

NESTING ECOLOGY OF LESSER PRAIRIE-CHICKENS IN SAND SAGEBRUSH PRAIRIE OF SOUTHWESTERN KANSAS

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ABSTRACT.—Despite the fact that the Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) is a species of conservation concern, little is known about its nesting ecology, particularly in sand sagebrush (*Artemisia filifolia*) habitats. To find and monitor nests, we captured and equipped 227 female Lesser Prairie-Chickens with transmitters (87 yearlings, 117 adults, and 23 of unknown age) from 1997 to 2002 in southwestern Kansas. Apparent nest success was similar for yearlings (31%, $n = 74$) and adults (27%, $n = 97$) but differed marginally ($P = 0.090$) between first nests (29%) and renests (14%). An estimated 31% of females that were unsuccessful in their first nesting attempt initiated a second nest. The probability that a female would initiate a second nest after failure of the initial attempt was negatively influenced by the day of incubation on which the initial attempt failed. Over 95% of all nests were initiated and completed between 5 May and 2 July. The primary cause of nest failure was predation by coyotes (*Canis latrans*) and gopher snakes (*Pituophis melanoleucus*). Mean clutch size, egg fertility, hatching success, nesting and renesting frequency, and incidence of interspecific parasitism were all similar across years and between yearlings and adults. Distances between nest sites were used as an index to nest-site fidelity between first nests and renests and for across-year nesting attempts. Mean distances between first nests and renests were similar for yearlings (1,071 m) and adults (1,182 m). Mean distance between nests constructed by the same female in subsequent years (918 m) did not differ between age classes or success of the first year's nest. Most females (80%) nested closer to a lek other than the lek where they were captured. Received 24 January 2005, accepted 21 September 2005.

Range-wide, Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*) have declined by an estimated 97% since the 1800s (Crawford 1980, Taylor and Guthery 1980). In Kansas, Lesser Prairie-Chickens are most abundant in the western part of the state—south of the Arkansas River in mixed and shortgrass prairie dominated by sand sagebrush (*Artemisia filifolia*). They also occur in mixed grass prairie north of the Arkansas River, but this habitat is generally devoid of sand sagebrush. Lesser

Prairie-Chickens currently occupy 31 of 39 counties believed to compose their historical distribution in Kansas, but counts of leks and individual birds suggest that Lesser Prairie-Chickens have experienced significant declines since 1964 (Jensen et al. 2000).

The mechanisms responsible for Lesser Prairie-Chicken population declines have not been identified; however, aspects of nesting ecology could be influential (Peterson and Silvy 1996, Wisdom and Mills 1997). Thus, identifying age-specific variation in nesting variables is important to understanding a species' demography or life-history strategy (Patton et al. 2005). Most research on Lesser Prairie-Chicken nesting ecology has been conducted in sand shinnery oak (*Quercus havardii*) habitats in New Mexico and Texas (Davis et al. 1979, Haukos and Broda 1989, Riley et al. 1992). The objectives of our study were to provide baseline information on age-specific variation in nesting ecology, record fidelity to previous nest sites (within-year renests and across-year attempts), and document nest-site locations relative to leks of Lesser Prairie-Chickens in sand sagebrush prairie of southwestern Kansas. We examined annual variation and the effects of age on reproductive parameters and nest-site placement.

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METHODS

Study area.—From 1997 to 2002, we studied Lesser Prairie-Chickens inhabiting sand sagebrush habitat south of the Arkansas River in Finney County, Kansas (37° 52' N, 100° 59' W). We initiated field work on a 7,700-ha area in 1997 and on a nearby 5,600-ha area in 2000; we continued work on both areas through summer 2002. Vegetation was similar in both areas; sand sagebrush was the most conspicuous vegetation present and was interspersed with grasses, including little bluestem (*Schizachyrium scoparium*), needle-and-thread (*Stipa comata*), sand lovegrass (*Eragrostis trichodes*), sixweeks fescue (*Vulpia octoflora*), blue grama (*Bouteloua gracilis*), sand dropseed (*Sporobolus cryptandrus*), sideoats grama (*B. curtipendula*), and western wheatgrass (*Agropyron smithii*). The most common forb species were Russian thistle (*Salsola kali*), western ragweed (*Ambrosia psilostachya*), sand lily (*Leucocrinum montanum*), and common sunflower (*Helianthus annuus*). Each study area was bounded almost entirely by center-pivot irrigated cropland and grazed seasonally by livestock. Annual precipitation averaged 50 cm (U.S. Department of Commerce 2003) and ranged from 42 cm (2000) to 59 cm (1997) during our study.

