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Factors Affecting Survival of Attwater's Prairie-Chicken Broods

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Factors Affecting Survival of Attwater's Prairie-Chicken Broods

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Abstract

Annual population changes of most grouse, including the imperiled Attwater's prairie-chicken *Tympanuchus cupido attwateri*, are driven by annual reproductive success. Previous research identified poor survival of chicks as a primary bottleneck for recovery of this species. We evaluated the relative importance of 26 factors in 5 categories (weather and topography, habitat, plant phenology, time and site, hen characteristics) on Attwater's prairie-chicken brood survival to 2 weeks post-hatch (the period when chick mortality is highest) and on the number of chicks per brood at 6 weeks post-hatch (when chicks are capable of independent survival). Factors with most support for predicting brood survival to 2 weeks included invertebrate dry mass, ordinal date, an index to maximum photosynthetic activity of vegetation from multispectral imagery, and proportion of brood locations within areas treated to suppress red imported fire ants *Solenopsis invicta*. Broods were most likely to survive if they hatched between early and late May and were located within areas (1) that were treated to suppress red imported fire ants, (2) where vegetation produced intermediate values for the maximum photosynthetic activity index, and (3) that supported high invertebrate biomass. The number of chicks per brood surviving to 6 weeks post-hatch was best predicted by a nonlinear relationship with a drought index during the first 2 weeks post-hatch, and was maximized when average values of the drought index indicated moderately depleted soil moisture, but not severe drought. Our finding that the average drought index during the first 2 weeks after hatch had more support for predicting the number of chicks per brood at 6 weeks than the average drought index for the entire 6 weeks emphasizes the importance of the first 2 weeks for Attwater's prairie-chickens. This comprehensive analysis of factors affecting Attwater's prairie-chicken brood survival provides valuable information to guide management and recovery efforts for this species.

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Introduction

The Attwater's prairie-chicken *Tympanuchus cupido attwateri* Bendire is endemic to grasslands of southeast Texas and southwest Louisiana (Bendire 1894; Lehmann 1941). It shares its subspecies status with the greater prairie-chicken *T. c. pinnatus* and the extinct heath hen *T. c. cupido.* (Johnson et al. 2020; Gill et al. 2021). Once abundant on expansive coastal prairie grasslands (Lehmann 1941, 1968; Lehmann and Mauermann 1963), the Attwater's prairie-chicken was listed as endangered with extinction in 1967 pursuant to the U.S. Endangered Species Preservation Act of 1966 (Udall 1967). Habitat conversion to cropland and residential areas and degradation of remaining grasslands by overgrazing, woody species encroachment, and invasion by exotic fauna and flora have driven this subspecies to near extinction (Lehmann 1941; Jurries 1979; U.S. Fish and Wildlife Service [USFWS] 2010; Morrow et al. 2015). Populations have remained below 200 individuals since 1993 despite intensive intervention, including habitat management and release of captive-reared individuals to supplement failing populations (USFWS 2010; Morrow et al. 2015; USFWS 2021). The Attwater's prairie-chicken is currently listed as endangered pursuant to the U.S. Endangered Species Act (ESA 1973, as amended; USFWS 2021).

The Attwater's prairie-chicken recovery plan pinpointed poor survival of chicks in the wild as "…the single-most factor limiting significant progress toward recovery" (USFWS 2010:40). Morrow et al. (2015) identified availability of invertebrate food as influenced by the invasive red imported fire ant *Solenopsis invicta* as a major limiting factor for survival of Attwater's prairie-chicken broods. However, other factors including habitat composition and structure (e.g., Lehmann 1941; Jones 1963; Kessler 1978; Svedarsky 1979), weather (e.g., Lehmann 1941; Jurries 1979; Flanders-Wanner et al. 2004), time of year (Riley et al. 1998; Fields et al. 2006; Matthews et al. 2011), or characteristics of the brood hen such as age or captive-reared versus wild (Moss et al. 1975; Fields et al. 2006; McNew et al. 2012, Rymesova et al. 2013) have been suggested as factors affecting brood survival for Galliformes.

