

Lesser Prairie-Chicken Brood Ecology on the Southern High Plains of Texas

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Abstract: The lesser prairie-chicken (*Tympanuchus pallidicinctus*) has declined precipitously in abundance and currently occupies a substantially reduced portion of its historic range. Within the sand shinnery oak (*Quercus havardii*) prairies at the southwestern extent of the lesser prairie-chicken's contemporary range, efforts to conserve the species have been constrained by limited information on how land management practices influence habitat quality, and subsequently, affect lesser prairie-chicken recruitment. From 2008–2011, we captured and radio-tagged hen lesser prairie-chickens to monitor broods during four breeding seasons in western Texas. We evaluated influences of vegetation structure and composition, insect availability, and weather on brood ecology on private lands with continuous cattle grazing but no recent herbicide treatment to control shrubs. We located 32 nests from 50 hens captured. Of these nests, 16 produced broods, with 69% of broods lost within the first 14 days. Brood survival was low, and few if any chicks monitored survived to adulthood. Brood sites were dominated by shrub cover and percentages of grass and forb cover were low compared to those reported from other studies. Mean vegetation cover percentages, insect abundance, richness, order, and families did not differ between brood and random sites. Insect abundance was negatively influenced by increased visual obstruction and grass cover, but positively influenced by increased litter, forb cover, and winter precipitation. As found in other studies, chick survival, especially within 14 days post-hatch, is the main limiting factor for population viability. Therefore, lesser prairie-chicken populations throughout the Sand Shinnery Oak Prairie Ecoregion will be largely dependent on management practices that restore healthy prairies, including reduced shrub cover and greater herbaceous groundcover.

Key words: grazing, habitat use, insects, sand shinnery oak, *Tympanuchus pallidicinctus*

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The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is a prairie grouse presumed to have been widely distributed throughout the western portions of the U.S. Central and Southern Great Plains historically. However, in the past century the species has declined precipitously in abundance and currently occupies a substantially reduced portion of its historic range due to conversion of native prairies to row-crop agriculture, energy development, unmanaged cattle grazing (e.g., high stocking densities and long grazing durations), woody-plant encroachment, and periods of intense drought (Giesen 1998, Hagen et al. 2004, Grisham et al. 2013, Ross et al. 2016). Collectively, these factors have likely decreased lesser prairie-chicken survival and impacted reproductive effort.

Lesser prairie-chickens occur in four ecoregions among varying temperature and precipitation gradients (Grisham et al. 2016).

Across all ecoregions, in 2022 the total range-wide population size was estimated at 26,591 individuals (90% CL: 16,321, 38,259; Nasman et al. 2022). Within the Southern High Plains of Texas and New Mexico, lesser prairie-chickens occur in the Sand Shinnery Oak (*Quercus havardii*) Prairie Ecoregion (Timmer et al. 2013). These prairies represent the extreme southwestern portion of lesser prairie-chicken distribution, where the population is geographically and genetically disconnected from other ecoregions (Hagen and Giesen 2005, Oyler-McCance et al. 2016). Populations occupying sand shinnery oak prairies remain dynamic, having decreased from 2967 (90% CL: 1119, 5016) individuals in 2012 to as few as 519 (179, 934) individuals in 2015 (Nasman et al. 2022).

Sand shinnery oak prairies were historically shaped by fire, precipitation, and grazing (Peterson and Boyd 1998, Grisham et al.

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2014). These ecological drivers created prairies that were a matrix of bunchgrasses, shrubs, and forbs (Smythe and Haukos 2009, Zavaleta et al. 2016), but their interplay has largely been altered due to land use changes and climate change. Fire suppression started during European settlement and remains common; reintroduction of fire may be the most important land management action to facilitate conservation efforts (Hagen and Elmore 2016). Precipitation directly influences plant and insect community structure, but on the Southern High Plains recurring intensive droughts are common and increasing in frequency. Extended periods of drought can drastically alter habitat quality, and subsequently, reduce lesser prairie-chicken reproductive output and recruitment (Grisham et al. 2014, Fritts et al. 2018). Precipitation is the most difficult ecological driver to address through management, and the Southern High Plains are forecasted to become drier with more frequent extreme heat events and fewer precipitation events (Grisham et al. 2013). Additionally, sand shinnery oak prairies were historically maintained in part by seasonal grazing by native mammals (Peterson and Boyd 1998). However, native grazers have mostly been replaced with domestic cattle that often graze continuously and at greater intensities than historical nomadic species.