Locating and monitoring nests.—Using walk-in funnel traps, we captured female Lesser Prairie-Chickens on leks from mid-March through mid-April (Haukos et al. 1990). Except in 1997 (when age was not determined), we classified captured birds as yearlings (~10 months of age) or adults (≥ 21 months of age) by examining the primaries (Copelin 1963). We equipped birds with 11-g necklace-style transmitters (life expectancy = 6–12 months; models from AVM Instrument Company, Colfax, California; Advanced Telemetry Systems, Isanti, Minnesota; and Hohil Systems, Carp, Ontario) and released them on-site immediately after capture. Each day, we determined locations of transmitter-equipped birds by triangulating bearings collected from a truck-mounted, null-peak telemetry system. Bird locations were determined until transmitter failure, emigration from the primary study areas, or bird death. When birds emigrated from our study area, we re-located them by extensive ground searches or from

fixed-wing aircraft. We monitored females that moved off our study area two to three times per week throughout the nesting season.

Using a hand-held antenna, we found nests by approaching transmitter-equipped females when their locations had remained unchanged ≥ 3 consecutive days. If the female was incubating, she was flushed so the eggs could be counted and the clutch examined for interspecific parasitism (Hagen et al. 2002). We marked nest locations with flags (1997) or transmitters (1998–1999) at a distance of 5 m from the nest bowl (Jamison 2000), or we recorded locations with a global positioning system (2000–2002). Nest sites were not visited again until the female departed the site with a brood or until the nest was depredated or abandoned. This technique allowed us to estimate apparent nest success only. Because we did not determine nest status throughout incubation, we did not estimate daily survival of eggs or nests according to the Mayfield method (Mayfield 1975).

After the departure of each nesting female, we classified nest fate as successful (produced at least one chick), unsuccessful, or abandoned. Beginning in 2000, we opened unhatched eggs to determine whether embryos had developed. If the nest was depredated, we systematically searched the area within a 10-m radius for tracks, scat, or eggshell fragments to help determine the predator's identity (Sargeant et al. 1998).

Statistical analyses.—We recorded clutch size and estimated the start of incubation for yearling and adult nests. We defined the start of incubation as the first day on which we detected no changes in the female's telemetry locations—typically, 3–5 days before a nest was located. We estimated the initiation date of each nest by backdating from the start of incubation by 1 day for each egg in the clutch (Coats 1955). We also calculated apparent nest success (the proportion of all known nests producing at least one chick $\times 100$), hatching success, egg fertility, percentage of females attempting a nest, percentage of females re-nesting, and the incidence of interspecific parasitism—separately for yearlings and adults. We defined hatching success as the number of eggs hatched divided by initial clutch size (Westemeier et al. 1998b). We defined percent fertility as the number of eggs hatching or

containing a developed embryo divided by the total number of eggs in the nest bowl at the time of hatching. We estimated incubation length as the time (days) between the start of incubation and the date when a female left the nest with a brood (as determined from telemetry locations). We estimated nesting frequency as the percentage of females that attempted a nest. Females that did not attempt a nest and died before 31 May were excluded from our estimate of nesting frequency. Because we documented some first nesting attempts after 31 May, it was uncertain whether birds dying prior to this date would have subsequently attempted a nest. Interspecific parasitism was reported as the percentage of nests containing eggs of both Lesser Prairie-Chickens and other bird species. Interspecific nest parasitism was previously described for the 1997 to 1999 field seasons (Hagen et al. 2002); here, we summarize all records of parasitism from 1997 to 2002. The percentage of females attempting to reneest was estimated as the percentage of females known to have incubated and lost a first clutch and that subsequently incubated a second. Because of some small expected cell counts, we used a Fisher's exact test for all comparisons (Agresti 1996). In addition, we used two-tailed *t*-tests for unequal variances (Zar 1999) to compare clutch size, incubation date, hatch date, and incubation length between yearlings and adults.

We used logistic regression to assess the relationship between the likelihood of reneesting and (1) age class, (2) clutch size of the initial nest attempt, and (3) day into incubation when the initial attempt failed. We excluded data from 1997 because we did not identify age class of birds that year. Initially, we fit seven *a priori* models to data associated with 59 failed first nest attempts recorded from 1998 to 2002. We considered all four additive models and main effect models for each of the three independent terms. We used the minimization of Akaike's Information Criterion for small sample sizes (AIC_c) to rank the models (Burnham and Anderson 1998). All models where $\Delta AIC_c \leq 2$ were considered to be competing models (Burnham and Anderson 1998). Because age class was not included in any of the competing models (all $\Delta AIC_c > 2$), we excluded this variable and developed models using an expanded data set ($n = 69$) that in-

cluded failed first nest attempts recorded from 1997 to 2002. We used the same model procedures previously described to fit three of our *a priori* models that included the main effects (1) clutch size and (2) day of incubation on which the initial attempt failed.

We calculated distances between first nests and reneests, nesting attempts in multiple years, and distances from nest sites to the lek of capture and the nearest lek. We used analysis of variance (ANOVA) to determine whether year or age class influenced the distance between an initial nest site and the reneest location and the affinity of nesting females to lek sites (capture lek and nearest lek). We also used ANOVA to determine whether age class or success of the first-year nest affected distance between nest sites in subsequent years. For these analyses, we excluded all data from 1997 because we did not identify age class that year; however, we included pooled age-class data from 1997 in the data tables to provide an overview of nesting parameters for the duration of our study. We interpreted simple effects with two-sample *t*-tests when significant interactions were found (Zar 1999). We considered all differences significant when $P < 0.05$ and marginally significant when $0.05 < P < 0.10$. We report parameter estimates and means as \pm SE (or SD as noted).