Removing poor chick survival as a bottleneck to Attwater's prairie-chicken recovery requires a thorough understanding of which factors most limit existing populations. Hannon and Martin (2006) identified two critical periods for survival of juvenile grouse: (1) the first 2 weeks after hatch when chicks are dependent on the hen for thermoregulation, habitat selection, and protection from predators, and (2) when independent young are dispersing. Hatch-year Attwater's prairie-chickens become capable of independent survival and dispersal from the brood hen at approximately 6 weeks of age (Lehmann 1941). Therefore, we evaluated the relative importance of hen attributes, weather, topography, ordinal day, site, and habitat characteristics, including plant phenology, vegetation structure, fire ant suppression, and invertebrate abundance on Attwater's prairie-chicken brood survival to 2 weeks post-hatch and on the number of chicks per brood alive at 6 weeks post-hatch.

Study Sites

We conducted our study at the Attwater Prairie Chicken National Wildlife Refuge and on private land in Goliad County, Texas (Figure 1). The 4,265-ha Attwater Prairie Chicken National Wildlife Refuge (APCNWR; Colorado County; 29.7°N, 96.3°W) near Eagle Lake, Texas, is part of the USFWS National Wildlife Refuge System and was established specifically to maintain habitat for Attwater's prairie-chickens (USFWS 2012). The Goliad County study area (28.7°N, 97.4°W) near Goliad, Texas, was located on a 2,670-ha private cattle ranch situated within approximately 20,445 ha of relatively contiguous grasslands (USFWS 2010).

The two study areas were located approximately 150 km apart. Both sites were within the gulf prairies and marshes vegetational area of Texas (Hatch et al. 1990) and consisted of managed open grasslands containing mid–tall native grass species. Climate of the region was subtropical, and dominated by warm, moist air masses derived from the Gulf of Mexico (Smeins et al. 1991). Total annual precipitation for Colorado County, Texas averaged 1,057 mm during 1960–1990, and average daily temperatures ranged from 10.8°C in winter to 27.9°C in summer (Brown 2006). Total annual precipitation for Goliad County, Texas averaged 1,016 mm from 1971–2000, and average daily temperatures ranged from 13°C in winter to 28.9°C in summer (Wiedenfeld 2010). Data on Attwater's prairie-chicken broods were collected during 2009–2019 at APCNWR and 2009–2012 at the Goliad County site. Annual precipitation during those periods averaged 1,076 [standard deviation (SD) = 329] mm at the Eagle Lake Agricultural Research Station 11 km southwest of APCNWR and 739 (SD = 314) mm at Coleto Creek Reservoir 18 km northeast of the Goliad County site (Wilson et al. 2015).

Cattle stocking rates at both study sites generally averaged 4.8–10.1 ha/animal unit year, and both sites used prescribed burning as a management tool. Prescribed fires at the Goliad County site were accomplished predominantly as whole pasture burns with pre- and post-fire grazing deferral, whereas APCNWR implemented patch burns within pastures (Fuhlendorf and Engle 2001; Fuhlendorf et al. 2006) with and without grazing deferral after prescribed fire. Portions of both sites, depending on funding availability, were treated aerially with 1.7 kg/ha of Extinguish Plus™ (0.365% hydramethylnon, 0.25% s-methoprene; Central Life Sciences, Schaumburg, IL) fire ant bait to suppress fire ants and increase abundance of invertebrates required by prairie-chicken broods for food (Morrow et al. 2015). Area and timing of treatment varied somewhat for each site and among years. For the Goliad County site, repeat treatments of

Extinguish Plus™ were applied in 2010 (November) and 2011 (September) on 294 ha of potential prairie-chicken brood habitat. At APCNWR, treatment area size increased from 308 ha in 2009 to a maximum of 2,381 ha in 2014–2015. During 2016–2019, treatment area size at APCNWR remained constant at 2,052 ha. APCNWR treatments ($1 \cdot site^{-1} \cdot year^{-1}$) occurred in autumn (September–November) or spring (March–early April). While we targeted prairie-chicken core use areas for fire ant treatment as indicated by long-term telemetry data and lek locations, we did not focus treatments on specific habitats (e.g., brood or nesting habitat).

