CHAPTER FIFTEEN

Reproductive Biology of a Southern Population of Greater Prairie-Chickens

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Abstract. We conducted a three-year study of the breeding chronology of Greater Prairie-Chickens (*Tympanuchus cupido*) to determine seasonal patterns of lek attendance and clutch initiation, and the duration of egg-laying and incubation for birds at the core of the species distribution. Our field study included three sites differing in landscape composition and rangeland management in the Flint Hills and Smoky Hills of Kansas. Counts of birds on leks were 30% higher when using counts from blinds compared to flush counts. Timing of lek attendance did not differ among study sites. Males attended leks from 2 March to 19 May, females were observed at leks from 20 March to 16 April, and peak lek attendance for 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 to 8 July. Females delayed initiation of first nests at the most southerly study site, possibly because of a lack of suitable nesting cover early in the season due to range management practices. Although previously undocumented for prairie chickens, egg-laying rates >1 egg/day suggested that intraspecific nest parasitism occurred in 6–15% of clutches. The probability of a female renesting after first nest failure was 50%, declining with date of nest failure, but was unaffected by stage of loss or study site. On average, females initiated renests 8 days after failure of first nests. Hatch dates ranged from 18 May to 8 July, brood-rearing extended from 18 May to 22 July, and juveniles were independent by 7 September at 60 days of age. Overall, the reproductive phenology of Greater Prairie-Chickens in Kansas occurred earlier and lasted longer than in other populations. 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 flotation, incubation, lek attendance, prairie grouse, reproduction, *Tympanuchus cupido*.

From Brett Sandercock, Kathy Martin, and Gernot Segelbacher, *Ecology, Conservation, and Management of Grouse,* Berkeley and Los Angeles: University of California Press, 2011.

Greater Prairie-Chickens (*Tympanuchus cupido*) have shown significant population declines across their continually shrinking range over the last century. Agriculture practices have caused a drastic decline of available usable habitat since the early 20th century (>95%; Schroeder and Robb 1993, Braun et al. 1994), and prairie chicken populations declined an estimated 75–80% as a result (Johnsgard 2002). The Flint Hills region of east-central Kansas, southern Nebraska, and northeastern Oklahoma consists of intact tallgrass prairie and has been identified as a stronghold for Greater Prairie-Chickens (hereafter prairie chickens; Johnsgard 2002). This area is characterized by rocky soils that are unsuitable for cultivation and encompasses over 1.6 million ha. For this reason, many authorities consider the Flint Hills to be vital to the long-term persistence of grassland birds (Svedarsky et al. 1999, With et al. 2008). Despite large tracts of relatively intact grassland, annual lek surveys conducted by the Kansas Department of Wildlife and Parks (KDWP) show that statewide prairie chicken populations have declined annually from 4.5 birds/km² in 1980 to 1.5 birds/km² in 2008 (Applegate and Horak 1999, Rodgers 2008). The cause of population declines remains unknown, but timing of declines coincides with the introduction of the range management practice of intensive early stocking and annual spring burning (IESB; Westemeier and Gough 1999, Robbins et al. 2002). IESB benefits cattle production by increasing grass production and allowing ranchers to stock ranges with cattle early. IESB may negatively affect prairie grouse production if complete burns of large contiguous range result in significant decreases in availability of quality nesting sites (Robbins et al. 2002, Patten et al. 2007). To date, studies of the effects of rangeland management on prairie chicken breeding ecology have been limited to the selection of nest sites and relative effects on nest survival (McKee et al. 1998, Patten et al. 2007). Data are lacking regarding how these practices impact other aspects of prairie chicken breeding behavior, such as breeding phenology.

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, 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). In addition, timing of nest initiation has implications for recruitment because chick development and survival is affected by abundance and seasonal phenology of insect food items (Johnson and Boyce 1990, Park et al. 2001, Gregg and Crawford 2009). Thus, timing of reproductive events is critical for maximizing fitness of prairie chickens and may vary among areas of different habitat conditions.