RESULTS

Nesting ecology.—We captured 227 female Lesser Prairie-Chickens and fitted them with transmitters (87 yearlings, 117 adults, and 23 of unknown age). We found 209 nests (77 yearling, 103 adult, and 29 unknown-age). The percentage of females initiating a nest was similar ($P = 0.50$) for yearlings (94%) and adults (92%; Table 1). We determined fate for 196 of 209 (94%) nests; apparent nest success was $26 \pm 3\%$ (51 of 196). The remaining nests were either abandoned (2%, $n = 5$) or success could not be determined from evidence remaining at the nest site (4%, $n = 8$). Nest success did not differ across years ($\chi^2 = 6.95$, $df = 5$, $P = 0.22$) or between age classes for first nests ($P = 0.60$) or reneests ($P = 0.82$; Table 1). An estimated 31% of all females that were unsuccessful in their first nesting attempt initiated a second nest, and this percentage did not differ ($P = 0.85$) between yearlings and

TABLE 1. Lesser Prairie-Chicken nesting statistics (mean ± SE), by nesting attempt and age, compiled over a 6-year period in the sand sagebrush prairie of southwestern Kansas, 1997–2002.

Attempt/Variable	n	Yearling	n	Adult	P	n	All females ^a
First nest							
Nest success (%)	60	35 ± 5	78	31 ± 5	0.60	157	29 ± 4
Clutch size	61	11.8 ± 0.2	81	12.3 ± 0.2	0.079	161	12.0 ± 0.1
Start of incubation (Julian date)	57	127.4 ± 0.9	76	127.3 ± 0.9	0.94	151	128.5 ± 0.7
Hatch date (Julian date)	20	156.7 ± 2.0	24	151.4 ± 1.6	0.044	45	153.8 ± 1.3
Second nest							
Nest success (%)	13	15 ± 10	16	13 ± 8	0.82	35	14 ± 6
Clutch size	11	8.2 ± 0.6	14	7.3 ± 0.6	0.30	29	7.6 ± 0.4
Start of incubation (Julian date)	13	153.9 ± 2.2	15	152.9 ± 1.9	0.73	34	153.3 ± 1.3
Hatch date (Julian date)	2	175.5 ± 1.5	2	167.0 ± 3.0	0.13	5	175.0 ± 4.3
Pooled							
Nest success (%)	74	31 ± 5	97	27 ± 5	0.54	196	26 ± 3
Incubation length (days)	21	27.3 ± 0.6	20	26.3 ± 0.6	0.25	43	26.7 ± 0.4
% eggs hatching	235	75 ± 3	323	72 ± 3	0.50	570	74 ± 2
% eggs fertile	87	94 ± 3	223	95 ± 2	0.90	311	94 ± 1
% females nesting ^b	70	94 ± 3	82	92 ± 3	0.50	176	92 ± 2
% females attempting a renest	39 ^c	33 ± 8	54 ^c	31 ± 6	0.85	112 ^c	31 ± 4
% nests parasitized ^d	77	4 ± 2	103	3 ± 2	0.72	209	3 ± 1

^a Includes females of unknown age.
^b Females that attempted a nest; females that did not attempt a nest and died before 31 May were excluded.
^c n = number of failed first nests.
^d Nests were parasitized by either Ring-necked Pheasants or Northern Bobwhites.

adults (Table 1). However, success of renests (14%) was marginally less than success of initial nests (29%; $\chi^2 = 3.31$, $df = 1$, $P = 0.090$). No females were known to have initiated a third nest in the same year. Mean hatch date (all years combined) was 1 June for first nesting attempts and 22 June for renests (Fig. 1), with a mean incubation length of 26.7 days (Table 1). More than 95% of all nests were initiated and completed between 5 May and 2 July (Fig. 1).

Mean clutch size did not differ between yearlings and adults for either first nesting or renesting attempts (Table 1). Mean clutch size was 7.6 ± 0.4 eggs for renests, significantly less ($t_{188} = 11.77$, $P < 0.001$) than the mean clutch size (12.0 ± 0.1 eggs) of first nests. Overall hatching success was $74 \pm 2\%$ and did not differ between yearlings and adults. Likewise, egg fertility was similar between the two age classes, with $94 \pm 1\%$ of all eggs containing a developed embryo (Table 1).

Six of 209 (3%) Lesser Prairie-Chicken nests were parasitized by other bird species. Four of the six nests contained Lesser Prairie-Chicken and Ring-necked Pheasant (*Phasianus colchicus*) eggs, and eggs of both species hatched in two of these nests. One nest was parasitized by a Northern Bobwhite (*Colinus virginianus*); 10 prairie-chicken eggs and 1 quail egg), and the remaining nest was parasitized by both Ring-necked Pheasant and Northern Bobwhite (3 prairie-chicken eggs, 1 pheasant egg, and 1 quail egg). Both of these latter nests were depredated before hatching.