Methods

Brood survival

We evaluated the relationship between Attwater's prairie-chicken brood survival and five categories of variables: (1) weather and topography, (2) habitat, (3) plant phenology, (4) time and site, and (5) hen characteristics (Data S1, Data S2, Table S1). We equipped hens with poncho-mounted radio transmitters (Amstrup 1980, Toepfer 2003) with tuned-loop (Telemetry Solutions, Walnut Creek, California; Advanced Telemetry Systems, Isanti, Minnesota) or whip antennas (American Wildlife Enterprises, Monticello, Florida). We coiled or trimmed whip antennas to extend only approximately 6 cm beyond the poncho to avoid potential interference with flight (Marks and Marks 1987). Most (n = 124; Table S1) Attwater's prairie-chicken females at both study locations were released from various captive rearing facilities (USFWS 2010). Although some (n = 53) were after-hatch-year, most (n = 83) brood hens were released as 8–12+ week-old poults during July–October after spending 2 weeks in pre-release acclimation pens at release sites (Table S1). Therefore, releases occurred roughly 5–8 months in advance of their first reproductive season (March-July) in the wild. Hens were equipped with transmitters (12–24 g, ≤ 3% of body mass; expected battery life > 365 d) at the time of transfer from captive rearing facilities. Survivors were recaptured by night-lighting in subsequent years as needed to replace transmitters nearing the end of their expected battery life. Transmitters were placed on wild-hatched hens (n = 14; Table S1) at ≥ 7 weeks of age after homing on their radioed mother at night.

We tracked broods (hen with chicks) using telemetry approximately 10 times (i.e., daily during the 5-day work week) during the first 2 weeks post-hatch, except when adverse weather hindered obtaining these data or hen movements (>1.6 km) indicated probable brood loss. We determined brood hen locations (hereafter brood location) either by triangulation using a vehicle-mounted 6-element yagi antenna system and computer software (DogTrack, Blacksburg, Virginia; Locate III, Tatamagouche, Nova Scotia, Canada), or by circling brood hens at 10–20 m with a hand-held telemetry system and recording location data with a global positioning system (GPS) unit. Radio-marking of hens and brood monitoring activities were authorized by Federal Fish and Wildlife Permit TE051839 and Texas Parks and Wildlife Department Scientific Research Permit SPR-0491-384.

We assessed if broods survived to 2 weeks post-hatch in one of two ways: (1) homing on radioed brood hens at dawn and visually checking for the presence of chicks, and (2) playing chick distress calls near brood hens. Through 2015, we approached radioed hens with hand-held telemetry equipment at 14 days post-hatch and observed them at dawn before they left night roosts to determine if any chicks remained with the hen. We encouraged hens to move only if necessary to be absolutely certain of chick presence. We considered a brood successful if we observed ≥ 1 chick with the hen. To reduce disturbance to the hen and brood, we did not attempt to obtain a total count of chicks at the 2-week assessment. During 2016–2019, we approached within approximately 20–30 m of brood hens during daylight hours and played an Attwater's prairie-chicken chick distress call recorded at the Houston Zoo, Inc. Visible and/or vocal response by the brood hen indicated positive presence of chicks (Healy et al. 1980). If, based on results of playing the chick distress call, we were uncertain whether chicks remained with the brood hen, we followed up by checking at dawn as previously described. At approximately 6–8 weeks post-hatch, brood survival was assessed again, this time with effort made to count all chicks. Brood hens were approached at night using telemetry and head-mounted spotlights, and all surviving chicks were counted. If counts of surviving chicks were assessed more than once, we used the maximum number of chicks observed on any one occasion for our analyses.