Nest and brood survival have been documented as the main demographic parameters affecting lesser prairie-chicken population persistence (Wisdom and Mills 1997, Hagen et al. 2009, Fritts et al. 2018, Ross et al. 2018). Using a sensitivity analysis, Hagen et al. (2009) found that the effect of chick survival on population growth rate was 1.7–2.1 times greater than the effect on any other demographic rate. Hence, effective management is best based on habitat management strategies that increase fecundity. Moreover, efforts that simultaneously increase nest success and chick survival are predicted to yield a greater effect on population growth rate than increasing female survival. Therefore, understanding brood-rearing ecology is critical to informing sand shinnery oak prairie management and restoration efforts to maintain viable populations of lesser prairie-chickens (Davis 2009).

Despite the importance of brood-rearing ecology for the persistence of lesser prairie-chickens, little is known about brood habitat use within sand shinnery oak-grassland communities (Riley and Davis 1993, Bell et al. 2010). Factors influencing lesser prairie-chicken brood survival appear to be synergistic among temperature and precipitation, concealment cover, ease of locomotion, and food availability (Merchant 1982). Fields et al. (2006) demonstrated that chick survival decreased as temperatures increased during drought periods and was greater when nests were initiated earlier in the nesting season, allowing chicks time to develop and self-thermoregulate prior to the onset of hotter summer temperatures. During periods of hotter temperatures, especially thermal

extremes, overhead vegetation structure provides important cover to avoid desiccation. Bell et al. (2010) reported hens with broods used areas that were warmer than random locations when temperatures were cool and used cooler locations when temperatures were warm, shifting depending on the time of day and diurnal variation in temperature. Therefore, retaining patches of dense shrub cover for thermal refugia is an important management consideration. Prairies with diverse plant communities, especially with abundant grasses and forbs, also support high insect biomass, critical components of lesser prairie-chicken brood-rearing foraging habitat. Conversely, areas with shrub monocultures, particularly those with mismanaged cattle grazing and lack of fire, limit habitat conditions for insects and therefore may result in malnutrition or starvation. Travel corridors are also important for chicks to easily navigate to feed and escape predation (Jones 1963, Riley et al. 1993).

Efforts to conserve lesser prairie-chicken throughout the Sand Shinnery Oak Prairie Ecoregion have been constrained by limited information on how land management practices influence habitat quality, and subsequently, affect lesser prairie-chicken recruitment. Therefore, to address these information gaps, we sought to assess the effects of prairie condition on brood-rearing ecology on privately owned lands in Texas. Our objectives were to evaluate: 1) brood survival on prairies experiencing continuous cattle grazing; 2) brood site selection and area; and 3) food availability for chicks including the influence of ground cover and weather on insect abundance and richness.

Study Area

Our research was conducted on 25,293 ha of privately owned lands in Cochran, Hockley, Terry, and Yoakum counties, Texas from 2008 to 2011. Most land use for this study area included cattle production, intensive row-crop agriculture, especially cotton and grain sorghum, and oil production (Haukos and Smith 1989, Grisham et al. 2014). Management records were incomplete, but the last reported herbicide treatment of sand shinnery oaks was between 1979 and 1983 (Olawsky and Smith 1991). Prairies throughout the entire study area were grazed continuously through the study period.

The landscape was composed of a matrix of rangeland, cropland, and gently undulating sandhills dominated by sand shinnery oak and sand sagebrush (*Artemisia filifolia*) with mixed grasses and forbs. Mesquite (*Prosopis glandulosa*) was encroaching on the periphery of sand shinnery oak grasslands (Hagen et al. 2004). Soils in the area included Brownfield and Tivoli series characterized by deep, loose, light colored, neutral sandy soils and deep, loose, light-colored sands that occur as dunes that were 2–5 m high with

slopes as much as 30%, respectively (Newman 1964). Precipitation for the study area averaged 45.9 cm, mostly occurring from May to October (Newman 1964). Temperatures ranged -33 to 44° C with minimum temperatures during January ($\bar{x} = 2.4$ C) and maximum temperatures during July ($\bar{x} = 25$ C; Newman 1964).

