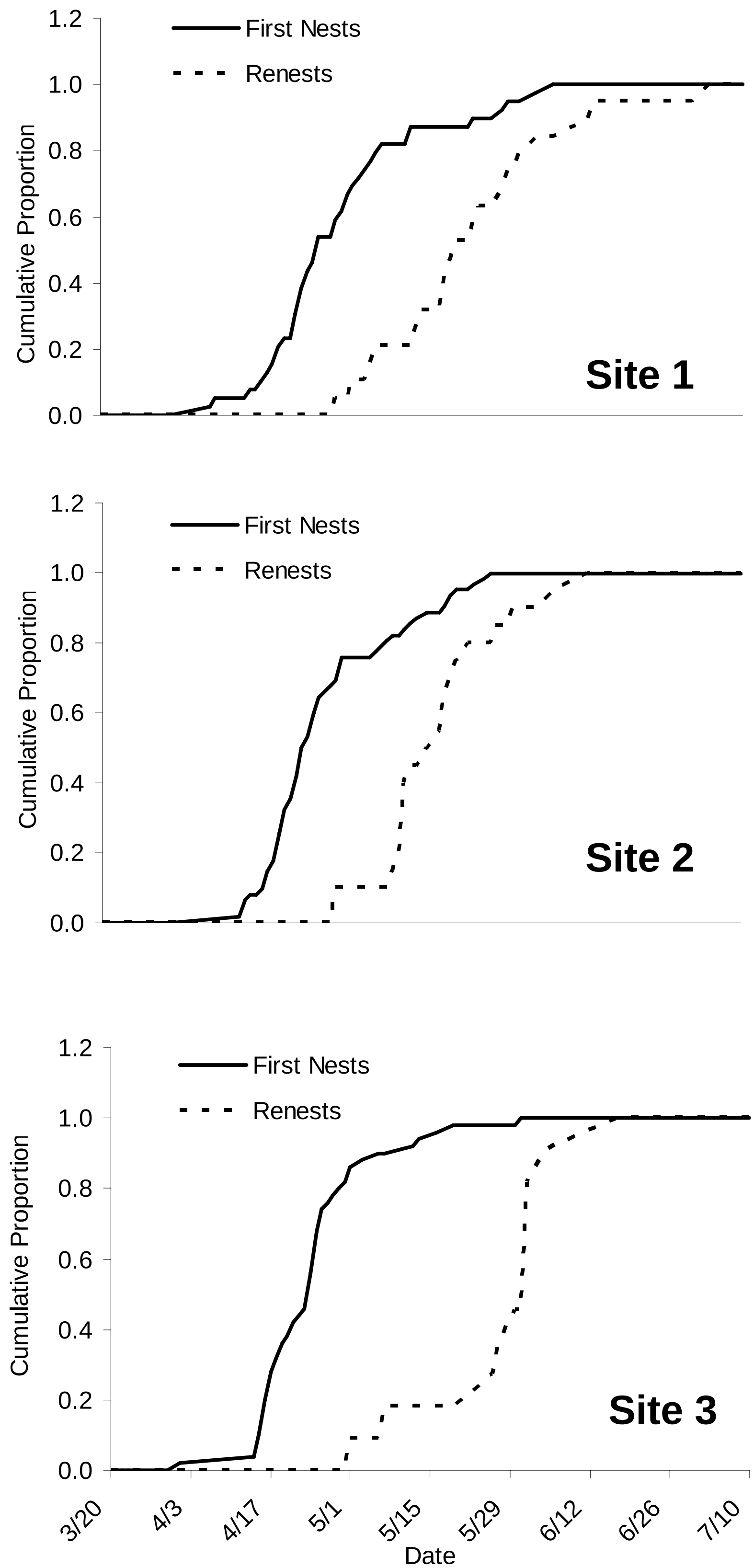

FIGURE 3. Cumulative clutch initiation dates for first nests and renests of female Greater Prairie-chickens at study sites 1 to 3 in eastern Kansas, 2006-08.