Nest predators.—Most (>80%) known predation events occurred >3 days after our initial nest visit (mean = 10.2 days \pm 6.9 SD). We assigned predator species to 112 of 161 (70%) unsuccessful Lesser Prairie-Chicken nests. Coyotes (*Canis latrans*) depredated the majority (64%) of the nests and were the primary cause of nest predation during most years (Table 2). Snakes were responsible for the loss of 31% and 42% of the unsuccessful Lesser Prairie-Chicken nests in 2001 and 2002, respectively. Most of the snake predation was probably by Gopher snakes (*Pituophis melanoleucus*) because they were the most observed snake species on our study areas. Other causes of nest loss included predation by ground squirrels (*Spermophilus* spp.) and trampling by cattle (Table 2).

Renesting probability.—The probability of a Lesser Prairie-Chicken renesting was influenced by both clutch size and the day of incubation on which the initial attempt failed. An additive model including both terms was the highest-ranking ($\Delta AIC_c = 0.00$; $AIC_c = 80.90$), but the model including only date of failure also had considerable support ($\Delta AIC_c = 1.48$). The model including only clutch size was not supported ($\Delta AIC_c = 15.24$). Females incubating initial nests later into incubation tended to have a lower probability of renesting ($\beta_{\text{date}} = -0.18$, 95% CI = -0.28 to -0.08 ; Fig. 2). Females laying a larger clutch in the initial nest attempt tended to be more likely to reneest ($\beta_{\text{clutch}} = 0.31$); however, the magnitude of this effect was not clear because the confidence interval overlapped zero (95% CI = -0.01 to 0.63). The odds of a female attempting to reneest decreased by 16.2% with each day into incubation of the initial attempt and increased 20.2% with each one-egg increase in clutch size (Fig. 2).

Nest-site location.—Between 1997 and 2002, we found 28 renests (Table 3). Distance between first nests and renests (1,271 m) was not influenced by age class ($F_{1,23} = 1.69$, $P = 0.21$) or year ($F_{4,23} = 1.65$, $P = 0.21$); there was no interaction effect ($F_{2,23} = 1.82$, $P = 0.19$; 1998–2002 data). Similarly, the distance between nests initiated by the same female in subsequent years (mean = 918 m, $n = 15$; Table 3) was not influenced by age class ($F_{1,14} = 0.16$, $P = 0.70$) or success of the first-year nest ($F_{1,14} = 0.05$, $P = 0.82$); there was no interaction effect ($F_{1,14} = 0.00$, $P = 0.98$).

The distance from a nest to the nearest lek (mean = 691 m, $n = 194$; Table 4) was not influenced by year ($F_{4,164} = 1.11$, $P = 0.36$) or age class ($F_{1,164} = 0.00$, $P = 0.99$), nor was there an interaction effect ($F_{4,164} = 1.41$, $P = 0.23$; 1998–2002 data). Of 184 nests, 147 (80%) were located closer to a lek other than the lek where the female was last captured. Ten nests (5%) were located >10 km from the lek at which the incubating female was captured (median = 20.6 km, range = 10.6–56.5 km). The female nesting 56.5 km from her lek of capture was successful in her nesting attempt. The distance from nest site to the lek where the female was captured (mean = 3,082 m, $n = 184$; Table 4) was not influenced by age class ($F_{1,158} = 0.12$, $P = 0.73$) or year