Reproductive chronology of prairie chickens also has implications for population monitoring, research, and range 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 population dynamics, such as the Greater Prairie-Chicken (Rodgers 2008, McNew et al., this volume, chapter 19). 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). Recent changes in regional land management practices over the last three decades may have altered the breeding phenology of prairie chickens in the Flint Hills, as changes in grazing and prescribed burning have affected the seasonal availability of lekking, nesting, and brood-rearing habitat (Patten et al. 2007). The landscapes of Kansas provide a unique opportunity to evaluate whether land management practices impact the breeding phenology of prairie chickens because land use and range management practices vary significantly across the species range within the state. In addition to occupying the large unfragmented grasslands of the Flint Hills, prairie chickens also occur in the more developed

Smoky Hills ecoregion (Rodgers 2008). Although grasslands in the Smoky Hills are highly fragmented by row-crop agriculture (>35% of the landscape) and improved roads (1.04 km per ha), they are not as intensively managed as grasslands in the Flint Hills and may be of better quality due to lower cattle stocking rates and less frequent burning (J. Pitman, pers. comm.).

In this paper, we describe the reproductive chronology of three declining populations of Greater Prairie-Chickens (*T. c. pinnatus*) occurring over a gradient of landscape alteration and rangeland management within the core of the species' extant range in Kansas. We expected (1) timing of breeding events to occur earlier than previous reports for northern populations due to advanced vegetation phenologies, and (2) differences in regional land use to affect the seasonal phenology and reproductive rates in our study populations. If prairie chickens require suitable cover in order to initiate nests (Pitman et al. 2005, Fields et al. 2006), clutch initiation, duration of laying and incubation, renesting propensity, and timing of brood-rearing and fledging might be delayed in areas where most residual cover is removed through extensive annual spring burning and early cattle stocking. We discuss the ecological and management implications of regional variation in the seasonal breeding chronology of prairie chickens in Kansas.

STUDY SITES

Our field study was conducted at three sites in Kansas: two sites in the Flint Hills and one site in the Smoky Hills. The three study sites differed in landscape composition and pattern, as well as rangeland management practices (Table 15.1). The southern Flint Hills site (South) was 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). The second study area was located in the northern Flint Hills (North). Annual spring burning is common at North and lands are managed with a mixture of IESB and season-long stock grazing and annual burning (SLSB; 1 head/1.6 ha for 180 days). The third study area (Smoky) was located in the Smoky Hills ecoregion and is more fragmented by agricultural land uses (Table 15.1). Cultivated crops include sorghum, corn, wheat, and soybeans. Native grass pastures at Smoky are burned infrequently at fire return intervals >1 year, are grazed at low intensity (1 head/>2 ha for 180 days), and cattle stocking occurs later in the season than at the Flint Hills sites. Thus, we expected the breeding phenologies of the sites to be ordered from earliest to latest: Smoky, North, and South.

TABLE 15.1

Comparison of southern Flint Hills (South), northern Flint Hills (North), and Smoky Hills (Smoky) study sites for population studies of Greater Prairie-Chickens in Kansas, 2006–2008.

	South	North	Smoky
Size (km^2)	1,106	671	1,630
Prairie-chicken density index[a]	0.10	0.19	0.17
Proportion grassland	0.90	0.81	0.53
Proportion cropland	0.03	0.10	0.38
Road density (km/km^2)	0.32	0.57	1.04
Mean (SE) precipitation (cm)[b]	12.3 (2.0)	11.4 (2.4)	8.2 (2.4)
Mean daily temperature (°C)[c]	15.0 (0.4)	12.9 (0.4)	12.1 (0.4)
Land management[d]	IESB	IESB, SLSB	SLSU, RG&B
No. of females radiomarked	54	77	72

[a] Males per km^2 = mean number of males per lek × number of leks/study site size.
[b] Mean monthly precipitation during March–May 2006–2008.
[c] Mean daily temperature during March–May 2006–2008.
[d] 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).

METHODS

Lek Attendance

During the spring lekking period (February–May), counts of birds at leks were conducted using two methods: (1) birds were flushed from untrapped leks between 0600 and 0930 hrs, and (2) prairie chickens were observed from blinds while birds were trapped at leks. We attempted to obtain counts of males and females prior to flushing by viewing leks from >100 m using binoculars when possible. For both methods, the maximum numbers of males, females, and total birds were recorded. Multiple flush counts were conducted for each lek within a breeding season but not on consecutive days. To assess whether survey method affected lek counts, 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 $\alpha = 0.05$ 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 (day 1 = 1 Jan) by the average number of birds attending leks:

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

where D_i is the Julian day i of lek observation, A_i is the mean lek attendance by males or females for day i, $\bar{A}_{1-N}$ is the mean lek attendance for all days of observation, and N is the total number of observation days per sex. Low numbers of surveys per day at each study area precluded comparisons of peak lek attendance among sites by year. We pooled daily surveys among years of study and compared timing of peak lek attendance among study sites using ANOVA. Female lek attendance data were log-transformed to meet the normality assumption of ANOVA (Sokal and Rohlf 2000).