Methods

We captured lesser prairie-chickens on leks during late winter (February) and spring (March–April) annually using walk-in funnel traps (Haukos et al. 1989, Schroder and Braun 1991) and magnetic drop-nets (Wildlife Capture Services, Flagstaff, Arizona). Upon capture, we used plumage characteristics (Copelin 1963) to sex and age birds. We banded hens with a uniquely numbered aluminum blunt-end leg band and fit those individuals with a radio-transmitter (9-g necklace style; American Wildlife Enterprises, Florida) equipped with an 8-hr mortality sensor. We released all individuals at their capture location. We located radio-tagged hens once daily throughout the breeding season (February–August) to monitor nesting activity and hatch date of successful nests (Grisham et al. 2014). All methods were approved under Texas Tech University Institutional Care and Use Protocol 1052-08. Capture and handling practices followed guidelines outlined by the Ornithological Council (Fair et al. 2010).

We located radio-tagged hens using a hand-held three-element Yagi antenna and receiver (R-2000; Advanced Telemetry Systems, Ashanti, Minnesota). We triangulated hens daily but waited to conduct flush counts until 14 days post-hatch (i.e., when chicks can fly) to minimize disturbance, then flushed broods to count the number of chicks at 7-day intervals until 60 days post-hatch (Hagen et al. 2005, Pitman et al. 2006a). Broods were flushed at daybreak and areas were thoroughly searched until we were confident all chicks had been located. We excluded hens from future sampling if they flushed >400 m with no evidence of chicks, were with other adult lesser prairie-chickens, or made continuous long-distance flights post-flush for two consecutive flush intervals. If hens made short-distance flights (i.e., <20 m) when flushed (a brooding behavior) and no chicks were located, we again flushed at the next interval to confirm brood loss (Pitman et al. 2006a).

We estimated ground cover at the location of the brooding hen and 7.5-m away along two perpendicular lines (one north-south, one east-west) emanating from the brood location (Hagen et al. 2005). We collected vegetation and insect samples immediately after determining fate status of the hen and chicks (see below) to reduce sampling bias and to minimize vegetation disturbance. We visually estimated the percentage of litter, bare ground, and canopy cover classes of grass, forb, and woody vegetation using a 20×50 -cm frame, for a total of five frames per brood location.

Additionally, we recorded visual obstruction readings (hereinafter, VOR; Robel et al. 1970) from a 4-m distance and 1-m eye height at each cardinal direction at the center location and each 7.5-m interval ($n = 20$ VOR readings per plot). To assess how lesser prairie-chickens used areas specific to vegetation structure, we used the same protocol to measure vegetation at paired-random locations within 360 m of the brood location in a random direction, consistent with observed reneating distance radii within sand shinnery oak-grassland communities by Grisham (2012). Random locations were sampled immediately after sampling brood locations.

We used a 30-cm insect net to sample insects at brood hen locations and corresponding random locations. We sampled four parallel lines 10 m apart with 20 sweeps per line. Insects were frozen at -17.5 C until each sample was sorted, counted, and identified to order and family. We obtained wet mass for each sample to account for water content given chicks' risk of dehydration. We summed all insects collected across orders to represent insect abundance and used the number of insect orders to represent insect richness.

We obtained 5-min averages of temperature and precipitation from the West Texas Mesonet's Sundown Station and used these data to develop weather variables unique to each season and brood. We selected seasonal weather parameters that influence vegetation cover, affect insect populations as food resources for chicks, and relate to physiological tolerance (Branson 2008, Grisham et al. 2013, Hovick et al. 2014). Weather variables included precipitation annually and during the previous winter (1 December to 28/29 February), and precipitation and maximum temperatures during the first 2 wk after a brood hatched (or for the number of days a brood survived if less than 14 days) and during the entire period for a brood (i.e., hatch until the last time known alive).