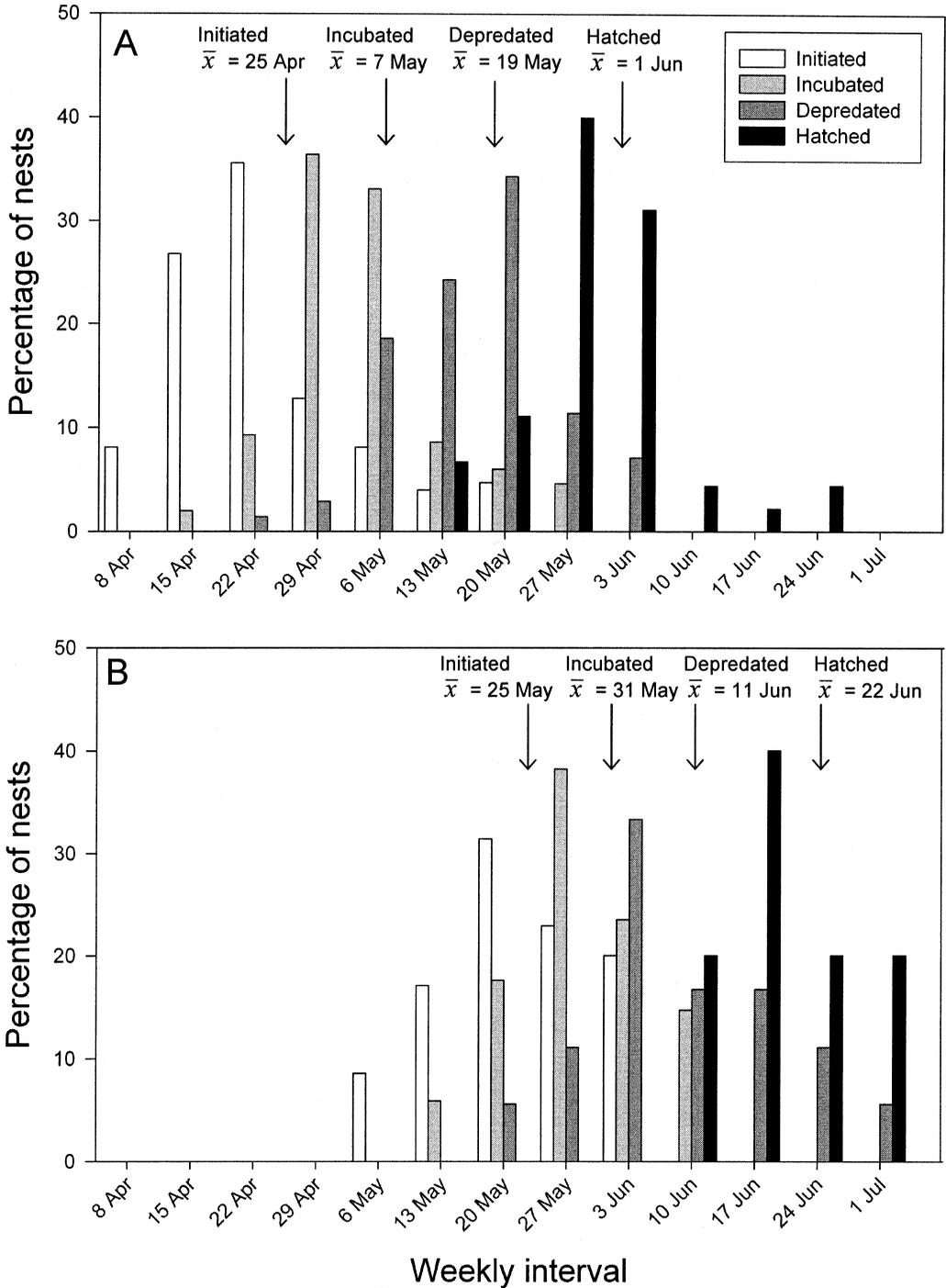


FIG. 1. Percentage of Lesser Prairie-Chicken first nests (A) and renests (B) in southwestern Kansas that were initiated, incubated, depredated, and hatched, by weekly intervals, 1997–2002. Mean dates for each variable are listed at the top of each figure.

TABLE 2. Probable causes of predation of Lesser Prairie-Chicken nests in the sand sagebrush prairie of southwestern Kansas, 1997–2002.

Predator	Depredation (%)						Total ^a (n = 161)
	1997 (n = 24)	1998 (n = 12)	1999 (n = 20)	2000 (n = 44)	2001 (n = 36)	2002 (n = 26)	
Coyote	71	100	70	34	22	27	45
Ground squirrel ^b	4	0	0	11	0	0	4
Snake ^c	13	0	5	11	31	42	19
Cattle	0	0	5	2	3	0	2
Unknown	13	0	20	41	45	31	30

^a Percentage of all nests destroyed by each predator.

^b We did not differentiate between thirteen-lined ground squirrels and spotted ground squirrels.

^c Gopher snakes appeared to be the most abundant snake species.

($F_{4,158} = 1.25$, $P = 0.29$), and there was no interaction effect ($F_{4,158} = 1.33$, $P = 0.26$; 1998–2002 data).

DISCUSSION

Although rainfall during the primary 4-month nesting period (April through July) var-

ied substantially during the 6 years of our study (range = 22.3–38.3 cm), we documented little annual variation in Lesser Prairie-Chicken nesting activity. Our ability to detect annual variation, however, may have been hindered by relatively small sample sizes within years, especially in the early years of the

