Survival of Juvenile Lesser Prairie-Chickens in Kansas
Author(s): James C. Pitman, Christian A. Hagen, Brent E. Jamison, Robert J. Robel, Thomas M. Loughin, Roger D. Applegate
Source: *Wildlife Society Bulletin*, Vol. 34, No. 3 (Oct. 1, 2006), pp. 675-681
Published by: Allen Press
Stable URL: http://www.jstor.org/stable/3784695
Accessed: 12/03/2010 09:26

Peer Reviewed

Survival of Juvenile Lesser Prairie-Chickens in Kansas

JAMES C. PITMAN,[1,2] *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
CHRISTIAN A. HAGEN,[3] *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
BRENT E. JAMISON,[4] *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
ROBERT J. ROBEL, *Division of Biology, Kansas State University, Manhattan, KS 66506, USA*
THOMAS M. LOUGHIN, *Department of Statistics, Kansas State University, Manhattan, KS 66506, USA*
ROGER D. APPLEGATE,[5] *Kansas Department of Wildlife and Parks, Emporia, KS 66801, USA*

Abstract

*Juvenile survival has been identified as the most critical demographic parameter influencing grouse populations. Little information currently exists on survival of juvenile lesser prairie-chickens (*Tympanuchus pallidicinctus*). We regularly flushed 51 individually identifiable lesser prairie-chicken broods over a 6-year period to estimate survival from hatch to 14 days post-hatch (early period) and from 15 to 60 days post-hatch (late period). Estimates of overall daily survival rates were 0.949 (95% CI = 0.932–0.966) for the early period and 0.978 (95% CI = 0.968–0.989) for the late period. Overall survival from hatch to 60 days posthatch was 0.177 (95% CI = 0.028–0.376). We used encounter histories of 31 transmitter-equipped juveniles to estimate survival from 1 August to 31 March (overwinter) using known-fate models. Juvenile overwinter survival was 0.70 (95% CI = 0.47–0.86), and chicks heavier than average for their age at 50–60 days posthatch were more likely to survive the 8-month overwinter period. Survival of juveniles from hatch to 31 March of the following year was 0.12 (95% CI = 0.01–0.32). We compared overwinter survival of juveniles and 93 transmitter-equipped full-grown lesser prairie-chickens using a second set of models. Overwinter survival rates for juveniles (0.64) and full-grown (0.63) birds were similar, but the timing of mortality events differed between age-classes. We recommend that managers in Kansas, USA, focus on improving early survival of juveniles by providing additional food resources to chicks. This can be accomplished by manipulating vegetation to increase forb cover, which will result in increased invertebrate biomass.* (WILDLIFE SOCIETY BULLETIN 34(3):675–681; 2006)

Key words

Artemisia filifolia, *chicks, juveniles, Kansas, lesser prairie-chicken, mortality, radiotelemetry, sand sagebrush, survival,* Tympanuchus pallidicinctus.

The lesser prairie-chicken occupies xeric grasslands dominated by sand sagebrush (*Artemisia filifolia*) or shinnery oak (*Quercus havardii*) in portions of southwestern Kansas, southeastern Colorado, western Oklahoma, northern Texas, and eastern New Mexico, USA (Copelin 1963, Giesen 1998). An estimated 92% of the land historically occupied by lesser prairie-chickens has been converted to cropland, and the species has experienced an estimated 97% range-wide decline since the 1800s (Crawford 1980, Taylor and Guthery 1980). In Kansas, the lesser prairie-chicken is most abundant south of the Arkansas River in mixed- and short-grass prairie dominated by sand sagebrush. Counts of leks and individual birds suggest the Kansas population has experienced a steady decline since 1964 (Jensen et al. 2000). Most of the decline in Kansas has been attributed to destruction of habitat for center-pivot irrigated cropland (Jamison 2000, Jensen et al. 2000). Populations have continued to decline even though little land conversion has occurred since the mid-1980s (Jensen et al. 2000), which suggests that habitat quality also may be declining.

Survival of juveniles from hatch to their first breeding season has been identified as the most critical demographic parameter associated with changes in prairie grouse population size (Wisdom and Mills 1998, Hagen 2003). Previous researchers have estimated survival of juvenile lesser prairie-chickens from hatch to late summer based on brood size (Davison 1940, Schwilling 1955, Copelin 1963, Merchant 1982). However, estimates of survival based on late summer counts fail to account for total brood loss. If losses of entire broods are common, chick survival estimates derived from late-summer brood counts will be biased high (Bergerud and Gratson 1988). We regularly flushed broods of transmitter-equipped female lesser prairie-chickens to provide a more reliable estimate of juvenile survival. We also modeled overwinter survival of transmitter-equipped juveniles from 1 August to 31 March. We report the first estimates of juvenile lesser prairie-chicken survival from hatch through the following breeding season.

Study Area

We conducted research in sand sagebrush prairie south of Garden City, Kansas, USA (37°52′N, 100°59′W), from spring 1997 through spring 2003 in 2 phases. Phase I was initiated on a 7,700-ha sand sagebrush prairie area (Site I) in 1997, and Phase II was started on a nearby 5,600-ha prairie area (Site II) in 2000; work continued on both areas through spring 2003. Each site was bounded almost entirely by center-pivot irrigated cropland and grazed seasonally by livestock. Sand sagebrush was the most obvious vegetation component on each site, and the primary grasses were native warm-season bunchgrasses typically associated with lesser prairie-chicken habitat in southwest Kansas (Hulett et

[1] *E-mail: jimp@wp.state.ks.us*
[2] *Present address: Kansas Department of Wildlife and Parks, Emporia, KS 66801, USA*
[3] *Present address: Oregon Department of Fish and Wildlife, Bend, OR 97701, USA*
[4] *Present address: Missouri Department of Conservation, Clinton, MO 64735, USA*
[5] *Present address: Tennessee Wildlife Resource Agency, Ellington Agricultural Center, Nashville, TN 37204, USA*

al. 1988, Pitman 2003). The principal invertebrate components on our sites were ground beetles (Carabidae), camel crickets (Gryllacrididae), short-horned grasshoppers (Acrididae), darkling beetles (Tenebrionidae), and ants (Formicidae) with Acrididae biomass constituting >70% of all sweepnet-collected invertebrate biomass (Jamison et al. 2002, Hagen et al. 2005). Annual precipitation averaged 50 cm (U.S. Department of Commerce 2003) and ranged from 42 cm (2000) to 59 cm (1997) during our study.

