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Age-Specific Survival and Probable Causes of Mortality in Female Lesser Prairie-Chickens

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ABSTRACT Long-term population declines and habitat reductions have increased concern over the status of the lesser prairie-chicken (*Tympanuchus pallidicinctus*). Robust estimates of demographic parameters are essential for identifying population declines and planning effective management. We evaluated the effects of age and season on the survival of female lesser prairie-chickens at 2 sites in southwestern Kansas, USA. Using telemetry data from a 7-year field study (from 1997 to 2003), we estimated seasonal (Apr–Sep) and annual (Apr–Mar) survival. We also examined daily survival rates of females attending nests during the 26-day incubation period and young during the 14-day early brood-rearing period. We evaluated the probable mortality causes of radiomarked birds by examining evidence at recovery sites. We captured 227 female lesser prairie-chickens (87 yearlings, 117 ad, and 23 age undetermined) and fitted them with radiotransmitters. Estimates of 12-month survival were lower among yearlings ($\hat{S}_{12} = 0.429$, SE = 0.117) and adults at site I ($\hat{S}_{12} = 0.302$, SE = 0.080) than among yearlings ($\hat{S}_{12} = 0.588$, SE = 0.100) and adults at site II ($\hat{S}_{12} = 0.438$, SE = 0.083). The patterns in timing of mortality and age-specific 6-month survival were consistent with those of 12-month estimates at site I from 1998 to 2002, with a peak in mortality during May and June. Females tending to nests or to prefledged chicks had lower daily survival ($D\hat{S}R_{\text{tend}} = 0.993$, SE = 0.001) than females not involved in these activities ($D\hat{S}R_{\text{failed-breeder}} = 0.997$, SE = 0.002). We recorded 92 mortalities from April 1997 to March 2003, and 59% and 11% were attributed to predation by mammals and raptors, respectively. Our research suggests that predation during the nesting season can have a major impact on lesser prairie-chicken demography, and conservation efforts should focus on enhancing female survival during the nesting and brood-rearing seasons. (JOURNAL OF WILDLIFE MANAGEMENT 71(2):518–525; 2007)

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Estimates of survival and the timing of mortality events are important components of avian demography in wildlife management and evolutionary ecology (Caizergues and Ellison 1997). Estimates of annual variation in survival are important in management and the development of demographic models. Understanding seasonal variation in timing of mortality is especially important to management of grouse because females provide sole parental care and may be exposed to greater mortality risk during incubation and brood-rearing periods (Bergerud 1988). The relationship between vegetation cover at nest sites and female survival may be of particular importance for grouse (Wiebe and Martin 1998). Moreover, yearling and adult females may have different survivorship due to age-specific variation in reproductive effort and success (Hannon and Smith 1984, Sæther 1990, Sandercock et al. 2005, Fields et al. 2006). Differential survival in gender and age classes provides the basis for use of gender or age ratios in harvest or count data (Amman 1957, Campbell 1972, Lindén 1981, Moss 1987, Flanders-Warner et al. 2004).

Most estimates of survival for grouse have been based on

age ratios (Bergerud 1988). Survival estimates from age ratios assume a stable age distribution, stationary population size, and equal sampling of different age classes. More recently, analyses of live encounter and dead recovery data have provided improved estimates (Zablan et al. 2003, Hagen et al. 2005, Sandercock et al. 2005).

Many grouse populations have been designated as at risk (14 of 18 species are internationally red-listed), and accurate survival estimates are needed for management actions (Storch 2000:195). Demographic information is critical for management of the lesser prairie-chicken, a species of conservation concern that is currently designated warranted but precluded from protection under the Endangered Species Act (United States Department of the Interior, Fish and Wildlife Service 2002). Available information on lesser prairie-chicken survival is incomplete, as there are no annual estimates for females, and there is limited information on the seasonal timing of mortality (Hagen 2005). Other work in Kansas, USA, estimated survival of adult male (Hagen et al. 2005) and juvenile lesser prairie-chickens (Pitman et al. 2006b). Two previous studies from New Mexico, USA, examined survival rates of female lesser prairie-chickens. Ten years of band recovery data from hunters were used to provide a pooled estimate of annual survival for both sexes of 35% (Campbell 1972). For a small sample ($n = 33$) of radiomarked females pooled over 2 years,

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Merchant (1982) estimated a survival rate of 52% for the breeding season (Apr–Aug).

We conducted a 7-year field study to address the paucity of data on female lesser prairie-chicken survival. The objectives of this study were to 1) examine seasonal and annual variation in survival, 2) compare age-specific differences between yearlings and adults, 3) calculate the relative risk of females tending to nests or chicks versus those not tending to nests or young during the nesting period, 4) evaluate the effects of horizontal and vertical cover at nest sites on daily survival of females, and 5) identify the probable causes of mortality.