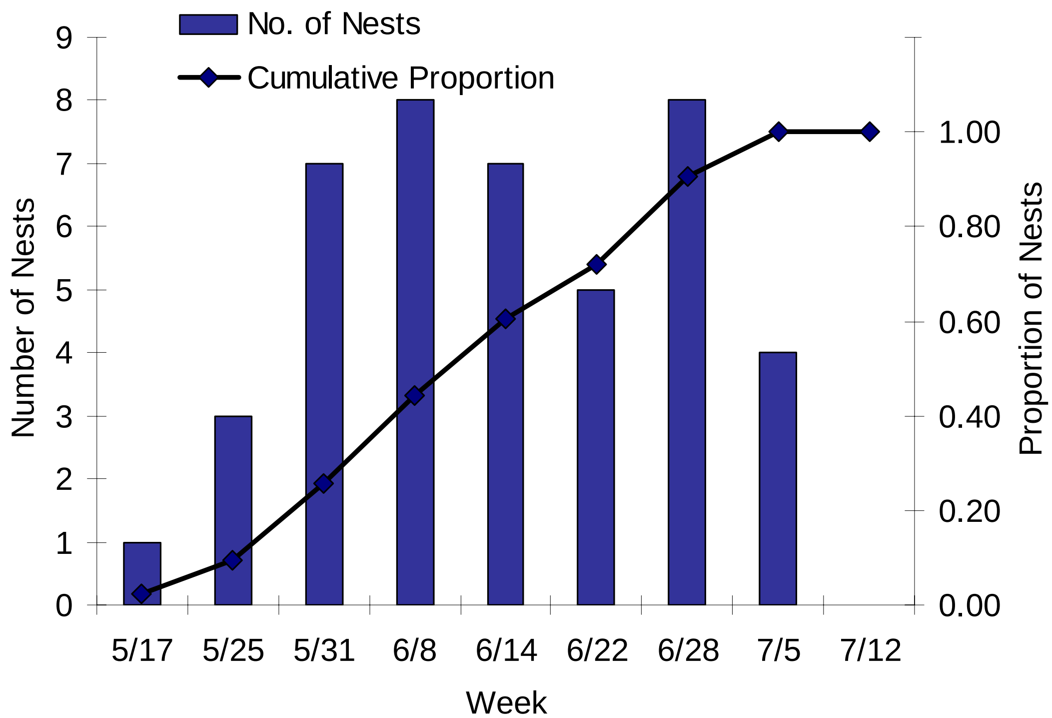

FIGURE 4. Weekly distribution of nest hatches and cumulative weekly hatch for female Greater Prairie-chickens in Kansas, 2006-08.