Egg-laying and Incubation

We captured prairie chickens with walk-in traps and drop-nets at leks during March–May of 2006–2008 (Silvy et al. 1990, Schroeder and Braun 1991). Captured birds were sexed by plumage characteristics (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 per 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 during laying and 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 successful if ≥1 egg successfully hatched chicks, or as failed if the clutch was depredated, abandoned, or destroyed for other reasons. Date of hatching was the last day the female was estimated to be incubating at a successful nest by triangulation with radiotelemetry.

To estimate duration of incubation in days, we subtracted the date of known clutch completion from the date of hatch. We assessed the influence of study site, nesting attempt, clutch size, and day of nest initiation on duration of incubation using forward 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 one 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 flotation (McNew et al. 2009). We used forward stepwise regression to model 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 and study site, clutch size of the first nest, day of incubation when the initial attempt failed, and the date of nest failure. Date of failure was considered to be the mid-point 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 $\pm$ 4 d. We excluded females that were unavailable to renest if 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). Logistic regression analyses were conducted using the logistic procedure in SAS 9.1 (SAS Institute, Cary, NC).

We located radio-marked hens with broods daily via triangulation. Brood flushes were conducted at 14 days post-hatching to estimate pre-fledge brood survival. Prairie chickens can sustain short flights at 14 days of age (Schroeder and Robb 1993). Although juveniles can survive without the brood hen when 40 days old, they are still generally associated with the hen and brood mates until 60–80 days post-hatch (Bowman and Robel 1977; L. B. McNew, unpubl. data). Therefore, dates of fledging and independence were estimated for successful broods and compared to predicted dates for all hatched broods. Sample sizes of successful broods were too small to conduct statistical analyses, and descriptive statistics are presented. Statistics were calculated with procedures of program JMP IN (ver. 4.0.4, SAS Institute, Cary, NC).

RESULTS

Lek Attendance

During 2006–2008, we conducted 673 lek surveys at our three study sites from 2 March to 19 May. We conducted 408 lek observations from blinds during trapping activities and 265 flush counts where no traps were deployed. To assess whether our trapping activities impacted lek attendance, 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 SE 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; $F_{1,367} = 30.7$, $P < 0.001$), suggesting that trapping activities did not negatively impact lek attendance and that counts from lek observations of trapped leks were suitable for further analysis.

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-day observation period (2 March–19 May; Fig. 15.1). Peak female attendance at leks was 10 April when data were pooled among years and sites, with 95% of female lek visitations occurring during a 28-day period between 20 March and 16 April (Fig. 15.1). Timing of peak lek attendance did not differ among study sites for males ($F_{2,172} = 0.38$, $P = 0.68$) or females ($F_{2,172} = 0.32$, $P = 0.73$), but the duration of female lek attendance appeared to be a shorter period at the South site. Copulations ($n = 13$) were observed during a 37-day period from 3 April to 9 May.