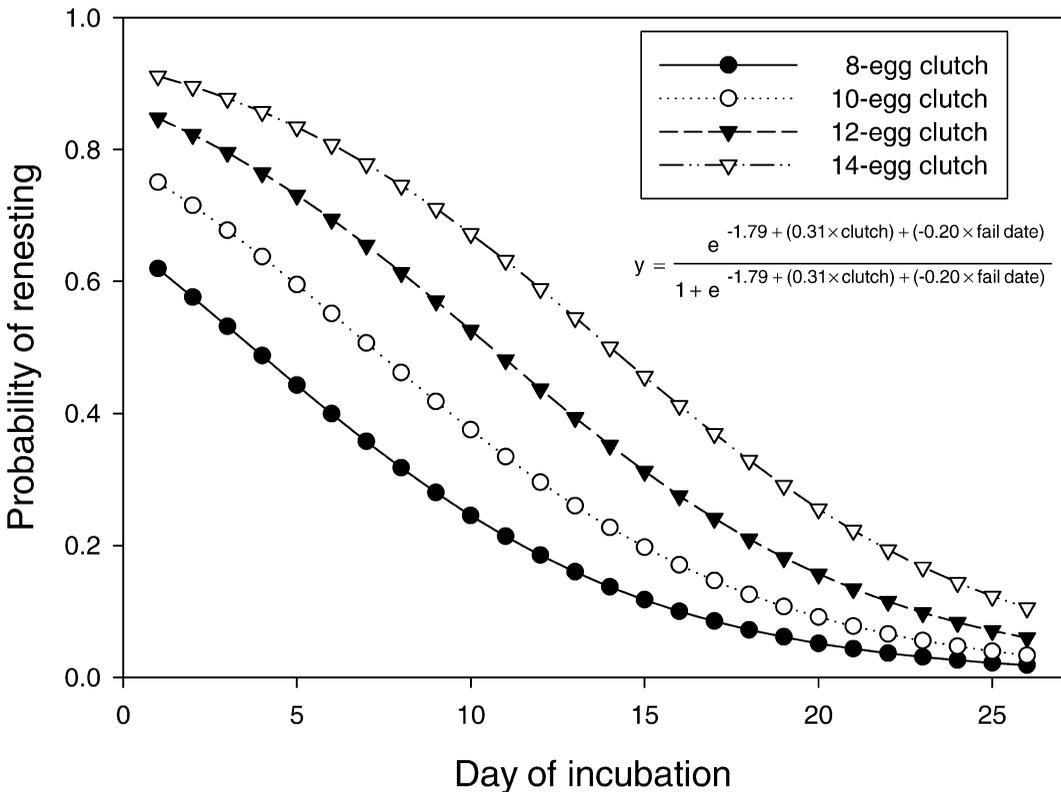


FIG. 2. Probability of Lesser Prairie-Chickens initiating renests after failure of the initial nest attempt in southwestern Kansas, 1997–2002. Probabilities are plotted for various clutch sizes (8, 10, 12, 14) and the day of incubation when the initial nest attempt failed.

TABLE 3. Evidence of nest-site fidelity as shown by mean distances (m) between nests for Lesser Prairie-Chickens in southwestern Kansas, 1997–2002. Within- and across-year distances are presented by age class and nest fate.

Category	Within-year ^a			Across years ^{b,c}		
	<i>n</i>	Distance	SE	<i>n</i>	Distance	SE
Age class						
Yearling	11	1,071	327	6	1,170	599
Adult	13	1,182	263	9	750	365
Nest fate^d						
Successful	—	—	—	6	712	438
Unsuccessful	—	—	—	9	1,055	453
Total^e	28	1,271	218	15	918	316

^a Distance between the first nest and the re-nest.

^b For two females that initiated ≥ 1 nest within a year, the mean coordinates of those nests were used to calculate the distance to the nest site in subsequent years.

^c Nests for one female were located in non-consecutive years; all other nests were located in consecutive years.

^d Nest fate refers to fate of first nests.

^e Age of four females was undetermined.

study. Additionally, we observed little age-specific variation—except that yearlings had slightly smaller clutches and marginally later hatch dates for first nest attempts than did adults.

For all known nests, initiation began in early May; peak hatching was 1 June for first nests and 22 June for re-nests (Fig. 1). Similar dates of nest initiation (mid-April through late May) and hatching (late May through mid-June) have been reported from studies throughout the species' range (Giesen 1998, Patten et al. 2005). Mean incubation length was 26.7 days (this study). Because nest at-

tentiveness of grouse increases throughout the laying period (Giesen and Braun 1979), we may have overestimated incubation length by misidentifying the start of incubation. However, the time required to hatch Lesser Prairie-Chicken eggs in an incubator (24–26 days; Coats 1955, Sutton 1968) was only slightly less than our estimate for eggs incubated by wild birds.

The success of all nests averaged 26% in our study, substantially less than estimates from New Mexico (42%) and Oklahoma (40%; Patten et al. 2005), but similar to the 28% reported by Giesen (1998) for 10 studies

TABLE 4. Distances (m) between Lesser Prairie-Chicken nest sites and leks in southwestern Kansas, 1997–2002.

Category	Nest site to lek of capture			Nest site to nearest lek		
	<i>n</i>	Median	Mean \pm SE	<i>n</i>	Median	Mean \pm SE
Year						
1997	25	1,528	1,647 \pm 226	26	556	557 \pm 52
1998	14	1,134	1,727 \pm 529	14	577	546 \pm 71
1999	24	2,357	2,317 \pm 332	25	726	701 \pm 55
2000	56	1,282	2,874 \pm 1,006	56	675	742 \pm 53
2001	37	1,396	3,241 \pm 983	41	727	740 \pm 54
2002	28	2,333	5,901 \pm 1,366	32	631	703 \pm 65
Age						
Yearling	68	1,893	3,580 \pm 853	68	633	702 \pm 48
Adult	91	1,258	3,104 \pm 591	97	675	718 \pm 32
Total	184^a	1,427	3,082 \pm 432	194^b	632	691 \pm 25

^a Includes 25 nests of females of unknown age.