Weather and topography variables

We characterized weather metrics for each brood by determining average temperature (°C; *temp*), total rain (cm; *rain*), number of days with rain (*days.rain*), total wind (km/day; *wind*), total pan evaporation (cm; *evap*), and average Keetch-Byram Drought Index (KBDI; Keetch and Byram 1968) over the first 2 and 6 weeks post-hatch (Tables S1, S2). The Keetch-Byram Drought Index ranges from 0–800 and estimates moisture deficits in the deep duff or upper soil layer. Each KBDI unit represents 0.25 mm of moisture deficit. Temperature, precipitation, wind, and evaporation data were downloaded for the Eagle Lake Agricultural Research Station (APCNWR broods; Colorado County; 29.6°N, 96.4°W) and Coleto Creek Reservoir (Goliad County broods; 28.7°N, 97.2°W) weather stations (Wilson et al. 2015). Daily KBDIs were calculated for each site from daily precipitation and maximum temperature (Alexander 1990).

We calculated a Topographic Position Index (TPI) as an index to flooding potential at brood sites during the first 2 weeks post-hatch based on light detection and ranging (LiDAR) data (Guisan et al. 1999; Tables S1, S2). Data collection for LiDAR occurred in June 2009 and January–February 2011 for Goliad County and APCNWR, respectively, with approximately 4 returns/m^2 (Strategic Mapping Program 2009, 2011). We processed the LiDAR data to produce a 3-m Digital Elevation Model, and then calculated the TPI using a 200-m radius neighborhood (Guisan et al. 1999). We used the 2-week mean TPI value for each brood in subsequent analyses to evaluate whether topographic position was related to brood survival. We also hypothesized that variation in TPI values might indicate the availability of potential refugia from flooding at the microhabiat level. Therefore, we also evaluated the relationship between brood survival and standard deviation (SD) of TPI (*TPI.SD*).

Habitat variables

Habitat data (Tables S1, S2) were collected at brood sites 1–4 days after determining their locations to avoid disturbance to the broods. Invertebrate samples were collected with 25 vigorous sweeps of vegetation along an approximately 20-m transect in a random direction from the predetermined brood location with a 38-cm diameter, canvas sweep-net. Each sweep consisted of a single approximately 2-m arc of the net. We did not collect samples when vegetation was wet. We labeled invertebrate samples and froze them until we could determine counts of individuals for each sample. Invertebrates were dried at 60°C for 24 h and then weighed to the nearest 0.0001 g on a digital analytical scale. We determined median invertebrate numbers (*num.inverts*) and mass (*dry.mass*) for each brood to control for pseudoreplication within brood unit. We also included the derived metric *mean.dry.mass* representing total dried mass (g) of invertebrates from samples divided by the count of invertebrates. We hypothesized that a mean mass per invertebrate >1 mg and <10 mg would represent prey sizes most available to foraging chicks.

We determined vegetation effective height (cm) using a 1.2 x 1.2-m white pegboard with holes spaced at 2.54 cm. We placed the pegboard at each pre-determined brood location, and at four locations 10 m away in each cardinal direction (Kobriger 1965; Toepfer 2003). We took digital photographs at each of the five locations from a distance of 4 m and height of 1 m (Robel et al. 1970). We then imported photographs into ArcGIS Desktop ArcMap (version 10.6.1 and earlier; ESRI 2018) and the height of vegetation which completely obscured all dots below it was determined at 10 equidistant (12.7 cm) points on the board, using the top of the board as a known distance to scale measurements. We used all 50 points (10 points/photograph, 5 photographs/brood site) to determine the mean and coefficient of variation of effective height at each brood location. Finally, we determined mean effective height (cm; *veg.ht*) and coefficient of variation (CV; *veg.ht.cv*) determined for each brood for the 2-week post-hatch period. We included the CV of effective vegetation height to assess the importance of variability in vegetation structure to brood survival in addition to height.