Statistical Analyses

We used the nest survival data type in Program MARK to estimate brood survival (White and Burnham 1999). We developed eight *a priori* models to model brood survival including: 1) a null model, and subsequent models incorporating temporal trends for broods known to be alive, including 2) daily survival; 3) weekly survival; 4) days post hatch grouped as early (0–3 days), pre-flight (4–10 days), mid (11–35 days), and late (36–71 days); 5) a linear relationship of brood survival increasing with brood age; 6) a quadratic relationship of brood survival increasing with brood age to an apex and then digressing; 7) brood hen age, and; 8) number of chicks at hatch (Fields et al. 2006, Pitman et al. 2006a).

To characterize brood areas and selection cues, we tested for differences in vegetation and insect abundance and richness between brood and paired random locations. We used logistic regression models with brood or random location as the response

variable (1 and 0, respectively) and each vegetation and insect covariate as predictors. To differentiate food availability for chicks between brood areas and random locations, we used generalized linear mixed-effects models with the R package lme4 (Bates et al. 2015) with brood identification as a random effect and a Poisson distribution for insect abundance and richness. We explored models with multiple variables, but limited our candidate set to single variables to better assess relative importance. First, we evaluated effects of vegetation covariates on insect abundance and richness by combining brood and paired random locations to understand insect availability for broods across the landscape. Second, with combined brood and random locations, we evaluated insect abundance in relation to weather parameters. We did not evaluate relationships between insect richness and weather parameters because of collinearity in fixed effects. Third, we assessed whether insect orders or families differed between brood and random locations. Fourth, we used a *t*-test to assess wet mass and differences in number of individual insects between brood and random locations. Lastly, we calculated the minimum boundary geometry using convex hulls in QGIS V3.32.0 (QGIS Development Team 2023) to estimate brood habitat area for the 13 hens and broods we located. To reduce biases from small sample sizes (birds with <15 relocations), we report area estimates for the eight brood-rearing hens whose broods survived the longest.

For all analyses, we *z*-standardized all continuous predictor variables (hereinafter, covariates) to improve model convergence. We examined relationships among covariates and retained one of a pair when the absolute value of their Pearson’s correlation coefficient was >0.70. We evaluated influences of covariates on response variables using Akaike’s Information Criterion corrected for small sample sizes (AIC_c; Akaike 1973). We considered covariates significant if 95% Confidence Limits (CL) on their regression coefficient (β) did not overlap zero.

Results

We captured and radio-tagged 50 hens and located 36 nests (14 in 2008, 9 in 2009, 10 in 2010, 3 in 2011) from 2008–2011, including re-nest attempts. Sixteen hens had broods during our study period, and we obtained locations of these hens throughout the brood-rearing period. Eleven (69%) of the broods were lost (i.e., all chicks died or otherwise could not be located) before the first flush date. The remaining five broods were monitored at 7-day intervals until they were lost or considered a successful brood at 49 days post-hatch. Only one brood may have been successful, but the hen dropped her radio-transmitter between days 42 and 49 in 2010. The brood-survival model that incorporated a quadratic time trend received the most support (Table 1). According to this

model, the probability of a brood surviving increased as the brood aged, and then decreased as the brood approached flock break-up. The probability of broods surviving the duration of the study was 0.002 (SE 0.004, 95% CL = 0.0001, 0.063).

We collected 23 vegetation samples from the brood-rearing hens whose broods survived beyond the first flush at 14 days post-hatch (Pitman et al 2006a) Most samples were collected at first flush and up to 28 days post hatch. None of our vegetation covariates differed between brood sites and paired random locations with litter, shrub, and bare ground coverages most common among all sites followed by grass and forbs and relatively low VOR (Table 2). Space use of the eight brood rearing hens averaged 156.8 ha, but was highly variable (minimum = 37.0 ha, maximum = 385.5 ha, SD = 126.8 ha). Of 13 hens and broods we located through daily triangulation and flushing, we found two brooding areas to overlap, each having only one location within the area used by the other (Figure 1).

We sampled insects at 23 brood and 22 random locations (one random location sample was lost) from brood-rearing hens. We collected an average of 0.48 (SD = 0.29) insects per sweep. There were 9 and 10 insect orders collected at brood and random locations, respectively (Table 3). Short-horned grasshoppers (Order Orthoptera, Family Acrididae) were the most abundant insect collected at brood and random locations. We found no differences

Table 1. *A priori* candidate models used to estimate brood survival rates for lesser prairie-chickens (*Tympanuchus pallidicinctus*) in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011. *K* = number of parameters; AIC = Akaike’s Information Criterion (AIC_c); *w_i* = AIC model weight.