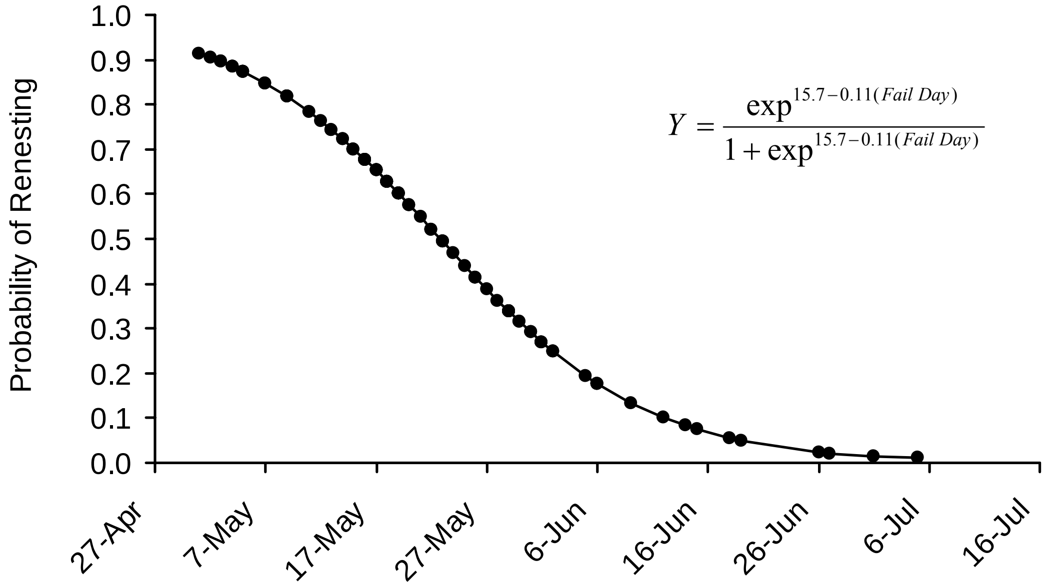

FIGURE 5. Probability of a female Greater Prairie-chicken initiating a renesting attempt as a function of date of failure for the first nest. Probability of renesting was not influenced by stage of loss, clutch size or study site (see text).

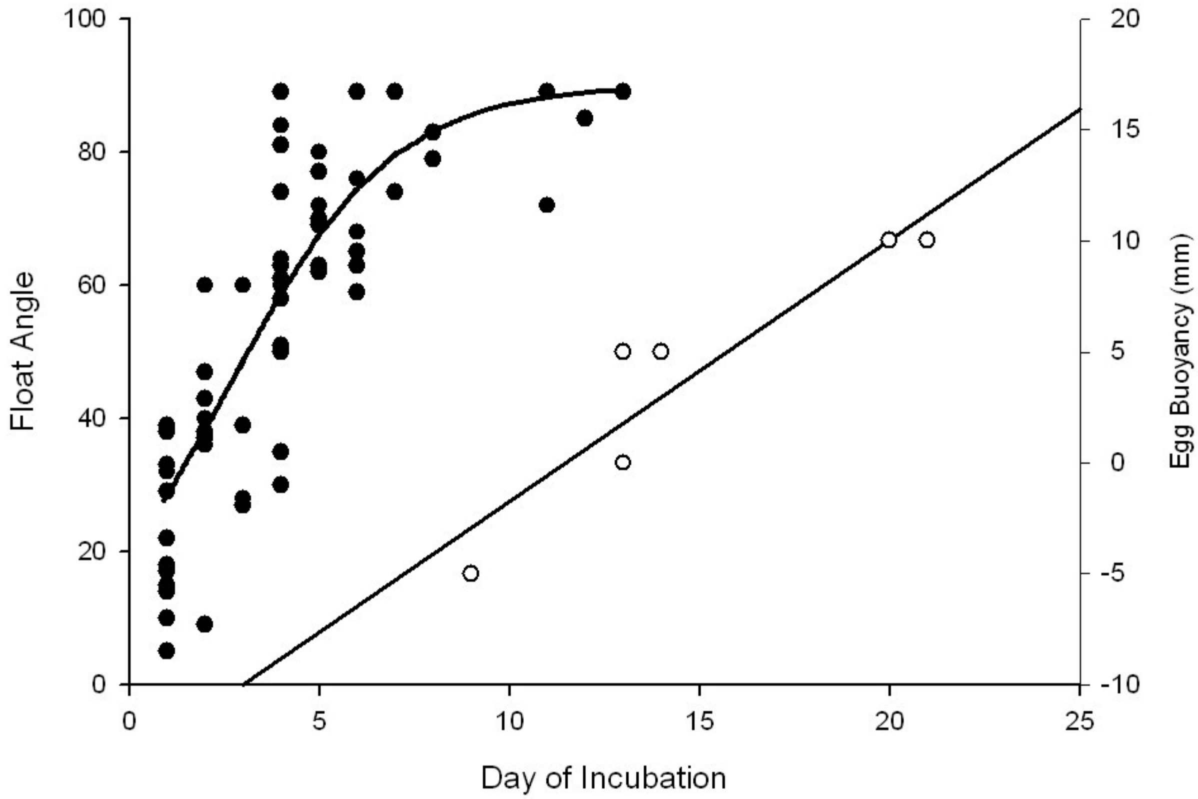

FIGURE 6. Egg angle (filled circles) and egg buoyancy (open circles) for prairie-chicken nests of known age that were floated during incubation. Egg buoyancy refers to distance from the top of the egg to the surface of the water (in mm).