STUDY AREA

The study region comprised 2 remnant patches (approx. 5,000 ha each) of native sand sagebrush (*Artemisia filifolia*) prairie near Garden City, Finney County, Kansas (37°52'N, 100°59'W). We conducted work on site I (southwest of Garden City) from 1997 to 2003. During 2000–2003, we expanded our trapping and monitoring efforts to include site II (southeast of Garden City). Hunting was legal on both sites during this study. Descriptions of the study sites can be found in Pitman et al. (2005) and Hagen et al. (2005).

METHODS

Capture, Marking, and Monitoring

Using walk-in funnel traps, we captured lesser prairie-chickens during late March and early April at 20 leks (Haukos et al. 1990, Schroeder and Braun 1991). We trapped for an average of 8 days on all known leks in native prairie (Hagen et al. 2005). At capture, we classified females as yearling (approx. 10 months of age) or adult (≥ 22 months) based on shape, wear, and coloration of the 9th and 10th primaries (Amman 1944, Copelin 1963). We measured body mass (± 2.5 g) with a Pesola spring scale.

We marked female prairie-chickens individually with numbered aluminum leg bands. We equipped all but 3 captured females with necklace-style transmitters (≤ 12 g), which were $\leq 1.9\%$ of female body mass ($\bar{x} = 731$ g, $SD = 50$ g, range = 610–855 g, $n = 203$) and below the recommended 3% maximum level (Withey et al. 2001). Transmitters had either a 6-month (1997–1999) or 12-month (2000–2003) battery life with an 8-hour or 12-hour mortality switch.

Throughout each year, we monitored radiomarked birds daily by triangulating with a vehicle-mounted null-peak twin Yagi antenna system from spatially referenced locations. We located nesting females by approaching transmitter-equipped females on foot when locations were unchanged for ≥ 3 days. We assumed females were still incubating if telemetry bearings were unchanged from the previous day. We did not revisit nest sites until females departed with a brood or the nest was depredated or abandoned. Once a mortality switch had been activated on a transmitter, we relocated females with a portable receiver (R4000; Advanced Telemetry Systems, Isanti, MN) and handheld Yagi antenna, and we retrieved most radios within

24 hours. We conducted aerial surveys from fixed-wing aircraft at least once a month to relocate missing signals. If we relocated them in aerial surveys, we located birds that had emigrated from our study sites from vehicle-based telemetry systems approximately every 10 days. We did not include birds off the study area in the analyses.

Probable Causes of Mortality

When we located a carcass or kill site, we classified the probable cause of mortality as mammal, avian, snake, hunter, accident, or unknown based on evidence at recovery sites. It is difficult to make unambiguous statements about causes of mortality (Bumann and Stauffer 2002), and we refer to “probable causes of mortality” in this article. We attempted to minimize confounding effects of scavenging by recovering of transmitters emitting a mortality pulse in ≤ 24 hours.

A mortality event was classified as mammal predation by bite marks on the transmitter, whole carcass cached in soil or under a shrub, chewed feathers or aluminum band, in addition to tracks or mammalian scat at the recovery site. Potential mammalian predators we observed on our study sites were coyote (*Canis latrans*), American badger (*Taxidea taxus*), and bobcat (*Lynx rufus*). We classified as avian predation carcasses that had been decapitated or cleaned of the breast muscle with no apparent chewing, the presence of bird feces, and evidence of feather plucking. Potential avian predators included red-tailed hawk (*Buteo jamaicensis*), ferruginous hawk (*B. regalis*), rough-legged hawk (*B. lagopus*), northern harrier (*Circus cyaneus*), prairie falcon (*Falco mexicanus*), and great horned owl (*Bubo virginianus*). Evidence for snake predation included feathers matted with saliva or residue from the head to just above the furcula, which indicated an attempted ingestion. Accidental deaths included carcasses we recovered near a powerline, fence line, or dismembered by farm machinery with no apparent marks of predation. Hunter deaths were birds recovered and reported by the public. Unknown causes included mortalities that went undetected for > 2 days and carcasses with multiple signs at the recovery site (e.g., mammalian chew marks on feathers but located under a powerline). In the event that we recovered a carcass unscathed, we recorded it as possible disease. We submitted these specimens for necropsy at the Diagnostic Laboratory, College of Veterinary Medicine at Kansas State University.

Survival Modeling

We estimated seasonal (Apr–Sep) and annual survival (Apr–Mar) using known-fate models in Program MARK 4.1 (Cooch and White 2005). We developed encounter histories in which each estimation period (biweekly or monthly) was coded as live, censored, or dead. We examined the effects of the covariates age, year, and month on 6-month survival estimates, in which we modeled age and year as group effects and month as the time-dependent variation in the data. Also, we examined the effects of covariates age, site, and month on 12-month survival estimates, in which age and site were group effects and month was time-dependent

Table 1. Numbers of yearling (Y) and adult (A) female lesser prairie-chickens captured and radiomarked at 2 study sites in Finney County, Kansas, USA, 1997–2002.