^b Includes 29 nests of females of unknown age.

conducted throughout the range of the Lesser Prairie-Chicken. Giesen (1998) suggested that nest success from those 10 studies was negatively biased due to observer disturbance at nest sites. Negative bias in our study was likely only slight because females were flushed from their nests only once. Westemeier et al. (1998a) reported that flushing incubating Greater Prairie-Chickens (*T. cupido*) once did not result in reduced nest success. Also, the number of days between our initial nest visits and predation events averaged >10 days. In addition, only 2% of the nests in our study were abandoned—a much smaller percentage than the 25% reported by Riley et al. (1992) for Lesser Prairie-Chickens in New Mexico. Further, one of five nests abandoned during our study was abandoned 9 days after the researcher's visit, indicating that it probably was not due to human disturbance.

The percentage of females initiating a second nest during our study (31%) was between previous estimates for Lesser Prairie-Chickens in New Mexico (15%) and Oklahoma (79%; Patten et al. 2005), and it was less than the 83% reported for Greater Prairie-Chickens (Svedarsky 1988) and the 67% estimated for Sharp-tailed Grouse (*T. phasianellus*; Roersma 2001). The percentage of Greater Sage-Grouse (*Centrocercus urophasianus*) initiating a renest was highly variable (5 to 87%) throughout their range (Schroeder et al. 1999), and most estimates were less than what we observed for Lesser Prairie-Chickens. Our models indicated that the low probability of Lesser Prairie-Chickens renesting in southwestern Kansas was influenced by the length of incubation before their clutches were depredated (>50% of unsuccessful initial clutches were incubated >12 days prior to predation). Similarly, Schroeder (1997) reported that Greater Sage-Grouse in Washington whose initial nests failed late in incubation were less likely to renest than those whose nests failed earlier in incubation. Clutch size of the initial nesting attempt was also somewhat associated with renesting probability in our study; however, the magnitude of this effect was unclear. The positive relationship that we observed may have been due to increased fitness associated with females laying larger clutches or the possibility that we misclassified some re-nests as initial nest attempts. We speculate that

the latter was not a common occurrence during our study, but our methods did not allow us to locate nests that were depredated prior to the onset of incubation.

Few prairie grouse researchers have reported nest success separately for first nest attempts and subsequent renestings. Bergerud and Gratson (1988) hypothesized that predation of grouse nests was density-dependent and that re-nests would be more successful than first nest attempts due to lower nest densities. They also believed that nest success should improve as new vegetative cover appears throughout the nesting season. Success of first and second nesting attempts of Lesser Prairie-Chickens in Kansas, however, does not support Bergerud and Gratson's (1988) hypotheses, as first nest attempts were marginally more successful than renestings. Likewise, Greater Prairie-Chicken nests initiated in Kansas prior to 30 April (presumably first attempts) were more successful than nests initiated after 1 May (presumably re-nests; Robel 1970). Initial nesting attempts for Attwater's Greater Prairie-Chicken (*T. c. attwateri*) also were more successful than re-nests in 4 of 5 years (Lutz et al. 1994). Similar nest success for first attempts and subsequent renestings has been reported for Greater Prairie-Chickens in Colorado (Schroeder and Braun 1992) and Greater Sage-Grouse in Washington (Schroeder 1997) and Alberta, Canada (Aldridge and Brigham 2001). The only support for Bergerud and Gratson's (1988) hypothesis comes from studies on Sharp-tailed Grouse in Minnesota and North Dakota, where success was higher for second attempts than first attempts (Christenson 1970, Schiller 1973). In our study, Lesser Prairie-Chicken nests initiated after 15 May were less successful (11.9%, $n = 42$) than earlier nests (31.5%, $n = 143$), regardless of nesting attempt. We speculate that nests initiated after 15 May were less successful due to an increase in predator efficiency later in the nesting season, corresponding to changes in the structure and composition of vegetation. Cattle grazing began on our study area around 15 May, and, after that date, grass cover and visual obstruction decreased substantially (JCP unpubl. data). Grazing coupled with normal drought conditions during the summer months in southwestern Kansas may result in declining habitat quality, and, there-

fore, the poor success of renesting Lesser Prairie-Chickens. Land management practices that maintain taller and denser vegetation structure later into the nesting season may promote the overall nesting success of Lesser Prairie-Chickens.

Clutch size in Kansas averaged 11.3 eggs in 191 completed clutches—greater than that reported in New Mexico (8.7) and Oklahoma (10.8; Patten et al. 2005) or in 60 completed clutches located in other states occupied by Lesser Prairie-Chickens (10.4; Giesen 1998). Our study is the first to document substantially different mean clutch sizes for first nests (12.0 eggs) and renests (7.6 eggs). Merchant (1982) reported mean clutch size for initial and second nesting attempts, but his estimates were similar for both (9.8 and 10.7 eggs, respectively). In our study, the percentage of eggs containing a developed embryo was 94% and hatching success was 74%. Egg fertility has not been reported previously for the Lesser Prairie-Chicken, but hatching success of eggs was estimated at >90% across three studies (see Giesen 1998). The lower hatching success observed in our study reflects partial nest losses that occurred in 32 of 48 (67%) successful nests.