Methods

We captured lesser prairie-chickens on leks in spring using walk-in funnel traps (Haukos et al. 1990, Schroeder and Braun 1991). We equipped each captured female with an 11-g necklace-style transmitter and released them on-site immediately following capture. We monitored transmitter-equipped birds on the 2 study sites daily throughout the nesting and brood-rearing season using a truck-mounted null-peak telemetry system. Capture and handling procedures were approved by the Animal Care and Use Committee at Kansas State University (ACUC #2609).

Brood Flush Counts

During both phases of our project, we used regular flush counts to gather data on the number of chicks in a brood (Hubbard et al. 1999). We approached transmitter-equipped females on foot at 14 days post-hatch and flushed them to determine whether chicks were present. At 14 days post-hatch, chicks were capable of only weak flights (Giesen 1998) and were more likely to hide than fly. Thus, to acquire more accurate counts, we conducted the initial flush at sunrise while the female was still brooding the chicks. We flushed broods 5 more times at approximately 10-day intervals until 60 days post-hatch. We conducted the subsequent 5 flush counts opportunistically during daylight hours with most counts occurring in the early morning. For every count, we thoroughly searched the flush area until the researcher was confident all chicks had been located and flushed. If no chicks were located, we used subsequent flush counts at normal intervals to confirm presence or absence of chicks. When we detected chicks in these later flush counts, we used the number flushed to update the previous count from zero.

Capturing and Releasing Chicks

During Phase II, we located transmitter-equipped females with chicks at night between 30 and 40 days post-hatch and used long-handled nets and spotlights to capture chicks. We transported captured birds to a vehicle in cotton bags and measured body mass with an electronic balance. We equipped chicks weighing ≥150 g with a 2-g necklace-style transmitter (60-d battery life) with a temperature-sensitive switch. This was a surrogate for a mortality switch in these small transmitters. We returned chicks to their capture location and released them immediately following handling. Beginning at approximately 55 days post-hatch, we used the same procedures to capture additional birds and all previously transmitter-equipped chicks. At this time, we fitted all captured chicks with an 11-g necklace-style transmitter (life expectancy of 1 yr) with an 8-hour activity switch. Midway through the 2000 field season, we collected blood samples from each bird and submitted them to a genetics lab (Zoogen Inc., Davis, California) where chromosome analysis of blood cells was used to identify the gender of each bird (Griffiths et al. 1998). Captures on lek sites during subsequent years were used to ascertain the gender of some birds not classified by chromosome analysis.

Monitoring Broods and Chicks

We used a truck-mounted null-peak telemetry system to monitor transmitter-equipped females with broods (Phases I, II) and individual chicks (Phase II) on a daily basis until death of the bird, dispersal from the primary study sites, or transmitter failure. We examined the remains of dead birds and systematically searched the surrounding area for tracks or scat to help establish the cause of death. When transmitter-equipped birds dispersed from the study areas, we located them from a Cessna 150 aircraft (Cessna Aircraft, Wichita, Kansas) using aerial telemetry equipment. We relocated chicks dispersing to areas other than the 2 primary study sites 2 or 3 times per week. In the final year of this project (2002–2003), we located transmitter-equipped birds daily only through mid-August. From mid-August to the following March, we monitored birds at approximately monthly intervals from a Cessna 150 aircraft.

Data Analyses

Mayfield estimates of brood survival.—We estimated daily survival rates from brood flush count data for early and late brood-rearing periods. We defined the early and late brood-rearing periods as hatch to 14 days post-hatch and 15–60 days post-hatch, respectively. We examined eggshell fragments in each successful nest and used the estimated number of hatchings as the initial brood size for the early period. When initial brood size was unknown, we censored the brood from the survival estimate for the early period. However, if ≥1 chick survived the early period, we included these broods in the estimate of survival for the late period. When flushes revealed fewer chicks than previous counts, we determined the midpoint between observations to be the time of disappearance (Mayfield 1975). We estimated Mayfield daily survival rates for chicks in individual broods ($D\hat{S}R_i$) and across all broods ($D\hat{S}R$) for each period (Mayfield 1975, Johnson 1979). One underlying assumption of the Mayfield estimator is independent survival of young within a brood (Johnson 1979). Violation of this assumption will not affect survival estimates but will cause underestimation of the variance (Pollock et al. 1989). Additionally, the Mayfield estimator does not account for mixing of young among broods, which has been documented for spruce grouse and lesser prairie-chickens (Keppie 1977, Pitman 2003). Thus, to account for dependence of brood mates and brood mixing, we assigned exposure days to both disappearances and adoptions equal to 50% of the observation interval (Flint et al. 1995). For example, if the initial size of a brood was determined to be 10 chicks, and only 7 chicks were observed at 14 days post-hatch, the exposure days for the brood would be 119 [(7 chicks × 14 d) + (3 chicks × 7 d) = 119]. We censored from the brood chicks that died as a result of capture or marking and adjusted exposure days accordingly. We calculated survival for each period by raising the $D\hat{S}R$ to the power of 14 and 46 for the early and late periods, respectively (Johnson 1979). We calculated confidence intervals (95% CI) by estimating the CI for the $D\hat{S}R$ and raising this upper and lower bound to the power of the period length (Johnson 1979). We estimated survival from hatch to 60 days posthatch as the product of overall survival for the early and late periods. We compared both early- and late-period $D\hat{S}R$s with a z-test (Johnson 1979) and used a χ^2 test to compare ≥ 3 $D\hat{S}R$s (Sauer and Williams 1989). We conducted all statistical analyses using SAS version 8.0 (SAS Institute 2000).