Timing of Clutch Initiation and Renesting

During 2006–2008, we located 231 nests of 155 females. A total of 167 nests were first nests, 61 nests were first renests, and three nests were third nesting attempts. Mean date of clutch initiation for first nests at all sites was 26 April (range = 1 April–22 May; $n = 162$). Mean date of clutch initiation for known renest attempts was 24 May (range = 29 April–4 July; $n = 64$). Forward stepwise regression revealed that nesting attempt and the interaction between study site and nesting attempt were significant predictors of date of clutch 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 ($\pm$SE) date of first clutch initiation differed significantly among study sites (South = 2 May $\pm$ 1.9 d, North = 30 April $\pm$ 1.5 d, Smoky = 24 April $\pm$ 1.7 d; $F_{2,150} = 3.4$,
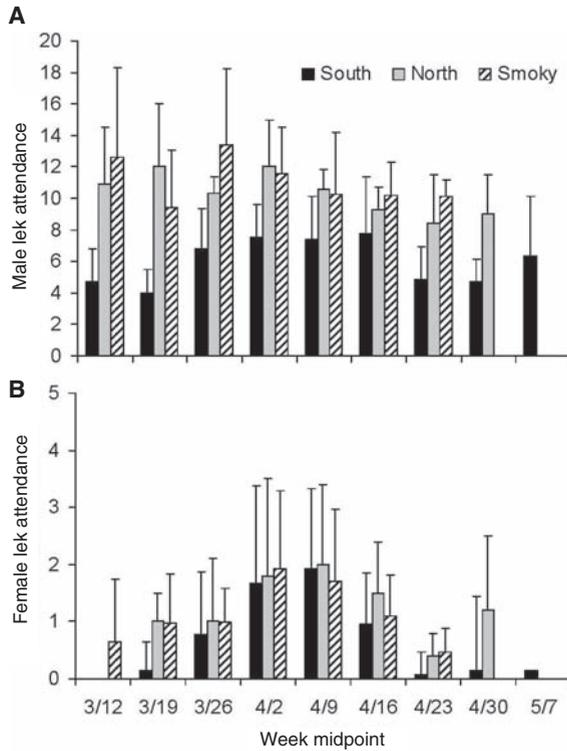
Figure 15.1. Mean daily lek attendance per week (birds per day ± SD) of male (A) and female (B) Greater Prairie-Chickens in Kansas, 2006–2008.
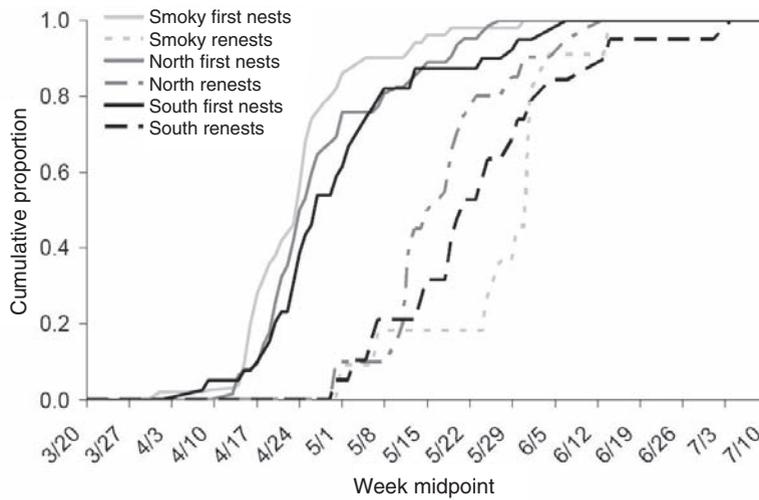

Figure 15.2. Cumulative clutch initiation dates for first nests and renests of female Greater Prairie-Chickens at three study sites in Kansas, 2006–2008.

$P = 0.03$), but timing of renests did not differ among study sites (Fig. 15.2). Mean date of hatching for all sites pooled was 6 June for first nests (range = 18 May–21 June) and 26 June for renests (7 June–8 July; Fig. 15.3), and date of hatching did not differ among study sites ($F_{2,40} = 2.0$, $P = 0.15$) or years ($F_{2,21} = 0.23$, $P = 0.79$).

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 day had 98% of the relative support of the data
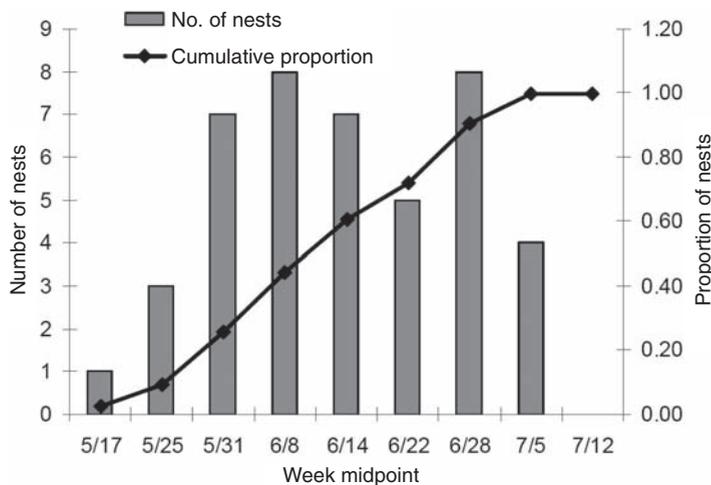
Figure 15.3. Weekly distribution of nest hatches and cumulative weekly hatch for female Greater Prairie-Chickens in Kansas, 2006–2008.