Identifying nest predators from nest remains is difficult because patterns of egg breakage overlap among, and even within, predator species (Larivière 1999). Uncertainties were reduced on our study area, however, because coyotes and gopher snakes were the only common species capable of preying on Lesser Prairie-Chicken nests. Studies in New Mexico and Texas revealed that Chihuahuan Ravens (*Corvus cryptoleucus*), badgers (*Taxidea taxus*), striped skunks (*Mephitis mephitis*), and ground squirrels were the primary predators of Lesser Prairie-Chicken nests (Davis et al. 1979, Haukos and Broda 1989, Riley et al. 1992). However, few corvids, badgers, or striped skunks were observed on our study area, and, although ground squirrels were abundant (estimated from casual roadside observations), they were identified as important nest predators during only 1 year (2000).

Davis et al. (1979) documented snakes preying on Lesser Prairie-Chicken nests in New Mexico. We found little evidence for snake predation of nests during the early years of our study (Jamison 2000), but snake abun-

dance appeared to increase (estimated from casual roadside observations), as did nest predation by snakes, in the later years (Pitman 2003). Snakes may have been responsible for most partial-nest depredations because of the lack of eggshell fragments at partly depredated nests. Also, three incubating Lesser Prairie-Chickens were likely killed by snakes because their intact carcasses were found with a thin film of mucus covering the heads. In each case, it appeared as if a snake had tried to swallow the bird.

Interspecific nest parasitism has been reported for Greater Prairie-Chickens and Sharp-tailed Grouse (Leach 1994, Westemeier et al. 1998b), but had not been reported for Lesser Prairie-Chickens before our work in Kansas (Hagen et al. 2002). Only 6 of 209 (3%) nests were parasitized by Ring-necked Pheasants and/or Northern Bobwhites, and 2 of the 6 (33%) nests produced Lesser Prairie-Chicken chicks. Hatching success of eggs in these two nests was 72%, similar to the 74% estimated for 46 unparasitized nests (Hagen et al. 2002). Our study provided no evidence that nest parasitism negatively affected nest success or hatchability of Lesser Prairie-Chickens.

Bergerud and Gratson (1988) hypothesized that successful female grouse would nest in the same area in the subsequent breeding season. In southwestern Kansas, female Lesser Prairie-Chickens nested within 712 m of the site of their previous year's nest site (if successful). This degree of philopatry is similar to that reported for Greater Sage-Grouse in Wyoming (Berry and Eng 1985) and Idaho (Fischer et al. 1993). Greater Sage-Grouse in Washington showed less philopatry to a previous year's successful nest location, moving an average of 1,600 m in the subsequent nesting season (Schroeder and Robb 2003).

The association between lek location and nest placement has important management implications for identifying critical nesting habitat. Bradbury (1981) hypothesized that female home ranges included only one lek and that >50% of all females should locate their nests nearer to that lek than other nearby leks. Studies of Greater Sage-Grouse and Sharp-tailed Grouse have provided support for this hypothesis (Bradbury et al. 1989, Giesen 1997). In Colorado and Minnesota, however,

only 23 of 89 (26%; Schroeder 1991) and 7 of 18 (39%; Svedarsky 1988) Greater Prairie-Chickens nested closer to their lek of capture than to other leks, respectively. Similarly, in Idaho Wakkinen et al. (1992) found 92% of Greater Sage-Grouse nests within 3 km of a lek, but only 55% were within 3 km of the lek of capture. Our Lesser Prairie-Chicken nesting data also do not support Bradbury's (1981) hypothesis: 80% of our females (147 of 184) nested closer to a lek other than that on which they were captured. More importantly, we located >80% of all nests within 1 km of a known lek site; thus, we believe that providing secure nesting habitat within 1 km of a lek site is an important management strategy.

Our study provides the first comprehensive description of Lesser Prairie-Chicken nesting ecology in terms of age-specific reproductive effort. Our estimates of Lesser Prairie-Chicken nesting parameters should be viewed as approximations, however, because our methodology did not allow us to locate nests that were destroyed during the laying process. Nevertheless, our estimates provide a much better understanding of Lesser Prairie-Chicken demography in sand sagebrush habitats. The low nest success we observed (26%) is troubling, especially if $\geq 50\%$ nest success is required for population stability (Westemeier 1979). Sensitivity analyses have revealed that nest success is one of the most influential demographic parameters affecting population growth of prairie grouse (Peterson and Silvy 1996, Wisdom and Mills 1997, Hagen 2003). Thus, habitat management designed to enhance nest success of Lesser Prairie-Chickens in southwestern Kansas should be a priority. Similar information on nesting ecology from Lesser Prairie-Chicken populations in other states and habitat types is needed to identify regional and site-specific conservation needs and to aid in the development of range-wide population models.

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