We also included metrics of vegetation height (cm) obtained from a LiDAR canopy height model (Tables S1, S2). We first processed the LiDAR data to provide an estimate of vegetation height above ground level using FUSION software v. 2.80 (McGaughey 2017). This layer was then summarized at multiple scales, using neighborhood analyses to calculate the mean and standard deviation of vegetation height at 9 and 21 m radii from each pixel. Mean values were calculated for brood locations taken during the first 2 weeks post-hatch only; specific brood locations were not determined after that time. These LiDAR-derived mean values provided information on the extent of vegetation along the vertical axis only. The field-collected effective height measurements we described previously were similar to visual obstruction measurements described by Robel et al. (1970) which were strongly correlated with the biomass of vegetation present in Kansas grasslands. These two vegetation height metrics provided information on different aspects of vegetation structure at Attwater's prairie-chicken brood sites.

Plant phenology, time and site, and hen variables

Remote sensing of land-surface plant phenology can characterize vegetation changes during the growing season and document specific events such as start of the growing season and its duration. These vegetation changes may in turn impact habitat characteristics (e.g., timing and density of invertebrate abundance, thermal cover, shelter from predators). We included metrics of plant phenology as derived from time-series Collection 6 Aqua EROS Moderate Resolution Imaging Spectroradiometer (eMODIS) Normalized Difference Vegetation Index (NDVI) data recorded at 7- to 10-day intervals and a 250-m grid cell size (Jenkerson et al. 2010). These metrics (Tables S1, S2) consisted of five annual phenological layers derived from NDVI values recorded over the course of the year (Jenkerson et al. 2010): (1) start of season (value at the beginning of measurable photosynthesis; *sosn*), (2) end of season (value at the end of measurable photosynthesis; *eosn*), (3) maximum increase in NDVI above the baseline level (*amp*), (4) maximum level of NDVI (*maxn*), and (5) sum of NDVI (*tin*).

Broods were classified according to year (*year*), study site (*site*), and ordinal date of hatch within year (*day*) to evaluate the relative importance of these variables on brood and chick survival (Tables S1, S2). Brood hens were classified by age (*age;* second year [SY] or after second year [ASY]), source (*source*; released from captivity or wild-hatched), years in the wild (*years.out*), whether they had successfully nested (*nest.prev*) or fledged (*fledge.prev*; chicks survived to minimum of 6 weeks) chicks in previous years, and the total estimated fresh weight (g; *total.egg.mass*) of eggs in the clutch as an index of energy invested by the hen. All eggs in a clutch were weighed (nearest 0.1 g) and measured (nearest 0.1 mm) with digital calipers, in most cases when hens were off their nests during morning or evening feeding forays. These data were used to estimate fresh egg weights as described by Hoyt (1979) and Burnham (1983). Table S1 provides summaries of data collected on broods and hens in our study.

Data analyses

We used a two-stage approach for analyzing both 2-week brood survival and the number of chicks per brood at 6 weeks. For both sets of analyses, we first fit models for each of the five predictor categories separately (stage one; Table S2). Models with support in each stage one category compared to the null model were then combined into additional models (stage two) using the ‘dredge’ function from the ‘MuMIn’ package (Barton 2020) to produce all possible combinations, provided the variables in these models were not highly correlated ($|r| < 0.6$). For each model, we examined β values for significance ($P \leq 0.05$) and removed models that had uninformative parameters (Arnold 2010). We took this modeling approach because missing values would have necessitated the removal of 16% of the observations had all data been initially analyzed together. By separating the analyses by predictor category, and then combining only terms with support in the final analysis, we were able to minimize the removal of observations with missing data. To aid in model convergence, all variables were scaled by subtracting the mean and dividing by the standard deviation.

Brood survival to 2 weeks. We modeled survival to 2 weeks using generalized linear models (GLM). The response variable was presence or absence of at least one chick at 2 weeks post-hatch. Although most hens (86%) had only one observation in the dataset, there were some hens with more than one observation because they were observed across multiple years: 16 hens with 2 broods and 1 with 3. Because there may have been some lack of independence among observations of the same hen, we initially ran the models as mixed effects models with hen as a random effect to account for any pseudoreplication. However, these models had difficulty converging and the estimated variation of the random effect was zero. Because these models did not support the inclusion of hen as a random effect, we instead used GLMs for the 2-week brood survival analysis.