Model	<i>K</i>	AIC _c	ΔAIC _c	<i>w_i</i>	Deviance
Quadratic	3	41.68	0.00	0.58	35.52
Hen age	2	44.81	3.13	0.12	40.72
Early, Mid, Late	4	45.34	3.66	0.09	39.18
Null	1	46.10	4.42	0.06	44.08
Weekly	4	46.94	5.25	0.04	38.67
Linear	2	47.13	5.45	0.03	43.05
Brood age	2	47.97	6.26	0.02	43.89
# Chicks	2	48.13	6.45	0.02	44.04

Table 2. Mean (SD) percentage of vegetation variables measured at lesser prairie-chicken (*Tympanuchus pallidicinctus*) brood locations and paired random points. Surveys were conducted in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011.

Survey method	Variable	Overall	Brood	Random
Ground cover	% grass	17.2 (11.1)	16.9 (10.7)	17.4 (11.8)
	% forb	3.7 (4.7)	2.8 (2.5)	4.6 (6.1)
	% bare ground	21.4 (12.4)	23 (13.9)	19.8 (10.8)
	% litter	33.6 (13.8)	31.6 (11)	35.7 (16.1)
	% woody	24.3 (10.1)	26 (10.6)	22.5 (9.4)
Visual obstruction reading	Decimeters	1.4 (0.8)	1.3 (0.9)	1.4 (0.7)

between insect abundance, richness, order, or families between brood and random points. Wet mass also did not differ between brood (\bar{x} = 5.10 g, SE = 1.14, 95% CL = 2.74, 7.46) and random points (\bar{x} = 2.94 g, SE = 2.11, 95% CL = 2.05, 3.84; P = 0.08).

Insect abundance increased with decreasing VOR (Tables 4, 5). Less grass coverage with greater litter and forb coverage were positively associated with insect abundance, but associated models had weak model weights (Tables 4, 5). Insect richness did not vary by vegetation covariates with our null model ranking first followed by all other models with minimal differences among weak model weights and CLs overlapping 0 (Tables 4, 5). Only one weather covariate, winter precipitation, influenced insect abundance, having a positive influence (Tables 4, 5).

Table 3. Insect orders and abundance (mean and SE) for lesser prairie-chicken (*Tympanuchus pallidicinctus*) brood and random locations. Surveys were conducted on private lands with no recent herbicide treatment and continuous grazing in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011.

Order	Family	Brood (n = 23)		Random (n = 22)	
		Mean	SE	Mean	SE
Blattodea	Blattidae	0.04	0.04	0.04	0.04
Carabidae	Carabidae	0.82	0.42	0.26	0.11
Coleoptera	Brentidae	0	0	0.08	0.08
Coleoptera	Cantharidae	0	0	0.08	0.04
Coleoptera	Chrysomelidae	0.34	0.13	0.34	0.17
Coleoptera	Coccinellidae	0.04	0.04	0.21	0.13
Coleoptera	Curculionidae	0.13	0.13	0.08	0.06
Coleoptera	Cycloneda	0	0	0.04	0.04
Coleoptera	Dryophthoridae	0.3	0.3	0.08	0.06
Coleoptera	Scarabaeidae	0.04	0.09	0.04	0.04
Coleoptera	Tenebrionidae	0	0	0.04	0.04
Diptera	Bombyliidea	0.26	0.09	0.04	0.2
Diptera	Muscidae	0.3	0.13	0.26	0.12
Diptera	Simuliidae	0	0	0.21	0.21
Diptera	Stratiomyidae	0.17	0.17	0	0
Hemiptera	Cicadellidae	3.36	0.94	3.5	1.06
Hemiptera	Cicadidae	0.17	0.13	0	0
Hemiptera	Miridae	0.13	0.07	0.34	0.16
Hemiptera	Pentatomidae	0.08	0.08	0	0
Hymenoptera	Formicidae	9.34	2.88	12.73	4.03
Hymenoptera	Halictidae	0	0	0.04	0.04
Hymenoptera	Sphécidae	0.13	0.07	0.08	0.06
Mantodea	Mantidae	0.69	0.2	0.26	0.09
Neuroptera	Chrysopidae	0	0	0.08	0.06
Neuroptera	Myrmeleontidae	0.04	0.04	0.04	0.04
Orthoptera	Acrididae	21.86	3.88	18.08	2.1
Phasmida	Heteronemiidae	0.08	0.08	0.17	0.08