TABLE 15.2

Model selection based on minimization of AIC$_c$ for the estimation of renesting probabilities of Greater Prairie-Chickens at three study sites in Kansas, 2006–2008.

Model[a]	K[b]	AIC$_c$	ΔAIC$_c$	w_i
Fail day + first nest age	3	91.4	0	0.41
Site + fail day + TCL + first nest age	5	92.0	0.5	0.32
Fail day + TCL + first nest age	4	92.4	1.0	0.25
Fail day	2	100.7	9.3	0.0
Site + fail day	3	101.4	10.0	0.0
Fail day + TCL	3	101.8	10.4	0.0
Site + fail day + TCL	4	105.1	11.2	0.0
TCL	2	128.4	37.0	0.0
Site	2	128.5	37.1	0.0

[a] Fail Day = date of failure for initial nesting attempt; First nest age = stage of development when initial attempt failed; Site = study site; TCL = clutch size of initial attempt.
[b] K = number of parameters; w_i = AIC$_c$ weight or relative support for model i.

(Table 15.2). However, the regression coefficient for First nest age ($\beta = -0.002$) was not significantly different than zero (95% CI = -0.06–0.06) and was considered spurious. Females losing first nests late in the season had a lower probability of renesting ($\beta = -0.11$, 95% CI = -0.17 to -0.05; Fig. 15.4), and the odds of a female attempting a renest decreased by 11% per day during the nesting season. Prairie chickens renested with an average interval between failure of the first nest and initiation of a renesting attempt of 7.8 ± 1.1 days (range = 0–27 d, $n = 45$).

The fledging period, defined as the period between the dates of fledging for our first and last brood, at all study sites ranged across a 53-day period from 31 May to 22 July (mean day of fledging was 30 June). Timing of fledging did not differ for broods that successfully fledged and the dates predicted for unsuccessful broods (difference = 2 d). Prairie chicken chicks at the Smoky site tended to fledge 5–6 days 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

$$Y = \frac{\exp^{15.7 - 0.11 \, (\textit{Fail day})}}{1 + \exp^{15.7 - 0.11 \, (\textit{Fail day})}}$$
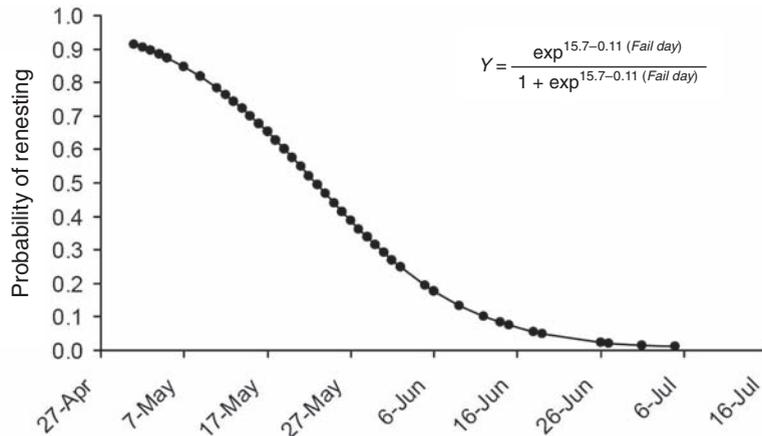
Figure 15.4. Probability of renesting for female Greater Prairie-Chickens as a function of date of failure for the first nesting attempt. Probability of renesting was not influenced by stage of loss, clutch size, or study site.

age would be predicted to occur from 16 July to 7 September.

Egg-Laying and Incubation

On average, prairie chickens laid an egg every 1.1 ± 0.3 days, but in 10 of 67 cases (15%), the estimated rates of egg-laying were >1 egg/day (range = 1.1–2.0). When we adjusted clutch initiation dates to account for the uncertainty of our egg flotation technique (± 2 d; McNew et al. 2009), egg-laying rates at 6 of 10 nests still were >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. Clutch sizes of first nests (12.4 ± 2.3 eggs) were larger than renests (10.5 ± 2.4 eggs). Prairie chickens incubated nests for 25.0 ± 2.5 days on average (range = 22–29 d, $n = 38$). Forward stepwise regression indicated that duration of incubation 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 ($F_{1,34} = 3.4$, $P = 0.08$; second and third nests pooled). Duration of incubation was positively related to clutch size by:

Duration of Incubation = 20.9 + 0.32 (Clutch Size)

but most of the variation was unexplained ($r^2 = 0.12$, $P = 0.03$, df = 1, $n = 35$).