We built GLMs using the 'glm' function in the R statistical system (R version 3.6.3, R Core Team 2020) and specified a binomial distribution with a logit link. We identified top models using change in Akaike's Information Criterion values (ΔAIC; Akaike 1973) and associated Akaike weights (*w*; Burnham and Anderson 2002). For the final (stage two) combined model analysis we considered the top models to be within 2 ΔAIC. To assess fit for the top model, we report the Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000). To evaluate performance, we calculated the accuracy of the top model predictions (% of broods with correctly predicted outcomes). We also calculated the Area Under a Receiver Operating Characteristic Curve (AUC; Hanley and McNeil 1982) for the top model. The AUC represents the probability of giving a brood that survived a higher probability of survival than a brood that did not survive. An AUC value of 0.5 indicates the model performs no better than expected by chance whereas a value of one indicates perfect predictive ability.

Number of chicks per brood at 6 weeks. For analysis of chicks per brood at 6 weeks, we followed the same procedure as the brood survival analysis at 2 weeks with the exception that 6-week weather metrics were added to candidate models, and the response variable, number of chicks per brood at 6 weeks, was modeled with a negative binomial distribution using the 'glm.nb' function from the 'MASS' package (Venables and Ripley 2002) in R. Detailed locations of broods were not determined and habitat metrics were not collected after 2 weeks post-hatch. However, we included habitat metrics collected from 0–2 weeks in our candidate models since most chick mortality typically occurs during this timeframe (Hannon and Martin 2006), and events during this time period could influence the number of chicks per brood at 6 weeks. We used a negative binomial rather than a Poisson model because the response variable, number of chicks, was overdispersed. To evaluate model fit, we used a chi-square test to compare the best supported model to the same model fitted with a Poisson distribution to verify that use of the negative binomial distribution was supported by the data. We also evaluated goodness-of-fit by comparing the observed deviance to the expected deviance under a chi-square distribution.

Results

We monitored 138 (APCNWR n = 115; Goliad n = 23) broods from 120 hens between 2009 and 2019 (Table S1). Of these, 58 (42.0%) survived to 2 weeks. Nine (15.5%) brood hens died during weeks 2–6, and we were unable to locate 4 (6.9%) brood hens at 6 weeks. Of the 45 surviving hens that we relocated at 6 weeks post-hatch, 13 (28.9%) had no chicks, and the remaining 32 (71.1%) had 1 or more chicks ($\bar{x}$ = 2.6, maximum = 8). Brood location coordinate data were available for 108 of the 120 hens during the first 2 weeks post-hatch. Location data from hens were available for all years at APCNWR, but only for 2009 and 2012 at Goliad. The mean number of locations per hen during the first 2 weeks after hatch was 7.4 (SD = 3.7, range = 1–18) with a total of 801 locations recorded for all hens combined.

Analysis of brood survival to 2 weeks

There was support for some candidate models in all categories except hen traits (Table 1). For stage one analyses, the best time and site model for 2-week brood survival contained a quadratic term for day of year (day^2; w = 0.53). All time and site models with support compared to the null model contained day or day^2 ($\Delta AIC_c \leq$ 4.31; cumulative w = 0.84); neither *year* nor *site* were competitive for predicting 2-week brood survival. The best stage one weather and topography model contained the 2-week mean value for KBDI along with a quadratic of mean temperature (*temp*^{2}) over the 2 weeks following hatching (w = 0.20; Table 1). The top three ($\Delta AIC_c \leq$ 2.33; cumulative w = 0.41) weather and topography models contained some form of KBDI or *temp*. The best supported stage one habitat model was a quadratic relationship with median dry mass of invertebrates along with a term for % of brood locations within fire ant treated areas (w = 0.51; Table 1). The second best stage one habitat model (ΔAIC_c = 0.93) also contained quadratic terms for *dry.mass* along with a binary variable indicating whether broods hatched in fire ant treated areas (*rifa.trt.hatch*). Cumulative weight for these two models was 0.83. The only other models for habitat that were competitive compared to the null model contained variations of these parameters. For the plant phenology metrics, there was some support for a quadratic brood survival relationship with both maximum level of photosynthetic activity (*maxn* + *maxn*^{2}; ΔAIC_c = 0.00; w = 0.22) in the canopy and level of photosynthetic activity at the beginning of measurable photosynthesis (*sosn* + *sosn*^{2}; ΔAIC_c = 0.43; w = 0.18; Table 1). No hen variables had support when compared to the null model, nor did any vegetation structure metrics (Table 1).