Table 4. *A priori* candidate models used to assess influences of vegetation structure and cover and weather variables on insect abundance and insect richness. Surveys were conducted in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011. K = number of parameters; AIC_c = Akaike's Information Criterion (AIC_c); w_i = AIC_c model weight, LL = Log-likelihood.

Analysis	Model	K	AIC_c	ΔAIC_c	w_i	LL
Abundance	Visual Obstruction Reading	3	728.033	0.000	0.980	-360.731
	Grass ground cover	3	735.879	7.846	0.019	-364.654
	Litter	3	742.006	13.973	0.001	-367.717
	Forb ground cover	3	749.112	21.079	0.000	-371.270
	Null	2	756.023	27.990	0.000	-375.872
	Woody ground cover	3	757.252	29.219	0.000	-375.341
	Bare ground	3	758.081	30.047	0.000	-375.755
Richness	Null	2	166.732	0.000	0.253	-81.226
	Forb ground cover	3	167.202	0.471	0.200	-80.316
	Bare ground	3	167.727	0.996	0.154	-80.578
	Grass ground cover	3	168.244	1.512	0.119	-80.836
	Visual Obstruction Reading	3	168.449	1.717	0.107	-80.939
	Woody ground cover	3	168.886	2.154	0.086	-81.157
	Litter	3	169.014	2.283	0.081	-81.221
Abundance	Winter precipitation	3	753.080	0.000	0.683	-373.254
	Null	2	756.023	2.943	0.157	-375.872
	Max. temp. – first 2 wk of a brood	3	756.891	3.811	0.102	-375.160
	Precipitation – brood-rearing	3	757.984	4.903	0.059	-375.706

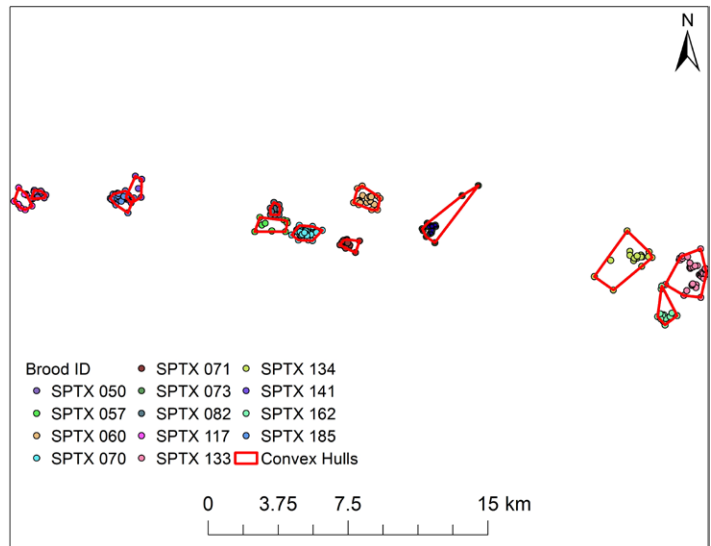


Figure 1. Point locations and convex hulls of 13 lesser prairie-chicken (*Tympanuchus pallidicinctus*) broods located to evaluate brood survival. Surveys were conducted in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011. Spatial data are accurate and precise, but scale/scope presented in figure have been modified to protect sensitive geospatial data.

Table 5. Estimates of beta coefficients (β), standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits, z-value, corresponding P-values of vegetation and weather covariates used to assess influences on insect abundance and insect richness, a primary food source for lesser prairie-chicken (*Tympanuchus pallidicinctus*) chicks. Surveys were conducted in Cochran, Hockley, Terry, and Yoakum counties, Texas, 2008–2011.