DISCUSSION

Compared to populations of prairie chickens in the northern extent of their 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. Moreover, regional differences in landscape pattern and rangeland management resulted in differences in timing of clutch initiation among sites in the Flint Hills and Smoky Hills ecoregions of Kansas, with delayed initiation in annually burned and heavily grazed grasslands. Duration of incubation and age at fledging were similar for all populations. Egg-laying rates >1 egg per day indicate that intraspecific nest parasitism may be more common in the core range of Kansas than in relict populations elsewhere.

Timing of Lek Attendance and Nesting

Lek attendance by both male and female prairie chickens in Kansas was highest during the second week of April, with no annual variation in seasonal timing during our three-year study. 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 prairie chickens 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). Sustained male attendance may be

driven by a propensity of females to initiate multiple nests or by extended nesting periods in our populations.

Clutch initiation for prairie chickens in Kansas (1 April) began earlier than populations in Minnesota and Wisconsin (20–27 April; Hamerstrom and Hamerstrom 1973, Svedarsky 1983), but later than a population of Attwater's Prairie-Chicken (*T. c. attwaterii*) in coastal Texas (12 March; Lutz et al. 1994), a latitudinal trend reported for other species of prairie grouse (Connelly et al. 1998, Schroeder et al. 1999). Latitudinal differences in the onset of clutch initiation may be due to variation in vegetation phenology across the species' range, which likely results in earlier availability of suitable resources at lower latitudes (Schoech and Hahn 2008). In addition, the nesting season was longer in Kansas than reported previously for both northern and southern populations of prairie chickens, with active nests located during a three-month period between 1 April and 4 July. Elsewhere, nests have been found during a two-month period for both interior Greater Prairie-Chickens (mid-April–early June; reviewed by Schroeder and Robb 1993) and coastal Attwater's Prairie-Chicken (mid-March–early May; Lutz et al. 1994). Early nesting and a longer breeding season may allow prairie chickens in Kansas to cope with nest failure due to initially poor nesting cover with higher rates of renesting (McNew et al., this volume, chapter 19).

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 and agricultural use 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 the South (~90%) and North (~70%) sites were burned during March and April, whereas none of the native tallgrass pastures at the Smoky site were burned during our study. Burning may affect timing of nesting if female prairie chickens delay egg-laying until vegetative cover is sufficient to conceal the clutch. Although delayed nesting in response to poor habitat conditions has not previously been reported for prairie chickens, female prairie grouse tend to initiate clutches in areas with greater residual cover and visual obstruction (Pitman et al. 2005, Fields et al. 2006, L. B. McNew, unpubl. data.). Alternatively, variation in timing of clutch initiation could have been due to site differences in food availability or weather. Prairie chickens and other grouse are income breeders that require exogenous nutritional resources for egg-laying (Meijer and Drent 1999), and site differences in rangeland quality or access to subsidies from agricultural crops could have affected variation in timing through effects on female nutritional status. Cultivated agricultural fields comprised a higher proportion of the landscape at the Smoky site, and prairie chickens will utilize grain sorghum and other crops prior to nesting (Robel et al. 1970). Females were heavier at the Smoky site (mean $\pm$ SE = 929 $\pm$ 8.8 g) than at the North (908 $\pm$ 8.7 g) or South (879 $\pm$ 7.9 g) sites. It is unclear whether females at the Smoky site were in better body condition, but larger females tended to initiate clutches earlier than smaller females (McNew et al., this volume, chapter 19). Weather can influence the timing of clutch initiation in grouse as well (Martin et al. 2000, Martin and Wiebe 2004). However, warmer average daily temperatures (~2–3°C; Table 15.1) during the period when initiation of first clutches would be impacted (March–May) did not result in advanced reproductive phenology at the South site. In contrast, clutch initiation occurred later at this site. We found no differences in mean monthly precipitation ($F_{2,18} = 0.9$, $P = 0.42$) among study sites during the clutch initiation period (Table 15.1), suggesting that weather was not responsible for the observed variation in clutch initiation timing among study sites.