The best supported stage two model for predicting brood survival to 2 weeks post-hatch contained day of year (*day*^{2}), % of brood locations within fire ant treated areas (*rifa.trt*), median invertebrate dry mass (*dry.mass*), and maximum level of photosynthetic activity (*maxn* + *maxn*^{2}) indicated by the NDVI (w = 0.42; Table 1; Figure 2). The two top stage two models with ΔAIC_c < 2 both contained the same *dry.mass*, *day*, and *maxn* terms, and both contained terms for fire ant treatment (*rifa.trt*, *rifa.trt.hatch*). These top stage two models accounted for 0.60 of cumulative model weight (Table 1). Of all the variables in the top model, support was strongest (P < 0.001) for median dry mass of invertebrates at brood sites (Table 2). Predicted brood survival increased from 0.38 (95% CI 0.21 - 0.58) to 0.96 (95% CI 0.83 - 0.99) when the median dry invertebrate biomass at brood locations increased from 0.12 g to 1.36 g. Similarly, predicted survival increased from 0.36 (95 % CI 0.20 - 0.55) to 0.64 (95 % CI 0.48 - 0.77) for broods with locations taken entirely outside of fire ant treated areas versus those with locations taken entirely within those areas, respectively (Figure 2). Model diagnostics did not uncover any issues with the final model. The Hosmer and Lemeshow goodness-of-fit test indicated adequate model fit ($P = 0.42$). The model predicted 74% of observations correctly and the AUC was 0.79, indicating the model had a moderate amount of predictive power.

Analysis of number of chicks at 6 weeks

Only three variables were supported in stage one models for predicting number of chicks per brood at 6 weeks: average KBDI^2 during the first 2 and 6 weeks after hatch, and median dry mass^2 of invertebrates collected at brood sites during the first 2 weeks post-hatch (Table 3). Overall, the mean KBDI^2 from hatch to 2 weeks had the most support in combined stage two models for predicting the number of chicks per brood at 6 weeks ($w = 0.90$; Table 3). No other predictor variables were found to be informative in the final stage two model. The highest number of chicks were predicted when KBDI values ranged from 200–400 (Figure 3), indicating conditions that were neither excessively wet nor dry. Model diagnostics revealed no issues with model fit. The negative binomial model, which estimated the dispersion parameter, was more appropriate ($P < 0.001$) than the Poisson model. Model diagnostics indicated an adequate fit of the model to the data ($P = 0.36$).

Discussion

We observed 42.0% survival for Attwater's prairie-chicken broods to 2 weeks post-hatch during our 11-year study. In comparison, McNew et al. (2011) observed 47–54% ($n = 15$) survival of Kansas greater prairie-chicken broods to 14 d post-hatch, and Matthews et al. (2011) observed 50% survival of Nebraska greater prairie-chicken broods ($n = 36$) to 10 d (38% when extrapolated to 14 d assuming constant daily survival). Pratt (2010) reported 69% survival for 83 Minnesota greater-prairie chicken broods to 2 weeks post-hatch. Not including 4 (2.9%) broods of unknown fate, at least 23.9% of brood units in our study survived to 6 weeks compared to 28–38% reported by others for lesser *T. pallidicinctus,* greater, and Attwater's prairie-chickens (Fields et al. 2006; Pratt 2010).