Analysis	Covariate	β	SE	LCL	UCL	z	P
Abundance	Intercept	4.192	0.126	3.939	4.446	32.411	<0.001
	Visual Obstruction Reading	-0.190	0.032	-0.255	-0.125	5.741	<0.001
	Grass ground cover	-0.144	0.028	-0.201	-0.087	4.943	<0.001
	Litter ground cover	0.119	0.026	0.067	0.171	4.460	<0.001
	Forb ground cover	0.071	0.020	0.030	0.112	3.380	<0.001
	Woody ground cover	-0.028	0.025	-0.078	0.021	1.123	0.262
	Bare ground	-0.016	0.025	-0.066	0.034	0.621	0.534
Richness	Intercept	1.356	0.092	1.171	1.541	15.210	<0.001
	Forb ground cover	-0.110	0.085	-0.281	0.061	1.265	0.206
	Bare ground	0.085	0.074	-0.064	0.233	1.119	0.263
	Grass ground cover	-0.069	0.080	-0.230	0.091	0.845	0.398
	Visual Obstruction Reading	-0.074	0.099	-0.273	0.126	0.725	0.469
	Woody ground cover	0.028	0.076	-0.125	0.181	0.361	0.718
	Litter ground cover	-0.008	0.076	-0.161	0.146	0.096	0.924
Abundance	Intercept	3.677	0.086	3.503	3.850	41.531	<0.001
	Winter precipitation	0.206	0.075	0.054	0.357	2.666	0.008
	Max. temp. – first 2 wk of a brood	-0.116	0.094	-0.305	0.072	1.209	0.227
	Precipitation – brood-rearing	-0.070	0.120	-0.311	0.172	0.565	0.572

Discussion

Lesser prairie-chicken brood survival in the Sand Shinnery Oak Ecoregion during our study was extremely low, suggesting that population level reproduction was also low. Chick survival was least during the first 2 wk post-hatch but increased weekly thereafter. Compared to populations at the northern extent of their range, adults in the Southern High Plains must invest more in survival and less in reproduction, maximizing reproductive efforts when environmental conditions are optimal (Patten et al. 2005, Hagen et al. 2009, Grisham et al. 2014). Moreover, lesser prairie-chickens in sand shinnery oak-grassland communities exhibit a boom-bust fecundity pattern, tied closely to recurring droughts (Merchant 1982, Fritts et al. 2018). The combination of these factors, in concert with their low population abundance and few days that most broods survived, makes conservation challenging, particularly in the sand shinnery oak prairies (e.g., Hagen et al. 2005). Despite these challenges, our results provide important baseline information regarding brood ecology of the species within the Sand Shinnery Oak Prairie Ecoregion.

In our study, 69% of the broods were lost before the first flush (<14 days). It is possible chicks moved away from the hen or became part of an amalgamated brood with another hen during surveys (Pitman et al. 2006b, Dahlgren et al. 2010, Orange et al.

2016). Nonetheless, if our assessments were correct, then of the 50 radio-tagged hens and 32 nests laid, there was little evidence that chicks successfully reached independence. Brood loss within 14 days of hatching likely has been a key vital rate influencing species' decline (Wisdom and Mills 1997, Pitman et al. 2006a, Davis 2009, Hagen et al. 2009). In Kansas, Fields et al. (2006) reported 28% of broods had at least one chick 60 days post-hatch and estimated the probability of a brood surviving to 60 days was 49% and 5% for those reared by adults and subadults, respectively. Also in Kansas, Pitman et al. (2006a) suggested overall chick survival for early brood-rearing (hatch to 14 days post-hatch) was 48%, 37% for the late period (15 to 60 days post-hatch), and 18% for the entire brood-rearing period of hatch to 60 days post-hatch. Estimates reported from the Southern High Plains are substantially lower than those from the northern populations. In the northeastern Texas panhandle, Holt (2012) estimated 63-day chick survival as 10%, while during a 2-yr study in New Mexico, Merchant (1982) reported yearly estimates of 0% and 27% for hens that produced a brood that survived until independence.