The influence of landscape composition and land use on prairie chicken nesting behavior and demography is well documented. Habitat conditions like residual cover directly affect the selection of nest and brood sites and the resulting success of these vital parameters (McKee et al. 1998, Pitman et al. 2005, Fields et al. 2006). Therefore, land management practices that alter habitat conditions, such as prescribed burning, grazing, and row crop agriculture, can have significant impacts on prairie chicken habitat use, reproductive success, and survival (Patten et al. 2007, McNew et al., this volume, chapter 19). Our data suggest that the effects of landscape alteration and management can influence not only vital rates directly through impacts on availability and quality of habitat, but through impacts on the effort and timing of reproduction as well. Although it is unclear whether nest initiation was delayed at the South site due to limited nesting cover or whether initiation was

advanced at the Smoky site because females were in better condition, human manipulation of prairie chicken habitats appears to be impacting the nesting phenology of prairie chickens in Kansas. Given the effects of temporal variation on nest survival and renesting propensity (Hannon et al. 1988, Sandercock et al. 2005, Martin et al., this volume, chapter 17), human activities that alter prairie chicken resources, such as range management practices, may have even greater influence on populations than previously recognized.

Egg-Laying and Incubation

The average egg-laying rate of female prairie chickens in Kansas was one 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 from 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. Intraspecific nest parasitism has not been documented for prairie chickens but has been reported in a few other species of grouse (Willow Ptarmigan, *Lagopus lagopus*, Martin 1984; Sharp-tailed Grouse, *T. phasianellus*, Gratson 1989, Yom-Tov 2001).

Duration of incubation for prairie chicken nests in Kansas (25 ± 2.5 d) was similar to values reported for northern populations in Wisconsin and Minnesota (23–25 d; Hamerstrom and Hamerstrom 1973, Svedarsky 1988, Schroeder and Robb 1993). Age-specific nest 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 (McNew et al., this volume, chapter 19).

Renesting Propensity

A minimum of 50% of female prairie chickens renested after failure, and the probability of renesting declined seasonally with the date of failure for first nesting attempts. Our reported estimates of renesting probability are conservative because our method of locating nests based on tracking of radio-marked females made it difficult to find nests during the laying period, possibly resulting in many undocumented first nests that failed before discovery. Nevertheless, renesting propensity is usually lower in other species of prairie and forest grouse (<36%) and has been explained by other factors, including stage of loss during the nesting cycle and female age-class (Sopuck and Zwickel 1983, Connelly et al. 1993, Storaas et al. 2000). Prairie chickens may have had high rates of renesting for three reasons. First, they are a relatively short-lived species that make a large investment in reproduction (Bergerud and Gratson 1988), and renests can contribute to the annual fecundity of single-brooded precocial birds (Martin et al. 1989, Milonoff 1991). Second, date of first nest failure impacted the probability of renesting, and a large proportion of first nests failed early in the season (>80%; L. B. McNew, unpubl. data). 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 (Sandercock et al. 2005). Last, differences in habitat conditions among the study sites could have influenced the probability of renesting. Because prairie chickens are income breeders, marked differences in landscape composition, fragmentation, and land management practices observed among study sites could have impacted the resources available for egg production. However, prairie chickens shared similar abilities to initiate renesting attempts among the three sites, suggesting that exogenous resources for follicle development during renesting attempts were not limiting for any of our populations. The resource availability hypothesis was also rejected for tundra grouse (Sandercock et al. 2005, Martin et al., this volume, chapter 17), suggesting alternate hypotheses may be more appropriate for explaining renesting abilities of Tetraoninae.

In summary, the reproductive chronology of prairie chickens in Kansas started earlier and lasted longer than in other populations, possibly due to a combination of longer summers at low latitudes and regional differences in landscape composition and rangeland management practices. 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. 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. For example, 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. Likewise, land managers can reduce negative impacts on prairie chicken populations by managing for a shifting mosaic of burned and unburned prairie to provide patches of residual nesting cover. Landowners should also delay haying and spraying during early April–late July, as this is the primary nesting and brood-rearing period in Kansas.

ACKNOWLEDGMENTS

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