Yr	Site I				Site II ^b			
	Y	A	Total	Months ^a	Y	A	Total	Months
1997	ND ^c	ND	23	6				
1998	18	5	23 ^d	6				
1999	18	16	34 ^d	6				
2000	7	19	26 ^{d,e}	12	11	14	25 ^e	12
2001	12	21	33 ^{d,e}	12	8	15	23 ^e	12
2002	3	11	14 ^{d,e}	12	10	16	26 ^e	12
Total	58	72	153 ^f		29	45	74	

^a Approx. battery life of transmitter and max. period for which overall probability of survival was estimated.

^b Field work commenced at site II in 2000.

^c ND = not determined.

^d Cohorts used to examine annual variation of age-specific survival rates for 6-month period.

^e Cohorts used to examine age- and area-specific rates in females for 12-month period.

^f Includes 23 birds of undetermined age.

variation in the data. We estimated overall survival for 6 months or 12 months using the derived parameter estimates output function in Program MARK.

Seasonal variation in survival could be due to general changes in predator communities or to increased vulnerability of incubating females. To examine these alternatives, we used breeding-season encounter histories from females attending offspring (yearling = 68, ad = 88) and females that were failed breeders (yearling = 39, ad = 58) to evaluate the mortality risk of tending a nest or preledged chicks using nest survival models in Program MARK (Cooch and White 2005). We refer to females incubating or tending to preledged chicks as tending females, and we refer to females that lost nests and remained on our study areas foraging as failed-breeders. We estimated daily survival rates ($D\hat{S}R$) of yearling and adult females during the nesting season based on nesting status, but we did not estimate nest survival. Use of nest-survival models for estimating survival with telemetry data is appropriate when date of loss is unknown (Cooch and White 2005). Because we modeled survival through early brood rearing and we estimated the actual day of brood loss, these models were appropriate for our data. We estimated $D\hat{S}R$ over a 40-day period for each nesting attempt, which included 26 days of incubation and 14 days posthatch (preledging of chicks). We estimated the probability of surviving the 40-day period by raising the $D\hat{S}R$ by a power of 40. A female's encounter history could contribute exposure days to both tending and failed-breeder groups. For example, a female that incubated a nest for 15 days prior to failure but was lost on day 15 provided 15 exposure days to the tending group and 25 exposure days to the failed-breeder group. However, if this female attempted a second nest, we added the number of days spent incubating that second nest to the exposure days for tending females. Thus, each nesting attempt by a female contributed to the total exposure days.

Variation in daily survival could be due to differences in vertical or horizontal cover at nest sites. To examine these alternatives, we evaluated 4 survival models for females during the incubation period only and included covariates of

horizontal cover (shrub cover) and vertical structure (visual obstruction readings [VOR]) at nest sites. A detailed description of nest-site vegetation measurements can be found in Pitman et al. (2005). We constructed all models using the design matrix tool and a logit link function in Program MARK 4.1 (Cooch and White 2005).

Global models were the most highly parameterized, but they were not necessarily fully saturated models. We based model selection on the minimization of Akaike's Information Criterion corrected for small sample size (AIC_c), and AIC_c weights (w_i). We used multi-model inference in cases in which the difference in AIC_c values (ΔAIC_c) between the best fit and alternative models was ≤ 2 (Burnham and Anderson 2002). We used model deviance to further evaluate the relative importance of adding one additional parameter to the best fit model when ΔAIC_c was ≤ 2 (Burnham and Anderson 2002).

Data Sets and Candidate Models

Battery life of transmitters and number of study sites differed among the 6 years of our study (Table 1). To examine seasonal, annual, and age-dependent variation in survival, we used different subsets of our data. To examine seasonal and age-specific survival during the breeding season, we restricted our analysis to site I during the period April to September from 1998 to 2002. However, we pooled across both sites and years (1998–2002) to estimate $D\hat{S}R$ s of tending and failed-breeder females. To examine site-specific and 12-month survival, we restricted our analysis to sites I and II from 2000 to 2003, when we deployed 12-month transmitters at both sites. To examine probable causes of mortality, we included data from all radiomarked females during 1997–2003.

RESULTS

We fitted 227 females (87 yearlings, 117 ad, and 23 age undetermined) with radiotransmitters (Table 1). We did not consider 7 birds that died within the 2-week acclimation period after initial marking. An additional 46 birds were right-censored in our analysis. Right-censoring was primar-

Table 2. Candidate models and model statistics for monthly survival over a 6-month period (Apr–Sep) for lesser prairie-chickens at site I, Finney County, Kansas, USA, 1998–2002.

Model structure	Model statistic ^a			
	Dev	<i>K</i>	ΔAIC_c	w_i
S_{month}	47.53	6	0.00 ^b	0.367
$S_{\text{year+month}}$	39.40	10	0.14	0.342
$S_{\text{age+month}}$	46.12	7	0.64	0.266
$S_{\text{age+year+month}}$	34.60	15	5.88	0.019
$S_{\text{age}\times\text{month}}$	43.36	12	8.30	0.006
S_{constant}	75.93	1	18.24	0.000
S_{year}	68.28	5	18.70	0.000
S_{age}	74.56	2	18.89	0.000
$S_{\text{year}\times\text{month}}$	15.46	30	19.69	0.000
$S_{\text{age+year}}$	61.99	10	22.73	0.000
$S_{\text{age+year}\times\text{month}}$	0.00	60	76.82	0.000

^a Model fit is described by deviance (Dev), the no. of parameters (*K*), the difference in Akaike's Information Criterion corrected for small sample size (ΔAIC_c), and the AIC_c wt (w_i).

^b $\text{AIC}_c = 237.98$ for the best fit model.

ily due to radio loss (30%), failure (24%), or known emigration outside of our study sites (46%).

Seasonal Survival

Monthly variation was an important structure within all competing models for seasonal survival, as either an additive or a main effect (Table 2). Much of the time-dependent variation in survival was centered on the nesting season in May and June and was lowest in 2000 and 2001 (Fig. 1A, B). Yearly variation in the seasonal survival of females was strongly supported by the data ($\Delta\text{AIC}_c = 0.14$, $w_2 = 0.34$), with an additive monthly effect (Fig. 1A). Although the model including age-specific survival of females had a $\Delta\text{AIC}_c = 0.64$ ($w_3 = 0.27$), the deviance was relatively unchanged from the best model, indicating that age was not as important as yearly variation to the observed survival estimates. The 6-month probability of survival (\hat{S}_6) varied from 0.571 to 0.855 from 1998 to 2002 ($S_{\text{year+month}}$), and survival of yearling females ($S_{\text{age+month}}$; $\hat{S}_6 = 0.759$, SE = 0.061) was greater than that of adult females ($\hat{S}_6 = 0.658$, SE = 0.058) during this period (Table 3). To explore the seasonal timing of mortality events, we examined survival with a 2-week instead of a monthly time step. The period of lowest 2-week survival occurred when a majority of females were incubating in June, and female survival rates increased once nesting activities ceased in July (Fig. 1C).

Survival of nesting females.—Daily survival during nesting was best modeled as separate probabilities for tending and failed-breeder groups (S_{tend} ; $w_1 = 0.61$). However, a model with constant survival across groups and time had some support from the data ($\Delta\text{AIC}_c = 2.53$, $w_2 = 0.17$; Table 4). Daily survival for tending females ($D\hat{S}R_{\text{tend}} = 0.991$, 95% CI = 0.987 to 0.994) was less ($D\hat{S}R_{\text{difference}} = -0.006$, 95% CI = -0.010 to -0.002) than failed-breeders during the nesting period ($D\hat{S}R_{\text{failed-breeder}} = 0.997$, 95% CI = 0.994 to 0.998). Differences in $D\hat{S}R$ led to marked differences ($\hat{S}_{\text{difference}} = -0.128$, 95% CI = -0.219 to -0.038) in period survival when extrapolated over the 40-day breeding period

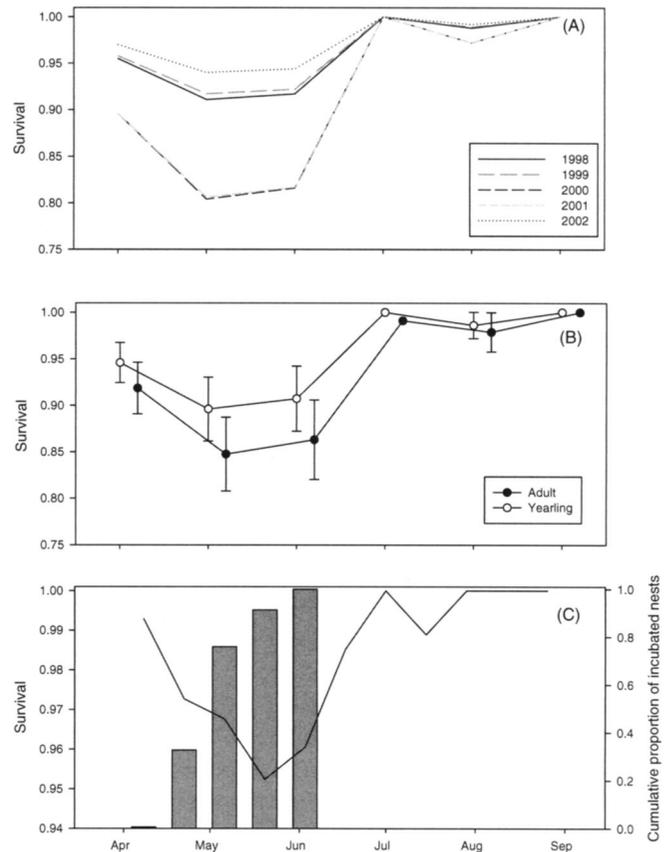


Figure 1. (A) Annual variation in monthly survival of female lesser prairie-chickens at site I ($n = 153$), in Finney County, Kansas, USA, 2000–2003, from the model $S_{\text{year+month}}$; we omitted standard errors for clarity. (B) We estimated yearling (white circles, $n = 58$) and adult (black circles, $n = 72$) female survival ($\pm\text{SE}$) at site I from the model $S_{\text{age+month}}$. We offset point estimates by age class at each interval for clarity; each estimate is for the same time period during an interval. (C) We also depict the relationship between biweekly survival estimates of females (solid line; $n = 199$) and cumulative frequency distribution of incubating females (gray bars; $n = 183$).

($\hat{S}_{\text{tend}} = 0.758$, 95% CI = 0.657 to 0.833; $\hat{S}_{\text{failed-breeder}} = 0.886$, 95% CI = 0.786 to 0.942).

Effects of nesting habitat on survival.—There was considerable model selection uncertainty and ΔAIC_c values were <2 for 3 of 4 models. However, incubating female survival was best modeled as a constant probability. Shrub cover and VOR tended to be positively ($\beta_{\text{shrub}} = 0.192$, 95% CI = -0.328 to 0.714) and negatively ($\beta_{\text{VOR}} = -0.062$, 95% CI = -0.556 to 0.432) associated with survival of nesting females, respectively, but neither covariate was significant.

Annual Survival

Site-specific survival with an additive time effect for females was strongly supported; however, monthly variation alone was a competitive model (S_{month} ; $\Delta\text{AIC}_c = 0.76$, $w_1/w_2 = 1.5$; Table 5). Age-specific differences in survival were present in the data but were not independent of study site or month, as evidenced by relatively small changes in the deviance. A parsimonious model with age-specific structure in survival included additive effects of both month and site ($S_{\text{age+site+month}}$ $\Delta\text{AIC}_c = 1.88$, $w_3 = 0.18$). Estimates from this

Table 3. Estimates of survival for a 6-month period (Apr–Sep) for radiomarked female lesser prairie-chickens on site I in Finney County, Kansas, USA, 1998–2002. Estimates derived from models $S_{\text{year+month}}$ and $S_{\text{age+month}}$.

Group	Parameter estimate		
	\hat{S}_6^a	SE	95% CI
Yr			
1998	0.788	0.094	0.551–0.918
1999	0.802	0.073	0.623–0.908
2000	0.571	0.098	0.378–0.744
2001	0.574	0.093	0.389–0.740
2002	0.855	0.095	0.568–0.963
Age specific			
Yearling	0.759	0.061	0.620–0.858
Ad	0.658	0.058	0.536–0.762

^a We estimated period survival (6 months) using the derived parameter estimates function in Program MARK.

model indicated that the annual probability of survival at site II was substantially higher ($\hat{S}_{12} = 0.499$, SE = 0.066) than that of site I ($\hat{S}_{12} = 0.347$, SE = 0.069). The annual probability of survival was less for yearlings ($\hat{S}_{12} = 0.429$, SE = 0.117) and adults at site I ($\hat{S}_{12} = 0.302$, SE = 0.080) than for yearlings ($\hat{S}_{12} = 0.588$, SE = 0.100) and adults at site II ($\hat{S}_{12} = 0.438$, SE = 0.083). Monthly variation in survival from the model $S_{\text{site+month}}$ indicated that the greatest mortality occurred during the breeding season in May (Fig. 2). Overall monthly survival, as estimated from the model S_{month} , during the nesting and brood-rearing season (\hat{S}_4 for Apr–Jul = 0.685,

Table 4. Candidate models and model statistics for daily survival rates over a 40-day period for female lesser prairie-chickens tending to nests or prefledged chicks and failed breeders at 2 sites in Finney County, Kansas, USA, 1998–2002.

Model structure ^a	Model statistic ^b			
	Dev	K	ΔAIC_c	w_i
Female parental care				
S_{tend}	371.66	2	0.00 ^c	0.613
S_{constant}	376.20	1	2.53	0.173
$S_{\text{age+tend}}$	370.70	4	3.04	0.134
S_{age}	375.75	2	4.08	0.080
$S_{\text{age+tend+t}}$	307.69	101	137.61	0.000
S_t	318.17	98	141.88	0.000
$S_{\text{tend}\times t}$	282.18	196	312.18	0.000
$S_{\text{age}\times t}$	292.94	196	322.94	0.000
$S_{\text{age+tend}\times t}$	255.08	392	719.91	0.000
Vegetation at nest sites				
S_{constant}	201.10	1	0.00 ^d	0.469
S_{shrub}	200.56	2	1.46	0.227
S_{VOR}	201.04	2	1.94	0.178
$S_{\text{shrub+VOR}}$	199.73	3	2.63	0.126

^a Subscripts: tend = tending nests or prefledged chicks and failed-breeders, age = yearling and ad, t = exposure d, VOR = visual obstruction readings.

^b Model fit is described with deviance (Dev), the no. of parameters (K), the difference of Akaike's Information Criterion corrected for small sample size (ΔAIC_c), and the AIC_c wt (w_i).

^c $\text{AIC}_c = 375.67$ for the best fit model of tending F.

^d $\text{AIC}_c = 203.10$ for the best fit survival model with nest-site vegetation covariates.

Table 5. Candidate models and model statistics for monthly survival of female lesser prairie-chickens in a 12-month period (Apr–Mar) at 2 sites in Finney County, Kansas, USA, 2000–2003.

Model structure	Model statistic ^a			
	Dev	K	ΔAIC_c	w_i
$S_{\text{site+month}}$	28.89	13	0.00 ^b	0.466
S_{month}	31.70	12	0.76	0.319
$S_{\text{age+site+month}}$	26.64	15	1.88	0.182
$S_{\text{age+month}}$	34.25	13	5.36	0.032
$S_{\text{site}\times\text{month}}$	19.34	24	13.38	0.001
$S_{\text{age}\times\text{month}}$	20.89	24	14.94	0.000
S_{age}	67.23	2	15.95	0.000
S_{site}	67.35	2	16.07	0.000
S_{constant}	70.11	1	16.82	0.000
$S_{\text{age+site}}$	64.69	4	17.45	0.000
$S_{\text{age+site}\times\text{month}}$	0.00	48	46.09	0.000

^a Model fit is described with deviance (Dev), the no. of parameters (K), the difference of Akaike's Information Criterion corrected for small sample size (ΔAIC_c), and the AIC_c wt (w_i).

^b $\text{AIC}_c = 455.56$ for the best fit model.

SE = 0.037) was less than winter survival (\hat{S}_4 for Nov–Feb = 0.770, SE = 0.056).

Probable Causes of Mortality

We recorded 92 deaths from April 1997 to March 2003 (Table 6). We attributed the majority of mortality to mammalian predation (59%). Four intact carcasses were cached under shrubs. Mammals killed 21 females incubating nests and 7 females attending broods. Most mortalities of females attending broods (6 of 7) occurred within 2 weeks of hatching, and they represented half of the non-nesting mortality during June. Raptor predation of radiomarked females occurred more frequently (15%) in early spring (Mar–Apr) and in winter (Nov–Feb) than in summer (11%). We attributed 3 female mortalities to snake predation, and these females were >20 days into incubation when they were killed. The gopher snake (*Pituophis catenifer*) was the probable predator because we discovered it consuming eggs at 4 nests, and it is the only snake on the study area large enough to constrict and attempt to swallow a female lesser prairie-chicken. In 2001, 2 females died of potential diseases during the nesting season. Avian cholera (*Pasturella multocoda*) was isolated from body tissues of one female and was likely the cause of death. This female had been incubating for 12 days at the time of death, and we recovered her <10 m from her undisturbed clutch of eggs. The other female had not been located on a nest, although the pattern of her radiolocations suggested she had been laying eggs for ≥ 8 days. Losses to hunting were small (1%) among our radiomarked birds ($n = 220$), and this rate did not increase appreciably (4%) if we included females collected for research (Robel et al. 2003).

DISCUSSION

Annual Variation in Survival

Annual variation in seasonal survival was evident and was closely related to mortality rates of incubating females on

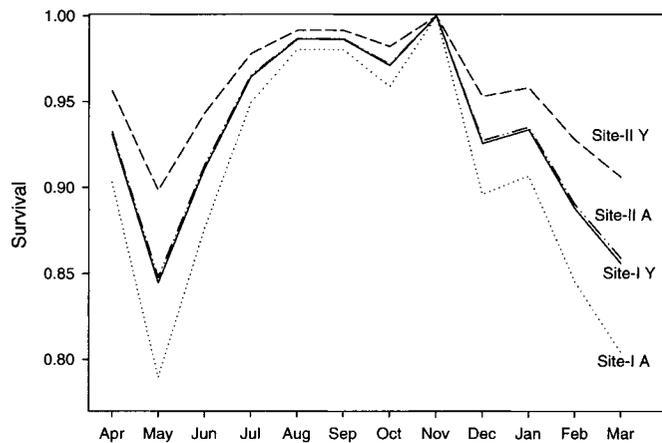


Figure 2. Monthly survival estimates (we omitted SE for clarity) of yearling (Y; $n = 51$) and adult (A; $n = 96$) female lesser prairie-chickens estimated from the model $S_{\text{age+site+month}}$ over a 12-month period on sites I and II in Finney County, Kansas, USA, 2000–2003.

nests (Fig. 1A, C); >30% of all female mortality was associated with the nesting and brood-rearing period. Annual variation in suitable nesting cover may have influenced nest success or female losses (Bergerud 1988, Wiebe and Martin 1998, Hannon et al. 2003). Female grouse select nest sites to optimize thermoregulation, detect predators, and elude predators during incubation. There may be a tradeoff between survival and the amount of cover at a nest site (Wiebe and Martin 1998). In our study, survival of incubating females was positively associated with nest sites with greater shrub cover but less vertical vegetation structure. Similarly, survival of female white-tailed ptarmigan (*Lagopus leucura*) during incubation was correlated with less vertical structure (Wiebe and Martin 1998). Because female grouse depend on cryptic plumage to avoid predators, predator detection and quick escape during incubation are important to survival. Therefore, optimum nest concealment should comprise moderate vertical cover and greater overhead cover.

In Oklahoma and New Mexico, USA, lesser prairie-chicken survival was positively correlated with greater shrub cover, and lesser prairie-chickens that occupied cooler and more humid sites throughout a year increased their survival (Patten et al. 2005a). Similarly in our study, site II had greater sand sagebrush density than site I (Hagen 2003) and may have had implications for avoiding predators and thermoregulation throughout the year. However, we hypothesize that relationship between survival of nesting females and cover is nonlinear, as there is likely an upper limit of shrub cover where predator detection and escape may be hindered (Wiebe and Martin 1998, Pitman et al. 2005). Mortalities during brood rearing suggest an added cost to survival for females during the reproductive period (Hannon et al. 2003). Annual fluctuations in female survival were largely dependent upon losses during the nesting season, and we hypothesize that these losses were likely attributed to the cost of reproductive effort.

Generally, annual variation in reproductive output may

Table 6. Number and percentage of female lesser prairie-chicken mortalities attributed to probable causes in Finney County, Kansas, USA, 1997–2003.

Probable cause	No. of mortalities ^a				%
	1997–1999		2000–2003		
	Summer ^b	Winter ^b	Summer	Winter ^b	
Predator					
Mammal	15	27	12	54	59
Raptor	1	5	4	10	11
Snake	0	3	0	3	3
Unknown	2	8	7	17	18
Disease	0	2	0	2	2
Accident ^d	1	1	3	5	5
Hunter	0	0	1	1	1
Total	19	46	27	92	100

^a Because transmitter battery life expectancy was 6 months from 1997 to 1999, we separated those mortalities from birds tracked throughout the yr 2000–2003.

^b We defined summer as months of Apr–Sep and winter as Oct–Mar.

^c Mortality during nesting was a considerable portion of all F losses, as 10 of 19 (53%) and 19 of 73 (26%) occurred during that period in 1997–1999 and 2000–2003, respectively.

^d Accidents included collisions with powerlines ($n = 4$) and one loss to farm machinery during nest incubation in an alfalfa field.

affect survival. Our examination of daily survival of females attending offspring and failed-breeders supported the idea that a tradeoff exists between reproductive effort and survival. In fact, tending females had lower daily survival than females who lost their nests and were foraging on the study areas during the nesting period. When rearing young, females may maximize reproductive output at the cost of survival, and yearlings may not be as effective in maximizing reproductive output as adults, thus manifesting as age-structured survival in our population.

Age-Specific Survival

Age-specific patterns in female survival were present, but study site and month had greater weight in describing survival. However, point estimates of yearling survival were higher than adults; this is opposite to several other avian species (Sæther 1990). A similar pattern but with a greater age effect on survival was found in an analysis of live encounter data for male lesser prairie-chickens at our study sites (Hagen et al. 2005). In males, it was hypothesized that costs associated with increased reproductive activity at lek sites may have contributed to lower survival for birds ≥ 2 years of age (Hagen et al. 2005). Behavioral responses of female grouse during the breeding season can affect survival rates (Hannon and Smith 1984, Hannon et al. 2003). Adult female willow ptarmigan (*Lagopus lagopus*) may have lower survival because adults were more tenacious (i.e., a fight response) in nest guarding or brood defense than were yearlings (Hannon and Smith 1984). Similarly, male willow ptarmigan were less defensive of chicks than females during brood rearing and had higher survival rates (Hannon et al. 2003). If similar age-specific behavioral responses occur in lesser prairie-chickens, this may explain the pattern of age-specific survival we observed in our study.

Probable Causes of Mortality

The possibility of mammalian scavenging makes predator classification from evidence at kill sites problematic (Bumann and Stauffer 2002). However, if a bias occurred in this study it was likely consistent across age classes and study sites. Thus, the magnitude of the difference in cause-specific mortality rates should be a reasonable index to compare proportional losses between groups.

Predation had a considerable effect on lesser prairie-chicken survival. Most mortality of lesser prairie-chicken females was classified as mammalian and nearly one-third of those events occurred during the nesting and brood-rearing periods. It is likely that coyotes were the primary mammalian predator because they were an important nest predator at both study areas (Pitman et al. 2006a), and the peak period of nest predation corresponded with increased adult mortality. The seasonal timing of avian predation on females in our study coincided with presence of wintering or migratory populations of raptors. Causes of mortality for juvenile lesser prairie-chickens on our study areas were proportional to causes of adult losses and most mortality occurred prior to November (Pitman et al. 2006b). Because we had no other studies with which to compare these losses, it is unclear if this level of predation is detrimental to the population.

Parasites and diseases can affect populations of prairie grouse, but few studies have examined such factors for a period long enough to detect such effects (Peterson 2004). Despite mortality associated with avian cholera, extensive disease surveys (assays of individual prairie-chickens; $n = 165$) in these populations did not reveal any clinical conditions of diseases (Hagen et al. 2002, Wiedenfeld et al. 2002). Similarly a parasitological survey of our populations from 1997 to 1999 recorded that parasite burdens and demographic rates did not differ between birds with heavy and low parasite burdens (Robel et al. 2003).

Accidental deaths due to powerline or fence collisions have a substantial impact on populations of European grouse (Miquet 1990, Bevanger 1995, Moss et al. 2000). In our study, this loss appeared to be relatively small, and collisions with powerlines occurred as birds were leaving the prairie to forage in adjacent agricultural fields. Our collision rate was similar to that of greater sage-grouse (*Centrocercus urophasianus*) in Idaho, USA (Connelly et al. 2000). Survival of lesser prairie-chickens in Oklahoma was negatively affected by the density of fences as compared to a population in New Mexico on an area with a lower fence density (Patten et al. 2005b). It is possible that some portion of the unknown cause of death category in our study was associated with powerline or other collisions; thus, our estimate may be conservative.

Hunting mortality was low among radiomarked females and similar to all banded birds (<1.5%; Hagen 2003). It has been hypothesized that fall hunting mortality of <10% should not impact spring breeding populations of European grouse (Ellison et al. 1988; Ellison 1991a, b). Connelly et al. (2000) suggested that harvest of female greater sage-grouse

was additive to overwinter mortality. Hunting mortality of 20% was mostly additive to both adult and juvenile ruffed grouse (*Bonasa umbellus*) in Wisconsin, USA (Small et al. 1991). If some cohorts are more susceptible to hunting mortality early in the season, the timing of hunting seasons can negatively affect populations if females are disproportionately harvested (Flanders-Warner et al. 2004). Current levels of hunting mortality appeared to have minimal impact on lesser prairie-chicken survival in southwestern Kansas.

MANAGEMENT IMPLICATIONS

Management of lesser prairie-chickens should focus on habitat manipulations that decrease female mortality during incubation and early brood rearing. In fragmented populations, predator control may achieve short-term goals of increased female survival but may be prohibitive to sustain over the long term (Schroeder and Baydack 2001). Long-term management should focus on creating suitable nesting habitat that minimizes loss of females to mammalian predation. Specifically, managers should identify habitat structure that lowers predation on nesting females. Maintaining moderate levels of vertical structure (2–3 dm) and shrub canopy cover (15–20%) will likely enhance female survival during the nesting period. The importance of residual grass (i.e., cover and ht) has been identified in nest-site selection, but additional information is needed on the link between these variables and female survivorship during the nesting period (Hagen et al. 2004, Pitman et al. 2005). Limiting harvest by hunters would probably have little impact on lesser prairie-chickens in Kansas because most mortality occurs during the nesting season. However, more accurate information is needed on harvest rates throughout the range of lesser prairie-chickens. Future assessments of demographic sensitivity and viability of lesser prairie-chickens are needed to evaluate the impacts of mortality during the breeding and fall hunting seasons to identify which factors best explain variation in rates of population growth.

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