Herbaceous vegetation structure is closely tied to precipitation, where above-average rainfall in the spring and summer maximizes vegetation growth, and tall, dense residual vegetation cover from the previous growing season contributes to quality nesting, and

subsequently brood-rearing habitat conditions (Bailey et al. 2000, Grisham 2012). During the 2010 season, following the most winter precipitation during our study (study area average = 11.56 cm), nest initiation occurred earlier (mean Julian date = 114) compared to other years (mean Julian dates = 129–144), and broods survived longer. Conversely, the 2011 season represented the other extreme of the precipitation gradient with an intense La Niña event and subsequent drought affecting lesser prairie-chicken reproductive ecology (Nielsen-Gammon 2012). In 2011, only 3 of 15 (20%) radio-tagged hens nested; however, all nests were abandoned within two days of initiation. The drought of 2011 was so severe that sand shinnery oak and grasses on our study sites did not leaf out, leaving no substantial cover for lesser prairie-chickens. Only 2.46 cm of precipitation occurred from 15 October 2010 to 31 August 2011, constituting the worst drought on record and warmest La Niña event in the area since 1950. Our study area had 56 days with temperatures >38 C, and at the time, made 2011 the hottest summer on record for the area (Grisham et al. 2016).

Habitat use by brood-rearing hens did not appear to be linked to specific structural vegetation variables. We found no differences between used and random locations, which may have been attributed to a true lack of selection or from small sample sizes that likely limited our ability to fully evaluate heterogeneity in habitat quality. The lack of differences between brood and random locations in our study differed from previous findings (Ahlborn 1980, Hagen et al. 2004, Bell et al. 2010). The overall uniformity and extent of shrub cover resulting from constant, unmanaged cattle grazing likely contributed to the low percentage of grass and forb cover and subsequently, decreased the quality of brood-rearing habitat. At brood sites, forb coverage was less (approximately 3%) than the 13–15% reported in other studies (Jones 1963, Hagen et al. 2004, Hagen et al. 2005). Lesser prairie-chicken brood-rearing habitat in the Sand Shinnery Oak Prairie Ecoregion should consist of approximately 50% of total overhead cover, with relatively equal proportions of shrub (20–25%), herbaceous cover (18–26%), and ground litter (38–44%; Hagen et al. 2013).

Increased precipitation prior to brood-rearing during winter and spring maximizes vegetation growth, promotes forb growth, and supports greater insect abundance (Noy-Meir 1973, Kingsolver 1998, Fields et al. 2006, Wenninger and Inouye 2008). Lesser prairie-chicken chick survival is positively correlated with insect availability, especially during the first 2 wk of life (Hagen et al. 2005). Davis et al. (1980) reported foods of chicks and young juveniles in New Mexico were 99–100% insects, especially short-horned (80.4%) and long-horned (7.7%) grasshoppers. We found grasshoppers (Order Orthoptera) and leafhoppers (Order Hemiptera) were the most common insects available for possible

consumption. While we found a positive significant relationship between winter precipitation and insect abundance, insects appeared to be limited even in years when precipitation was near average (e.g., 2008 = 41.1 cm).

Low heterogeneity in vegetation composition may have contributed to the lower insect availability, and possibly, lower brood survival due to malnutrition or starvation. Our sand shinnery oak dominated stands lacked sufficient forb cover to support insect communities and may be the underlying reason why chicks failed to survive the first 14 days post hatch. This is further supported by the negative relationship between insect abundance and visual obstruction, which was mostly related to shrub cover. Additionally, while maximum temperature was not a good predictor of food availability in our study and may not be a good predictor of brood survival (Fields et al. 2006), it may lead to decreased survival if chicks must decrease feeding time to seek shade during periods of higher temperatures (Ahlborn 1980).

We found no evidence that chicks born in our study survived to adulthood. We acknowledge that repeated disturbances via flushing may have contributed to low brood survival probabilities. Beyond this, chick survival in our study was a clearly affected by synergistic effects of severe drought and unmanaged cattle grazing with high stocking densities that resulted in poor prairie conditions. Shrub-dominated prairies at our study site, and likely elsewhere, may not support properly interspersed brood-rearing habitat in relation to lekking and nesting habitat. Long-term survival of lesser prairie-chickens in the Sand Shinnery Oak Prairie Ecoregion will be largely dependent on management practices that promote healthy prairies. When possible, it would be prudent for land managers to employ practices such as short duration, low intensity grazing that mimic native grazers, and prescribed burning and herbicide treatments to reduce woody shrub cover and promote conditions for grass and forb cover, and subsequently, support greater food resources for chicks.

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