Survival of transmitter-equipped birds.—We estimated survival of transmitter-equipped chicks using known-fate models in program MARK (White and Burnham 1999). We modeled chick survival as a monthly rate from 1 August to 31 March and included in the analyses only chicks surviving 5 days beyond the time of capture. Data were not sufficient to estimate survival separately for each year or study site. Thus, we used data pooled across all 3 years of Phase II to estimate overwinter survival. We considered 11 a priori candidate models. Because of small sample sizes, we added covariates primarily to constant survival models. We evaluated simple interactions only for time-specific (monthly) models. We examined age at capture (days posthatch), gender (dummy variable $1 = M$, $0 = F$), and chick body mass at capture (between 50 and 60 d post-hatch) as individual covariates. We standardized chick body mass as the difference between the observed mass (g) of a chick at capture from the predicted value for the chick's age (Pitman et al. 2005*a*). This provided a residual mass (g) for each chick adjusted for gender and age at capture. We evaluated relative importance of each covariate by the magnitude of the parameter estimate (β) and the 95% confidence intervals from the logistic equation. We considered parameters with confidence intervals not inclusive of zero to have a measurable effect.

We considered the model with the lowest Akaike's Information Criterion (AIC_c) value to be best supported by the data. We ranked all other models from greatest to least support based on differences in AIC_c values (ΔAIC_c) between each remaining model and the highest-ranking model. We considered models with a ΔAIC_c value <2 as competing models. We used Akaike's weights (w_i/w_j) between 2 models to quantify the relative degree of support of one model over the other (Burnham and Anderson 1998). Because gender was never identified for 2 chicks, we fit models using all gender possibilities for these chicks. The model selection was not changed by any combination, and we dropped these 2 chicks from this analysis.

We conducted another known-fate survival analysis to compare overwinter survival of juvenile and full-grown (yearling and adult) lesser prairie-chickens between 1 August and 31 March. We did not consider gender in this analysis, and we included all juveniles and full-grown birds in the data set. Five a priori models were fit to the data. We examined survival of juvenile and full-grown birds as a group effect (S_{age}) against the alternatives S_{month} and S_c. If support was greater for the latter 2 model structures, we concluded that age effects were not measurably different between juvenile and full-grown birds. We conducted all model development and selection procedures in program MARK, version 4.1 (White and Burnham 1999).

Juvenile survival to the first breeding season.—Survival from hatch to the breeding season (31 Mar) was the product of the Mayfield survival estimate (hatch to 60 d post-hatch) and the known-fate survival estimate for transmitter-equipped juveniles (1 Aug–31 Mar). Confidence intervals for this estimate were the product of the lower and upper bounds surrounding the Mayfield and known-fate survival probabilities. We derived the Mayfield survival estimate used in this calculation from broods across all years and both study sites. The known-fate survival estimate was the point estimate from the highest-ranking model.

Results

We captured and equipped 226 females with transmitters during this 6-year study and located 209 nests from these birds: 118 on Site I, 84 on Site II, and 7 off of the 2 study sites. We ascertained fate for 196 nests. Fifty-one nests (26.0%) were known to have produced ≥ 1 chick, and 17 of these broods (33.3%) suffered complete losses of chicks prior to 14 days post-hatch. Only 21 broods (41.2%) were known to have ≥ 1 chick surviving beyond 60 days post-hatch.

Survival Estimates

Flush counts.—Across the 6 years of this project, overall $D\hat{S}R$ was 0.949 (95% CI = 0.932–0.966) for the early period, and the pooled $D\hat{S}R$ estimate did not differ ($z = 1.131$, $P = 0.258$) between Site I (0.963) and Site II (0.943). Yearly estimates of $D\hat{S}R$ for the early period ranged from 0.849 to 0.975, but the annual variation in early-period survival was not significant ($\chi^2 = 5.635$, df = 4, $P = 0.228$) for years in which >1 brood were monitored (1998–2002). Overall chick survival for the early brood-rearing period was 0.480 (95% CI = 0.373–0.616).

The $D\hat{S}R$ for the late brood-rearing period (0.978, 95% CI = 0.968–0.989) was greater ($z = 2.897$, $P < 0.01$) than the early brood-rearing period. The $D\hat{S}R$ for the late period did not differ ($z = 1.074$, $P = 0.283$) between Site I (0.985) and Site II (0.972) or across the 5 years for which yearly estimates were calculated ($\chi^2 = 0.050$, df = 4, $P = 0.998$). Overall chick survival for the late brood-rearing period was 0.368 (95% CI = 0.221–0.610), and survival from hatch to 60 days post-hatch (early brood-rearing survival × late brood-rearing survival) was 0.177 (95% CI = 0.028–0.376).

Transmitter-equipped birds.—During Phase II, we captured 41 chicks from 20 broods and equipped them with transmitters between 35 and 60 days post-hatch. We recorded mortalities for 19 transmitter-equipped chicks prior to their first breeding season (31 Mar) and attributed 13 (68.4%) to mammals, 3 (15.8%) to unknown predators, 2 (10.5%) to raptors, and 1 (5.3%) to collision with a power line. In addition to the 19 observed mortalities, 1 juvenile was lost to an injury sustained during a recapture attempt, 1 juvenile died when it became entangled in its transmitter, and the fate of 4 juveniles was not ascertained due to either transmitter failure or dispersal beyond the search area. Fourteen of the 19 mortalities (73.7%) occurred prior to 1 November, and 26.3% of all juvenile mortality was recorded in October.

We used encounter histories of 31 transmitter-equipped chicks (17 M, 12 F, 2 unknown) from 16 broods to model survival from 1 August to 31 March. We transmitter-equipped all birds from 22 July to 1 September at 50–60 days post-hatch. Chick mass at capture ranged from 357 to 618 g. Sixteen of 29 (55.2%) lesser prairie-chicken chicks used to examine gender-specific survival were alive at the end of March. There was some model-selection

Table 1. Candidate known-fate models used to describe juvenile lesser prairie-chicken survival as a function of covariates gender, age at capture (age), and body mass at capture (mass), 1 Aug–31 Mar. A second set of models (age effects) was used to draw comparisons between the survival of juvenile and full-grown (yearling and adult) birds during the same period. Thirty-one juveniles and 93 full-grown birds were used to model survival in Finney County, Kansas, USA, 2000–2003.

Model structure	Model statistics				
	AIC_c	ΔAIC_c	w_i[a]	K[b]	Deviance
Juvenile survival					
S_{mass}	72.80	0.00	0.32	2	68.73
$S_{mass+age}$	73.22	0.42	0.26	3	67.08
$S_{gender+mass}$	73.86	1.06	0.19	3	67.72
$S_{gender+mass+age}$	73.93	1.13	0.18	4	65.70
$S_{constant}$	78.80	6.00	0.02	1	76.78
$S_{month \times mass}$	79.61	6.81	0.01	9	62.75
S_{gender}	80.84	8.04	0.01	2	76.77
S_{age}	80.84	8.05	0.01	2	76.77
S_{month}	81.20	8.41	<0.01	8	64.34
$S_{gender+age}$	82.90	10.10	<0.01	3	76.76
$S_{month \times gender}$	88.70	15.90	<0.01	9	71.83
Age effects[c]					
$S_{age \times month}$	292.79	0.00	0.43	16	0.00
$S_{constant}$	293.41	0.62	0.32	1	31.39
S_{age}	295.24	2.44	0.13	2	31.20
S_{month}	295.99	3.19	0.09	8	19.77
$S_{age+month}$	297.91	5.11	0.03	9	19.64

[a] Generalized Akaike weights that can be interpreted as the relative degree of certainty associated with each model.
[b] Number of parameters in the model.
[c] Subscript "age" refers to juvenile or full-grown birds in this model set.

uncertainty (ΔAIC_c <3) for the top 4 models examining gender-specific survival rates. The highest-ranking model, S_{mass}, for this 8-month period was 1.23 (w_1/w_2) times more likely to be supported by the data than the next-best model and 1.68 times (w_1/w_3) more so than a model with gender effects included (Table 1). This indicated that survival was best modeled as a single rate ($\hat{S}$ = 0.70, 95% CI = 0.47–0.86) for both male and female chicks when adjusted for body mass. Chick body mass (g) at 50–60 days post-hatch was greater ($\beta_{bodymass} = 1.042$, 95% CI = 0.218–1.867) for chicks that survived the entire period ($\bar{x} = 476$, SE = 21, n = 17) than chicks that died prior to 31 March of the following year ($\bar{x} = 419$, SE = 17, n = 10) and was included in each of the competing models. Gender ($\beta_{gender} = 0.384$, 95% CI = –0.356 to 1.244) and age ($\beta_{age} = 0.412$, 95% CI = –0.237 to 1.060) did not measurably affect 8-month survival of chicks, although model selection indicated these covariates were of some importance to survival.

We examined the evidence for age-specific overwinter survival rates between juveniles and full-grown prairie chickens using encounter histories of 93 transmitter-equipped full-grown birds (17 M, 76 F) and 31 juveniles from 1 August to 31 March. There was some model-selection uncertainty (ΔAIC_c <3). The most parsimonious model, $S_{age \times month}$, indicated differences in monthly estimates of survival (Fig. 1), but overall rates for the 8-month period were similar for juveniles ($\hat{S} = 0.64$, 95% CI = 0.46–0.79) and full-grown birds, ($\hat{S} = 0.63$, 95% CI = 0.51–0.74; Table 1). The evidence for similar survival rates between age classes was supported by the second-highest-ranking model, $S_{constant}$, which

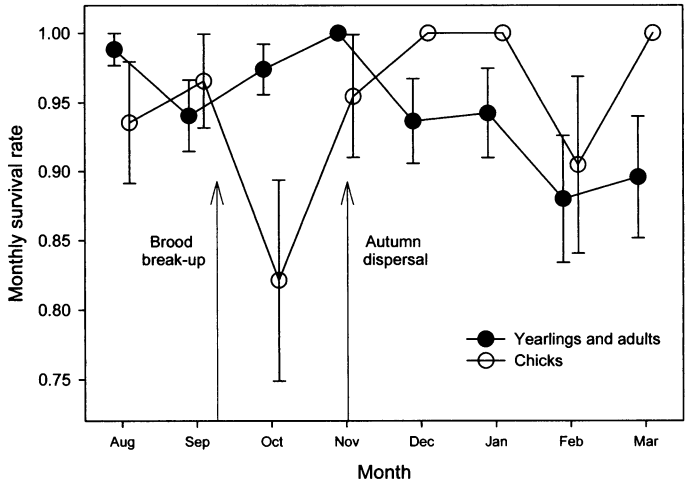


Figure 1. Monthly survival estimates from Aug through Mar for juvenile and full-grown (yearling and adult) lesser prairie-chickens in southwestern Kansas, USA, 2000–2003. Estimated time of brood break-up and autumn dispersal are indicated with arrows (Pitman 2003).

estimated a constant survival across age and month ($\hat{S}$ = 0.65, 95% CI = 0.56–0.74).

Combining overall survival estimates from brood-flush counts (hatch to 60 d = 0.177) and transmitter-equipped chicks (60 d to 243 d = 0.698) yielded a survival estimate from hatch to their first breeding season of 0.12 (95% CI = 0.01–0.32).

Discussion

Daily survival of lesser prairie-chicken broods was relatively consistent across the 6 years of our study for both the early and late brood-rearing periods. However, daily survival of chicks was different between periods and greatest during late brood-rearing. We examined the effects of gender, age at capture, and body mass on overwinter survival of transmitter-equipped juveniles and concluded that body mass was the most influential covariate. However, juvenile survival during this period was similar to that of full-grown birds. Overall recruitment into this population was low, with only 12% surviving from hatch to first breeding.

Prior to our study, no other researcher had estimated survival of juvenile lesser prairie-chickens using regular flush counts. Jamison (2000) estimated chick survival using average late-summer brood sizes previously reported from Kansas (Schwilling 1955) and Oklahoma (Davison 1940, Copelin 1963, Merchant 1982). Assuming an average clutch size of 12 eggs, Jamison (2000) estimated survival from hatch to early autumn at 0.27 in Kansas and 0.43–0.65 in Oklahoma. These survival rates are similar to estimates reported for other grouse species (~50%) over approximately the same period (Jenkins et al. 1963, Watson 1965, Rusch and Keith 1971) but substantially higher than survival of juvenile lesser prairie-chickens observed in our study. Only our estimate of juvenile survival for lesser prairie-chickens and survival of Chinese grouse through 8 weeks post-hatch (0.17; Yue-Hua et al. 2003) were calculated from regular flush counts. These estimates could have been negatively influenced by observer disturbance, but, in our study, >50% of all mortality occurred from complete brood losses prior to our initial observation at 14

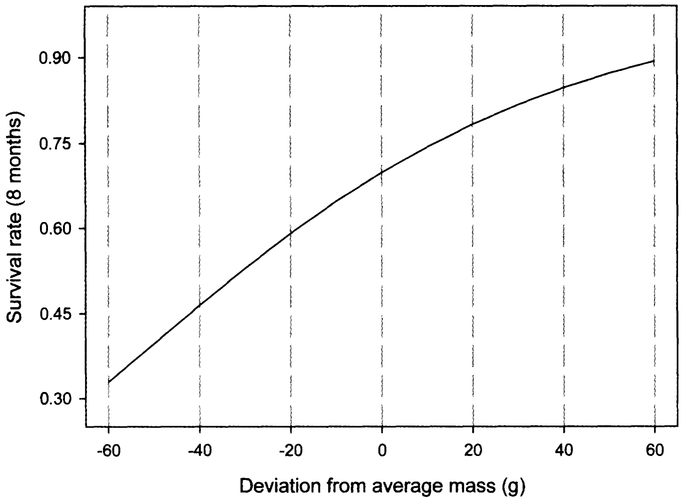


Figure 2. Eight-month (Aug–Mar) survival rates of juvenile lesser prairie-chickens as predicted from body mass (g) at 50–60 days post-hatch in southwestern Kansas, USA, 2000–2003. Mass data are standardized by gender and age and reported as a mean of 0 ± 1 SD (SD = 60 g).

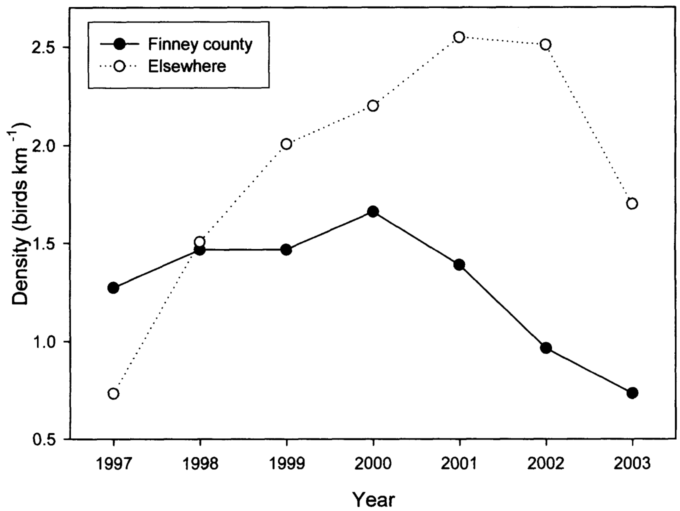


Figure 3. Estimated lesser prairie-chicken density calculated from lek counts in Finney County and elsewhere within 7 other Kansas counties (Kearny, Meade, Morton, Clark, Hamilton, Ford, Comanche), USA, 1997–2003 (Kansas Department of Wildlife and Parks, unpublished data).

days posthatch. When early and complete brood losses are common, apparent brood survival is overestimated using late-summer brood counts (Jamison 2000). Because most researchers have estimated juvenile survival using late-summer brood sizes, it is not clear whether lesser prairie-chicken brood survival is truly less than estimates for other grouse species.

Body mass was positively associated with overwinter survival in our study. At 50–60 days post-hatch, heavier-than-average juvenile lesser prairie-chickens had a greater probability of surviving until the following March (Fig. 2). A predicted 20-g increase or decrease from average body mass changed 8-month survival rates by 11 and 15%, respectively. This suggests that relatively small differences in growth can have a measurable effect on survival. Likewise, heavier red grouse (*Lagopus lagopus scoticus*) chicks survived better than lighter chicks and mass of chicks at 14 days post-hatch was positively correlated with survival to 21 days post-hatch (Hudson et al. 1994). Survival of juvenile lesser prairie-chickens in our study was estimated at 0.70 from 1 August to 31 March. This estimate is greater than the apparent overwinter survival of juvenile greater prairie-chickens (*T. cupido*, 0.55; Halfmann 2002). The overall effect of gender to lesser prairie-chicken juvenile survival was small and likely was correlated to body mass of males. This ambivalence was similar for black grouse (*Tetrao tetrix*; Caizergues and Ellison 2002) and ruffed grouse (*Bonasa umbellus*; Small et al. 1993) in which gender did not substantially influence overwinter survival. However, in the more dimorphic grouse species (e.g., greater sage-grouse [*Centrocercus urophasianus*]), differential survival rates may be more common, where males require more resources to reach adult size (Swenson 1986).

Overwinter survival of juvenile and full-grown lesser prairie-chickens was similar and best explained by an age × month interaction. This similarity was further supported by the relative weight of a model with a constant survival rate and indicated the age × month interaction likely was a result of different mortality periods for juvenile and full-grown birds (Fig. 1). In Kansas, depressed juvenile lesser prairie-chicken survival occurred in October between brood break-up and the onset of autumn dispersal (Pitman 2003; Fig. 1). There are no previous reports of depressed juvenile survival rates during this period; however, several researchers have examined the possibility of differential survival during dispersal. Juvenile greater prairie-chickens were highly susceptible to predators during autumn dispersal and almost twice as vulnerable as full-grown birds during this time (Bowman and Robel 1977). However, most other grouse species do not exhibit depressed survival rates during dispersal periods (Hines 1986, Beaudette and Keppie 1992, Small et al. 1993, Caizergues and Ellison 2002).

Estimated survival of juvenile lesser prairie-chickens from hatch to their first breeding season was 0.12 in our study. Similar estimates of annual survival have been reported for juvenile black grouse (0.11; Lindén 1981), capercaillie (*Tetrao urogallus*; 0.07; Lindén 1981), and ruffed grouse (0.07; Small et al. 1991). Gender-specific survival of spruce grouse (*Falcipennis canadensis*) from hatch to the following spring has been reported in 2 different studies (Ellison 1974, Keppie 1979) and ranges from 0.02–0.23 and 0.20–0.22 for females and males, respectively. Another study examining ruffed grouse reported survival of 0.21–0.34 for juvenile birds during their first year of life (Rusch and Keith 1971). These poor survival rates are troubling considering that juvenile survival has been identified as one of the most critical demographic parameter regulating grouse populations (Peterson and Silvy 1996, Peterson et al. 1998, Wisdom and Mills 1998, Hagen 2003).

Concurrent spring lek count data collected in the county where our study was conducted (Finney County) were reflective of the poor recruitment we observed (Kansas Department of Wildlife and Parks, unpublished data). From 1997–2003, the average annual change in estimated lesser prairie-chicken density was −7.1% (SE = 7.9%) in Finney County (Fig. 3). However, over that same period, average annual change in lesser prairie-chicken density throughout 7 other Kansas counties was +22.8% (SE =

19.7%; Fig. 3). Thus, juvenile survival observed in our study was most likely not indicative of lesser prairie-chicken recruitment into other Kansas populations. We speculate that low juvenile survival on our study areas was due to a poor interspersion of nesting and brood-rearing habitats (Pitman 2003). On our study areas, hens often were >1 km from a critical habitat component (e.g., optimal brood or nesting cover) due to large pastures (>800 ha) with seemingly homogenous vegetative characteristics. Young chicks hatched in dense cover likely experienced less mobility and lower invertebrate availability than those in more sparsely vegetated pastures. Conversely, chicks hatched in the more sparsely vegetated pastures were more conspicuous to predators and often far from dense escape cover.

Management Implications

To stabilize or increase lesser prairie-chicken populations in Kansas, managers should focus efforts on creating conditions that will optimize chick survival. In our study, chick body mass had a substantial impact on overwinter juvenile survival. Because body mass of juvenile grouse has been correlated with invertebrate biomass (Park et al. 2001, Hagen et al. 2005), we believe that habitat manipulations that increase invertebrate biomass can indirectly improve juvenile lesser prairie-chicken survival. In sand sagebrush habitats, invertebrate biomass can be increased by conducting management practices that result in increased forb cover (Jamison et al. 2002). Strip-disking at a depth of 7–15 cm on flat areas of firm soil during March should produce habitat dominated by native forbs (Litton et al. 1994). It is possible that prescribed burning or an appropriate grazing system could increase the native forb component, but the impact of these methods on vegetative composition and lesser prairie-chicken populations is not well understood in sand sagebrush habitats (Engle and Bidwell 2001, Hagen et al. 2004). We believe that vegetative manipulations designed to improve brood habitat should occur within preferred nesting habitat typically composed of dense stands of mature sand sagebrush (Pitman et al. 2005*b*). This will ensure that quality brood habitat will be easily accessible to females with recently hatched chicks. However, reliable knowledge is needed on the optimal timing and juxtaposition of these treatments in sand sagebrush habitats.

Acknowledgments

J. O. Cattle Co., Sunflower Electric Power Corporation, Thornton Cattle Co., Brookover Cattle Co., R. A. Greathouse, and the P. E. Beach family provided property access. G. C. Salter, T. L. Walker, Jr., C. C. Griffin, and T. J. Whyte assisted with fieldwork. R. D. Rodgers provided annual indices to lesser prairie-chicken density throughout Kansas. Our study was supported by Kansas State University (KSU), Division of Biology; KSU Agricultural Experiment Station (Contribution 05-308-J); Kansas Department of Wildlife and Parks, Federal Aid in Wildlife Restoration Grants W-47-R and W-53-R; and Westar Energy, Inc.

Literature Cited

Beaudette, P. D., and D. M. Keppie. 1992. Survival of dispersing spruce grouse. Canadian Journal of Zoology 70:693–697.

Bergerud, A. T., and M. W. Gratson. 1988. Adaptive strategies and population ecology of northern grouse. Volume II. Theory and synthesis. University of Minnesota, Minneapolis, USA.

Bowman, T. J., and R. J. Robel. 1977. Brood break-up and dispersal, mobility and mortality of juvenile prairie-chickens. Journal of Wildlife Management 41: 27–34.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information–theoretic approach. Springer, New York, New York, USA.

Caizergues, A., and L. N. Ellison. 2002. Natal dispersal and its consequences in black grouse *Tetrao tetrix*. Ibis 144:478–487.

Copelin, F. F. 1963. The lesser prairie-chicken in Oklahoma. Technical Bulletin No. 6. Oklahoma Wildlife Conservation Department, Oklahoma City, USA.

Crawford, J. A. 1980. Status, problems, and research needs of the lesser prairie-chicken. Pages 1–7 *in* P. A. Vohs and F. L. Knopf, editors. Proceedings of the Prairie Grouse Symposium. Oklahoma State University, Stillwater, USA.

Davison, V. E. 1940. An 8-year study of lesser prairie-chickens. Journal of Wildlife Management 4:55–62.

Ellison, L. N. 1974. Population characteristics of Alaskan spruce grouse. Journal of Wildlife Management 38:383–395.

Engle, D. M., and T. G. Bidwell. 2001. Viewpoint: the response of central North American prairies to seasonal fire. Journal of Range Management 54:2–10.

Flint, P. L., K. H. Pollock, D. Thomas, and J. S. Sedinger. 1995. Estimating prefledging survival: allowing for brood mixing and dependence among brood mates. Journal of Wildlife Management 59:448–455.

Giesen, K. M. 1998. Lesser prairie-chicken (*Tymapanuchus pallidinctus*). Number 364 *in* F. Gill and A. Poole, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; and The American Ornithologists' Union, Washington, D.C., USA.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1076.

Hagen, C. A. 2003. A demographic analysis of lesser prairie-chicken populations in southwestern Kansas: survival, population viability, and habitat use. Dissertation, Kansas State University, Manhattan, USA.

Hagen, C. A., B. E. Jamison, K. M. Giesen, and T. Z. Riley. 2004. Guidelines for managing lesser prairie-chicken populations and their habitats. Wildlife Society Bulletin 32:69–82.

Hagen, C. A., G. C. Salter, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2005. Lesser prairie-chicken brood habitat: invertebrates biomass and vegetation. Wildlife Society Bulletin 33:1080–1091.

Halfmann, D. A. 2002. Natal dispersal of greater prairie-chickens in Wisconsin. Thesis, University of Wisconsin, Stevens Point, USA.

Haukos, D. A., L. M. Smith, and G. S. Broda. 1990. Spring trapping of lesser prairie-chickens. Journal of Field Ornithology 61:20–25.

Hines, J. E. 1986. Survival and reproduction of dispersing blue grouse. Condor 88:43–49.

Hubbard, M. W., D. L. Garner, and E. E. Klaas. 1999. Wild turkey poult survival in south-central Iowa. Journal of Wildlife Management 63:199–203.

Hudson, P. F., F. Booth, M. Hurley, and D. Howarth. 1994. Problems with red grouse chick survival. Game Conservancy Annual Review 25:120–122.

Hulett, G. K., J. R. Tomelleri, and C. O. Hampton. 1988. Vegetation and flora of a sandsage prairie site in Finney County, southwestern Kansas. Transactions of the Kansas Academy of Science 91:83–95.

Jamison, B. E. 2000. Lesser prairie-chicken chick survival, adult survival, and habitat selection and movements of males in fragmented rangelands of southwestern Kansas. Thesis, Kansas State University, Manhattan, USA.

Jamison, B. E., R. J. Robel, J. S. Pontius, and R. D. Applegate. 2002. Invertebrate biomass: associations with lesser-prairie chicken habitat use and sand sagebrush density in southwestern Kansas. Wildlife Society Bulletin 30:517–526.

Jenkins, D., A. Watson, and G. R. Miller. 1963. Population studies on red grouse *Lagopus lagopus scoticus* in northeast Scotland. Journal of Animal Ecology 32:317–376.

Jensen, W. E., D. A. Robinson, and R. D. Applegate. 2000. Distribution and population trends of lesser prairie-chicken in Kansas. Prairie Naturalist 32: 169–176.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

Keppie, D. M. 1977. Inter-brood movements of juvenile spruce grouse. Wilson Bulletin 89:67–72.

Keppie, D. M. 1979. Dispersal, overwinter mortality, and recruitment of spruce grouse. Journal of Wildlife Management 43:717–727.

Lindén, H. 1981. Growth rates and early energy requirements of captive juvenile capercaille, *Tetrao urogallus*. Finnish Game Research 39:53–67.

Litton, G., R. L. West, D. F. Dvorak, and G. T. Miller. 1994. The lesser prairie chicken and its management in Texas. Texas Parks and Wildlife Federal Aid Report Series No. 33, Austin, USA.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

Merchant, S. S. 1982. Habitat use, reproductive success, and survival of female lesser prairie-chickens in two years of contrasting weather. Thesis, New Mexico State University, Las Cruces, USA.

Park, K. J., P. A. Robertson, S. T. Campbell, R. Foster, Z. M. Russell, D. Newborn, and P. J. Hudson. 2001. The role of invertebrates in the diet, growth and survival of red grouse (*Lagopus lagopus scoticus*) chicks. Journal of Zoology 254:137–145.

Peterson, M. J., W. T. Grant, and N. J. Silvy. 1998. Simulation of reproductive stages limiting productivity of the endangered Attwater's prairie-chicken. Ecological Modeling 111:283–295.

Peterson, M. J., and N. J. Silvy. 1996. Reproductive stages limiting productivity of the endangered Attwater's prairie-chicken. Conservation Biology 4:1264–1276.

Pitman, J. C. 2003. Lesser prairie-chicken nest site selection and nest success, juvenile gender determination and growth, and juvenile survival and dispersal in southwestern Kansas. Thesis, Kansas State University, Manhattan, USA.

Pitman, J. C., C. A. Hagen, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2005*a*. Gender identification and growth of juvenile lesser prairie-chickens. Condor 107:87–96.

Pitman, J. C., C. A. Hagen, R. J. Robel, T. M. Loughin, and R. D. Applegate. 2005*b*. Location and success of lesser-prairie chicken nests in relation to vegetation and human disturbance. Journal of Wildlife Management 69: 1259–1269.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Rusch, D. H., and L. B. Keith. 1971. Seasonal and annual trends in numbers of Alberta ruffed grouse. Journal of Wildlife Management 35:803–822.

SAS Institute. 2000. SAS/STAT user's guide. Release 8.0. SAS Institute, Cary, North Carolina, USA.

Sauer, J. R., and B. K. Williams. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management 53:137–142.

Schroeder, M. A., and C. E. Braun. 1991. Walk-in funnel traps for capturing greater prairie-chickens on leks. Journal of Field Ornithology 62:378–385.

Schwilling, M. D. 1955. A study of the lesser prairie-chicken in Kansas. Kansas Forestry, Fish and Game Commission, Pratt, USA.

Small, R. J., J. C. Holzwart, and D. H. Rusch. 1991. Predation and hunting mortality of ruffed grouse in central Wisconsin. Journal of Wildlife Management 55:512–520.

Small, R. J., J. C. Holzwart, and D. H. Rusch. 1993. Are ruffed grouse more vulnerable to mortality during dispersal? Ecology 74:2020–2026.

Swenson, J. E. 1986. Differential survival by sex in juvenile sage grouse and gray partridge. Ornis Scandinavica 17:14–17.

Taylor, M. A., and F. S. Guthery. 1980. Status, ecology, and management of the lesser prairie-chicken. U.S. Forest Service General Technical Report RM-77, Fort Collins, Colorado, USA.

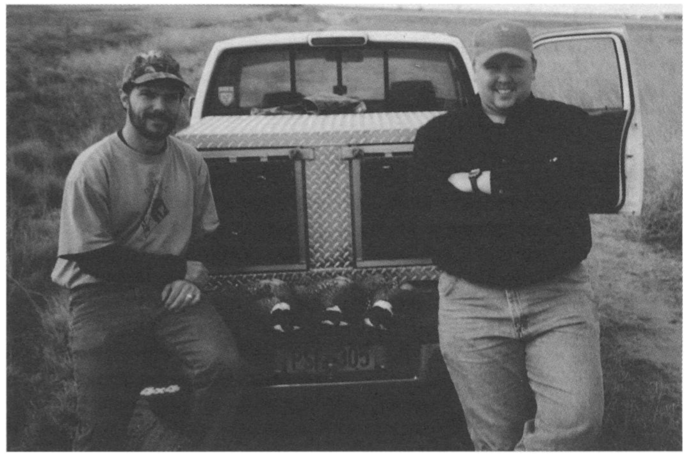
U.S. Department of Commerce. 2003. National Oceanic and Atmospheric Administration. National Climatic Data Center. http://www.ncdc.noaa.gov/. Accessed: 2003 Jan 7.

Watson, A. 1965. A population study of ptarmigan (*Lagopus mutus*) in Scotland. Journal of Animal Ecology 34:135–172.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

Wisdom, M. J., and L. S. Mills. 1998. Sensitivity analysis to guide population recovery: prairie-chicken as an example. Journal of Wildlife Management 61: 302–312.

Yue-Hua, S., J. E. Swenson, Y. Fang, S. Klaus, and W. Scherzinger. 2003. Population ecology of the Chinese grouse, *Bonasa sewerzowi*, in a fragmented landscape. Biological Conservation 110:177–184.



James C. (Jim) Pitman (right) recently began working as the small game coordinator for the Kansas Department of Wildlife and Parks. He formerly was employed by the Indiana Division of Fish and Wildlife as the farmland research biologist. He received a B.S. in wildlife science from Purdue University in 1998 and an M.S. in ecology and systematics from Kansas State University in 2003. His professional interests include management of upland game bird habitats and populations. He has been a member of The Wildlife Society (TWS) since 1997 and a Certified Associate Wildlife Biologist since 2000. ***Christian A. Hagen*** (left) is the sage grouse conservation coordinator for the Oregon Department of Fish and Wildlife. He received his Ph.D. in ecology and systematics from Kansas State University (2003), a master's degree in natural resource management from University of Manitoba (1999), and a B.A. in political science from Fort Lewis College (1993). He has been an active member of TWS since 1997. His interests include habitat and population management of upland game birds, demographic modeling, habitat selection analyses, and almost any activity that takes him to the backcountry. ***Brent E. Jamison*** (not pictured) is a resource scientist with the Missouri Department of Conservation. He holds a B.S. in fisheries and wildlife from the University of Missouri-Columbia and an M.S. in biology from Kansas State University. ***Robert J. (Bob) Robel*** (not pictured) received his B.S. in fisheries and wildlife management from Michigan State University, an M.S. in forest and wildlife sciences from the University of Idaho, and a Ph.D. in wildlife science from Utah State University. He is professor emeritus at Kansas State University after 43 years of service, but remains active in wildlife management in the United States and abroad. He has served numerous natural resource organizations and as an advisor to state and federal governments. ***Thomas M. (Tom) Loughin*** (not pictured) is a professor in the Department of Statistics at Kansas State University. He holds a half-time appointment with K-State Research and Extension, collaborating with and providing statistical consulting for researchers in the agricultural and biological sciences. He received his Ph.D. in statistics in 1993 from Iowa State University, his M.S. in statistics in 1987 from the University of North Carolina, Chapel Hill, and his B.S. in mathematics in 1985 from Rensselaer Polytechnic Institute. ***Roger D. Applegate*** (not pictured) currently is small game coordinator with Tennessee Wildlife Resources Agency. At the time of this research, he was small game coordinator with Kansas Department of Wildlife and Parks. He has served on several TWS committees and as an associate editor of the *Wildlife Society Bulletin.*

Associate Editor: Chamberlain.