Post-hatch survival of broods represents a critical stage in the life cycle of grouse, and is potentially influenced by a myriad of biological and environmental factors (Hannon and Martin 2006; Manzer and Hannon 2008). It is important to evaluate the relative influence of as many of those factors as possible so management strategies may be formulated within an efficient and logical framework where feasible. We evaluated 20 environmental factors and 6 characteristics of brood hens on Attwater's prairie-chicken brood survival (Tables 1–3). Broods were most likely to survive the first 2 weeks post-hatch if they hatched between early and late May, were located within areas treated to suppress red imported fire ants where vegetation produced intermediate values for maximum NDVI, and supported high invertebrate biomass (Figure 2). Numerous studies have identified the importance of invertebrate abundance to survival of prairie-chicken broods (e.g., Lehmann 1941, Jones 1963, Hagen et al. 2005, Morrow et al. 2015). Morrow et al. (2015) identified invertebrate abundance as a limiting factor specifically for Attwater's prairie-chicken brood survival, and in turn implicated red imported fire ants in limiting invertebrate abundance. However, that study did not explore the relative importance of other factors (e.g., habitat, weather, hen characteristics) that may influence brood survival.

Surprisingly, field-collected metrics related to habitat structure (*veg.ht*, *veg.ht.cv*) were not supported as predictive of Attwater's prairie-chicken brood survival within the range of habitat conditions we observed (Tables 1, S2). This suggests that other resources or environmental conditions (i.e., invertebrate abundance, ordinal date, fire ant management) were more limiting to Attwater's prairie-chicken broods than habitat structure in our study. These findings are consistent with those of Matthews et al. (2011) and Flanders-Wanner et al. (2004) who also failed to find support for habitat variables in explaining daily survival rates of greater prairie-chickens broods or sharp-tailed grouse *Tympanuchus phasianellus* production indices, respectively. Lutz and Silvy (1980) suggested that for nesting Attwater's prairie-chickens, vegetation characteristics beyond critical minimum thresholds may have little influence on susceptibility of nests to predation. Our data, along with those of Flanders-Wanner et al. (2004) and Matthews et al. (2011) suggest the same principle may apply to prairie grouse brood habitat as well.

However, it is also possible that we did not collect field data on habitat variables most pertinent to brood survival. Maximum NDVI, collected remotely by satellite sensors, was included in our final model for predicting 2-week brood survival. The NDVI is derived from canopy reflectance of the red and near-infrared wavebands, and serves as an indicator of canopy structure, green biomass, nitrogen content, and potential photosynthetic activity of vegetation (Gamon et al. 1995). The quadratic relationship for maximum NDVI indicates that 2-week brood survival was highest at intermediate values (50–150) and declined sharply on either side of those values (Figure 2). In addition to providing an abundant supply of invertebrate food, prairie-chicken brood habitat must allow for chick movement, provide concealment from predators, and provide shelter from the weather (Lehmann 1941; Kessler 1978; Svedarsky et al. 2003). Thus, to maximize brood survival a balance must be achieved that optimizes provision of food, concealment and shelter, while facilitating chick movements. The relationship of 2-week brood survival to maximum NDVI we observed suggests that overhead canopy structure may be more important to brood survival than the vertical effective vegetation heights we measured in the field at brood sites. It is also possible that maximum NDVI may be related to potential invertebrate abundance supported by green vegetation. However, if that were the case, we would expect the maximum NDVI – 2-week brood survival relationship to become asymptotic as the ability of the habitat to support invertebrate biomass reached saturation levels necessary to maximize survival.

We found little support for Topographic Position Index in predicting Attwater's prairie-chicken brood survival. This may be due to the relative lack of variability in topographic relief for our study areas, which are typical of much of the Attwater's prairie–chicken's historic range. In a Nebraska study, where topographic relief is more prominent than in the coastal prairie habitat of Attwater's prairie-chickens, greater prairie-chicken brood hens showed a strong preference for intermediate topographic positions, but topographic position was not supported for predicting brood survival (Matthews et al. 2011). Topographic position may be relevant to brood survival only when extreme precipitation results in flooding.

Consistent with other studies (e.g., Fields et al. 2006, