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Source: Wildlife Biology, 15(1) : 89-96

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/07-083

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Wildl. Biol. 15: 89-96 (2009)
DOI: 10.2981/07-083
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Short communication

Breeding and non-breeding survival of lesser prairie-chickens *Tympanuchus pallidicinctus* in Texas, USA

Eddie K. Lyons, Bret A. Collier, Nova J. Silvy, Roel R. Lopez, Benjamin E. Toole, Ryan S. Jones & Stephen J. DeMaso

Lesser prairie-chickens *Tympanuchus pallidicinctus* have declined throughout their range because of loss or fragmentation of habitat from conversion of native prairie to agricultural cropland, exacerbated by overgrazing and drought. We used data from radio-marked lesser prairie-chickens to determine whether differences in survival existed between populations occurring in two areas dominated by different vegetation types (sand sagebrush *Artemisia filifolia* vs shinnery oak *Quercus havardii*) in the Texas Panhandle from 2001 through 2005. We used a model-selection approach to evaluate potential generalities in lesser prairie-chicken survival. Our results indicated that survival of lesser prairie-chickens differed between breeding and non-breeding periods, and between study populations. We estimated annual survival of lesser prairie-chickens at 0.52 (95% CI: 0.32-0.71) in the sand sagebrush and 0.31 (95% CI: 0.12-0.58) in the shinnery oak vegetation type. Our results suggest that demographic differences in lesser prairie-chicken within sand sagebrush and shinnery oak vegetation types throughout the Texas Panhandle should be evaluated, especially during the breeding season. Based on our results, higher mortality of birds during the breeding season illustrates the need to manage for vegetation components such as sand sagebrush and residual bunchgrasses as opposed to shinnery oak such that potential breeding season mortality may be lessened.

Key words: Lesser prairie-chicken, radio-telemetry, survival, Texas Panhandle, Tympanuchus pallidicinctus

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Received 2 November 2007, accepted 5 May 2008

Associate Editor: Ilse Storch

Continued declines, extirpation and extinction of pinnated grouse (prairie chickens *Tympanuchus* spp.) across their historic ranges in North America have been extensively documented (Johnsgard 1983, Silvy et al. 2004, Storch 2007). Although lesser prairie-chickens *Tympanuchus pallidicinctus* inhabit rangelands in all five states of their historic range, they have one of the most restricted ranges of any native North American grouse, second only to Gunnison's sage-grouse *Centrocercus minimus* (Giesen & Hagen 2005). Habitat loss in the form of range-wide land conversion from native short and mid-grass prairies to agricultural cropland, and urban and energy development have been hypothesized as causes of declines in lesser prairie-chicken populations (Taylor & Guthery 1980). Compounding the effects of habitat loss is fragmentation and degradation of remaining habitat by drought and overgrazing (Crawford 1980, Taylor & Guthery 1980). Many grouse populations have experienced declines and are considered at risk (14 of 18 species are red-listed in at least one country; Storch 2007). Lesser prairie-chickens have been classified as vulnerable by the International Union for Conservation of Nature and Natural Re-

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sources (IUCN) since 2004 (IUCN 2007) and "warranted but precluded" by the United States Fish and Wildlife Service (United States Department of the Interior, Fish and Wildlife Service 2007).

Survival estimates are important components to avian demography and are essential for grouse management (Caizergues & Ellison 1997, Hagen et al. 2007). Parental input between male and female grouse differs in promiscuous mating systems and the two sexes would be expected to have different survival, a difference which may be exacerbated during the breeding compared to the non-breeding season (Bergerud & Gratson 1988). Factors involved in population declines are not known with certainty; however, increased mortality during the breeding season has been observed in several grouse species including lesser prairie-chickens (Hannon et al. 2003, Patten et al. 2005, Hagen et al. 2007). Studies have quantified differing aspects of lesser prairie-chicken survival (Patten et al. 2005, Pitman et al. 2006, Hagen et al. 2005, 2007), yet information on annual or seasonal survival of lesser prairie-chickens is incomplete, as no recent studies have evaluated survival of the two remaining Texas populations (Sell 1979, Haukos 1988). Because of uncertainty surrounding lesser prairie-chicken recovery, we initiated studies to determine survival of lesser prairie-chickens in these two populations in Texas. We used radio-telemetry to 1) estimate survival in differing regions of the Texas Panhandle, and 2) determine whether generalizations about factors contributing to variation in lesser prairie-chicken survival can be made to Texas populations.

Material and methods

Study area

We conducted our study from April 2001 through August 2005 in two areas in the Texas Panhandle (Fig. 1). In 2001, trapping sites were located in portions of Hemphill (36°01'N, 100°11'W) and Wheeler (35°33'N, 100°06'W) counties (northeast region). This region was dominated by sand sagebrush *Artemisia filifolia*, with lesser amounts of Chickasaw plum *Prunus angustifolia* and fragrant sumac *Rhus aromatica*. In 2002, trapping sites were expanded to include the southern portion of Lipscomb County (36°07'N, 100°03'W), Texas, and added Yoakum and southern Cochran counties (33°23'N, 102°50'W; southwest region) in 2003. This region was dominated by shinnery oak *Quercus havardii*. Environmental conditions were similar across both study regions and a severe drought occurred on both sites in 2003 (NOAA 2005).

Our study areas ranged within 5,000-18,000 ha and were bordered by center-pivot irrigated cropland, conservation reserve program lands (CRP) and grazed rangelands. Primary land uses were ranching and natural gas and oil extraction. Average precipitation across the regions was approximately 48 cm/year during our study (NOAA 2005).

Data collection

We trapped lesser prairie-chickens using non-explosive Silvy drop nets on leks (Silvy et al. 1990). Birds were trapped during the breeding season from late March to 1 June from 2001 through 2005. At capture, birds were sexed and aged as juvenile or adult based on shape, wear, and coloration of the ninth and tenth primaries (Amman 1944, Copelin 1963). All birds were equipped with a numbered leg band, and fitted with a 12-15 g battery-powered, mortality-sensitive radio transmitter. Two models of necklace-style radio transmitters were used during the study; non-adjustable collar-style radio

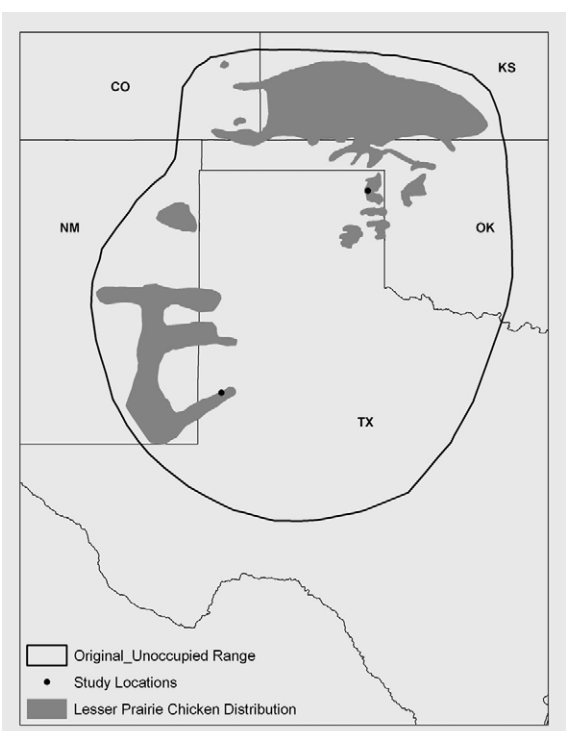


Figure 1. Lesser prairie-chicken distribution (from Silvy & Hagen 2004). Black dots represent the location of study sites in the Texas Panhandle during 2001-2005.

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transmitters with fixed-loop antennas (Telemetry Solutions, Walnut Creek, California USA) and adjustable collar-style transmitters with whip antennas (Wildlife Materials Inc., Carbondale, Illinois USA or AVM Instrument Company, Ltd., Livermore, California, USA).

We monitored radio-marked lesser prairie-chickens three days per week year round throughout the study, using triangulation (White & Garrott 1990) or homing during random tracking periods. We used a vehicle mounted with a 5-element Yagi antenna or 3-element handheld Yagi antenna. Observations were increased to five times a week during spring and early summer to estimate nest and brood success and breeding season mortality.

Statistical analyses

We estimated survival of adult lesser prairie-chickens using a staggered-entry (Pollock et al. 1989), known-fate design in program MARK 4.3 (White & Burnham 1999). We defined encounter occasions monthly, and we based survival estimates on the best fitting model. We estimated period survival (monthly) for radio-marked individuals beginning on 20 April 2001. We used 20 April as the initial date on which individuals entered the survival data set and we allowed at least two weeks after capture before entering individuals for analysis to ensure that transmitter effects had declined (Hagen et al. 2006).

We used an information-theoretic approach to model selection (Burnham & Anderson 2002) as implemented in MARK to evaluate factors contributing to variation in survival. When we found evidence of model selection uncertainty, we used multimodel inference and provided model-averaged estimates of survival (Burnham & Anderson 2002). We used the delta method to calculate standard errors and confidence intervals for the model-averaged annual survival estimates (Seber 1982). For each region (northeast and southwest), we independently analyzed the survival data using a standardized candidate model set in an effort to determine if generalities in factors contributing to variation in survival were assumable for lesser prairie-chickens in different populations during different time frames. In order to evaluate temporal variation, we divided the breeding season into segments based on reproductive phenology. We developed candidate models which evaluated variation in survival between the initial nesting and renesting-brooding periods, models that hypothesized a linear decline in survival over the breeding period, and evaluated these temporal trends both within and between years (Table 1). We applied our standardized candidate set to the data collected on both sites during 2003, removing those models which included a year effect. Because parameters for region and time were confounded based on our study design, we focused primarily on inter-annual variation. Because of our expectation of sex and regional variation, we incorporated both into the best fitting model after analyzing our initial model set, in an attempt to optimize model selection procedures (Norman et al. 2004). However, if addition of these variables did not change $AIC_c \geq 2$ units, we considered that model non-competitive and focused interpretation on the best fitting model without inclusion of sex or regional variation (Burnham & Anderson 2002:131).

Table 1. Notation and description of models used to estimate survival of lesser prairie-chickens in Texas during 2001-2005.

Model	Model notation	Model description
1	S_{Sex}	Survival differs by sex
2	S_{Site}	Survival differs by site
3	$S_{Breed\ (AMJJ;\ ASOCNJFM)}$	Survival differs between breeding and non-breeding season; constant within each season
4	$S_{Breed\ (AMJ;\ JASOCNJFM)}$	Survival differs between early to mid-breeding season and non-breeding season; constant within each season
5	$S_{Breed\ (T\text{-}AMJJ;\ ASOCNJFM)}$	Survival varies according to linear trend during breeding season and is constant during non-breeding season
6	$S_{Breed\ (AM;\ JJ;\ ASOCNJFM)}$	Survival differs between early breeding, mid to late breeding, and non-breeding season; constant within each season
7	$S_{Year:\ Breed\ (AMJJ;\ ASOCNJFM)}$	Survival differs between years, between breeding and non-breeding season; constant within each year-season combination
8	$S_{Year:\ Breed\ (AMJ;\ JASOCNJFM)}$	Survival differs between years, between early to mid-breeding season and non-breeding season; constant within each year-season combination
9	$S_{Year:\ Breed\ (AM;\ JJ;\ ASOCNJFM)}$	Survival differs between years, between early breeding, mid to late breeding, and non-breeding season; constant within each year-season combination
10	$S_{Year:\ Breed\ (AM;\ JJASOCNJFM)}$	Survival differs between years, between early breeding, and non-breeding season; constant within each year-season combination
11	S_{Year}	Survival differs between years; constant within a year
12	S_{Region}	Survival differs between regions

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Results

We trapped and monitored 187 lesser prairie-chickens during 2001-2005 (Table 2); 115 birds in the northeast region during 2001-2003, and 72 in the southwest region during 2003-2005. We trapped 98 males (68 adults, 30 juveniles) and 89 females (35 adults, 54 juveniles) over the course of the study. We excluded from our analysis those individuals lost within two weeks of capture due to mortality (N = 30), transmitter failure, or slipped radios (radios with fixed loop antennas mounted during 2001 were too large and many were lost).

Table 2. Number of lesser prairie-chickens (by sex) captured and radio-marked in the Texas Panhandle during 2001-2005.

Year	Region	Site	County	Male	Female	Total
2001	NE	1	Hemphill	15	12	27
	NE	2	Wheeler	12	7	19
2002	NE	1	Hemphill, Lipscomb	19	7	26
	NE	2	Wheeler	5	6	11
2003	NE	1	Hemphill, Lipscomb	9	8	17
	NE	2	Wheeler	6	9	15
	SW	3	Yoakum, Cochran	9	14	23
2004	SW	3	Yoakum, Cochran	16	9	25
2005	SW	3	Yoakum, Cochran	7	17	24

We found evidence of model selection uncertainty, as several models in each set were viable models based on $AIC_c < 2$ (Table 3). Models which included year effects had little support in our candidate model sets, which indicated that within-year variation is less relevant than between-year variation to lesser prairie-chicken survival. For both study regions and for both study periods the best approximating models consisted of those which outlined differences between breeding and non-breeding season survival. The pattern of lower breeding season survival was supported by the data collected on both sites during 2003 (see Table 3). In addition, our model selection procedures indicated that models for breeding vs non-breeding, which included differences based on study region or sex, were supported

Table 3. Plausible candidate models[a] used to estimate survival of radio-tagged lesser prairie-chickens in the Texas panhandle during 2001-2005.

	Model notation	-2 log likelihood	Number of parameters	AIC[c]	w_i
Northeast area	$S_{Breed\ (AMJJ;\ ASOCNJFM)}$	244.90	2	0.00	0.287
	$S_{Breed\ (AM;\ JJ;\ ASOCNJFM)}$	244.13	3	1.25	0.154
	$S_{Breed\ (T\text{-}AMJJ;\ ASOCNJFM)}$	240.19	5	1.39	0.144
	$S_{Breed\ (AMJ;\ JASOCNJFM)}$	246.36	2	1.45	0.139
	$S_{Year:\ Breed\ (AMJJ;\ ASOCNJFM)}$	241.12	5	2.31	0.090
	S_{Sex}	248.22	2	3.31	0.055
	S_{Site}	248.43	2	3.53	0.049
	S_{Year}	247.31	3	4.43	0.031
	$S_{Year:\ Breed\ (AM;\ JJ;\ ASOCNJFM)}$	237.19	8	4.56	0.029
	$S_{Year:\ Breed\ (AM;\ JJASOCNJFM)}$	242.65	6	5.89	0.015
	$S_{Year:\ Breed\ (AMJ;\ JASOCNJFM)}$	244.29	6	7.53	0.006
Southwest area[b]	$S_{Breed\ (AM;\ JJ;\ ASOCNJFM)}$	182.59	3	0.00	0.213
	$S_{Year:\ Breed\ (AM;\ JJASOCNJFM)}$	176.73	6	0.34	0.180
	$S_{Breed\ (AMJJ;\ ASOCNJFM)}$	185.49	2	0.86	0.139
	S_{Sex}	185.59	2	0.96	0.132
	$S_{Breed\ (AMJ;\ JASOCNJFM)}$	185.88	2	1.24	0.115
	$S_{Year:\ Breed\ (AMJ;\ JASOCNJFM)}$	178.51	6	2.12	0.074
	$S_{Breed\ (T\text{-}AMJJ;\ ASOCNJFM)}$	180.62	8	2.15	0.073
	$S_{Year:\ Breed\ (AMJJ;\ ASOCNJFM)}$	182.38	8	3.91	0.030
	$S_{Year:\ Breed\ (AM;\ JJ;\ ASOCNJFM)}$	176.46	8	4.28	0.025
	S_{Year}	187.46	3	4.87	0.019
Combined (2003)[c]	$S_{Breed\ (AM;\ JJ;\ ASOCNJFM)}$	141.62	3	0.00	0.348
	S_{region}	144.53	2	0.85	0.228
	S_{Sex}	145.99	2	2.31	0.109
	$S_{Breed\ (T\text{-}AMJJ;\ ASOCNJFM)}$	139.79	5	2.34	0.108
	$S_{Breed\ (AMJJ;\ JASOCNJFM)}$	146.11	2	2.43	0.104
	$S_{Breed\ (AMJ;\ JASOCNJFM)}$	146.14	2	2.46	0.102

[a] The lowest AIC_c values for the best fitting models for each group were: Northeast = 248.929; Southwest = 188.674; Combined (2003) = 147.737.

[b] The Southwest area has one less model tested than the Northeast area because we did not evaluate differences between sites in this region.

[c] Model selection results for the combined 2003 comparisons of birds in both the Southwest and Northeast areas do not include Year effects.

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based on AIC_c values changing < 2 units; however, these additional parameters provided no additional information (Burnham & Anderson 2002:131), so we did not interpret these models in our analysis.

For two of the three candidate model sets (southwest and combined 2003), the best fitting model was the one in which survival differed between early breeding, mid to late breeding, and non-breeding season, but was constant within each season ($S_{Breed\ (AM;\ JJ;\ ASOCNJFM)}$; see Table 3). For the northeast, the best fitting model was the one in which survival differed between breeding and non-breeding seasons, but was constant within each season ($S_{Breed\ (AMJJ;\ ASOCNJFM)}$) with the aforementioned model ($S_{Breed\ (AM;\ JJ;\ ASOCNJFM)}$) also being plausible (see Table 3).

Because model ($S_{Breed\ (AM;\ JJ;\ ASOCNJFM)}$) was one of the best two models for each model set, we estimated survival and associated variance measures by model averaging over parameters in this candidate model. Model-averaged monthly survival in the northeast was higher during both breeding season periods (0.92, SE = 0.02 and 0.93, SE = 0.02, respectively) and the non-breeding period (0.96, SE = 0.01) than survival in the southwest for the breeding season periods (0.85, SE = 0.04 and 0.89, SE = 0.03, respectively) and the non-breeding period (0.93, SE = 0.03). Based on our monthly survival estimates, model-averaged estimates of annual survival for the northeast region were 0.52 (95% CI: 0.32-0.71), while model-averaged estimates of annual survival for the southwest region were 0.31 (95% CI: 0.12-0.58). When we combined areas for analysis based on the 2003 data, monthly survival for the breeding season periods was 0.88 (SE = 0.03) and 0.92 (SE = 0.02) with non-breeding season survival of 0.89 (SE = 0.04).

Period (monthly) survival estimates indicated that survival was ~4% lower during breeding than during non-breeding seasons for both study areas. A period estimate of 0.92 (for the breeding season) indicated that breeding season survival for four months was 0.71, while a period estimate of 0.96 (for the non-breeding season) indicated that non-breeding season survival for eight months was 0.72.

Discussion

Breeding season survival of both males and females was lower compared to the non-breeding season on both study sites as an equal proportion were likely to die during the four month breeding season compared to the eight month non-breeding season. Similar results were found for populations of lesser prairie-chickens in New Mexico and Oklahoma as mortality of both males and females peaked during the breeding season (Patten et al. 2005, Wolfe et al. 2007). Hagen et al. (2007) also reported higher mortality during the reproductive season (0.69, SE = 0.04) compared to the non-breeding season (0.77, SE = 0.06) in Kansas, and estimated that approximately 30% of all female mortalities were directly related to breeding season activities. Other grouse species show similar trends in survival during breeding and non-breeding seasons. Populations of sharp-tailed grouse *Tympanuchus phasianellus*, black grouse *Tetrao tetrix*, willow ptarmigan *Lagopus lagopus*, sage grouse *Centrocercus urophasianus* and spruce grouse *Falcipennis canadensis* exhibited increased mortality associated with breeding season activities (Marks & Marks 1988, Boag & Schroeder 1992, Caizergues & Ellison 1997, Schroeder & Baydack 2001, Hannon et al. 2003, Leupin 2003).

Understanding the mechanisms driving survival during the breeding and non-breeding seasons is critical for lesser prairie-chickens and other grouse species given the conservation status of grouse around the world (Storch 2007). The most critical component for female survival during the breeding season may be nest placement, and survival of females may be lower during the breeding season because of the costs incurred during reproduction (Bergerud & Gratson 1988, Hagen et al. 2007). The relationship between cover at nest sites and hen survival may be of importance to grouse demographics (Wiebe & Martin 1998). For males, survival may be lower during the breeding season than during the non-breeding season because of increased vulnerability and conspicuousness on the display grounds (Bergerud & Gratson 1988, Hagen et al. 2005).

Results suggest that differences between regions, likely tied to differences between sand sagebrush and shinnery oak vegetation types throughout the Texas Panhandle, may be important to survival of lesser prairie-chickens. Patten et al. (2005) found that annual survival in New Mexico and Oklahoma was maximized when shrub cover was ~20%, and survival was positively correlated with lower temperatures and higher relative humidity. Hagen et al. (2007) found that survival of females during the breeding season was associated with nest sites with greater shrub cover, but less vertical vegetation

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structure. Specific differences in vegetation for nesting and brooding may be factors related to lower survival in the southwestern compared to the northeastern populations in the Texas Panhandle. Hagen et al. (2004) suggested that although lesser prairie-chicken declines have slowed, their continuation is probably a result of poor habitat quality and quantity. We agree as shrub cover on the southwestern study site exceeded 20% and was related to poor survival. Lesser prairie-chicken habitat use is selective in regard to microclimate (Patten et al. 2005), and a monoculture of shinnery oak (i.e. southwestern study site) may be detrimental to lesser prairie-chicken survival if arthropod density and residual cover in the form of bunchgrasses are decreased. Restoration of current habitat or creation of patchy habitats may be essential for providing adequate habitat for lesser prairie-chickens throughout the Texas Panhandle.

Annual survival estimates from our study were similar to those reported elsewhere in the literature (Hagen et al. 2005). Estimates from the southwestern region were similar to estimates from other studies in shinnery dominated areas (Campbell 1972), and estimates from the northeastern study site were similar to studies in Kansas (Jamison 2000, Hagen et al. 2005, 2007) where lesser prairie-chicken populations continue to occupy the majority of their historic range (Taylor & Guthery 1980, Hagen 2003). However, caution should be taken when making direct comparisons of annual survival estimates because of the variety of methods used to calculate survival estimates (Hagen et al. 2005). Increasing breeding season survival of lesser prairie-chickens is important if not imperative, to the short-term conservation and long-term recovery of lesser prairie-chickens in Texas. Although nest and brood success are vital stages critical for grouse recovery (Bergerud & Gratson 1988, Peterson & Silvy 1996, Wisdom & Mills 1997), Patten et al. (2005) suggested that even small declines in adult survivorship can affect nest production and ultimately population persistence. Since the majority of mortalities occurred during the breeding season, this also is likely the case in Texas. Based on our estimates of survival and given the mounting evidence of continued population declines (Storch 2007), it is likely that current populations are not sustainable, thus without immediate management attention focused on large-scale habitat restoration, the future of lesser prairie-chickens in Texas is bleak. Without changes in policies and attitudes towards recovery of the species by scientists and agencies (McCleery et al. 2007) the lesser prairie-chicken will continue towards extinction in Texas.

Acknowledgements - we are grateful to the landowners and land managers who allowed us access to their properties over the course of this study. We also are grateful to Duane Lucia (Texas Parks and Wildlife Department) and John Hughes (U.S. Fish and Wildlife Service) for logistical support. This project was funded by Texas Parks and Wildlife Department.

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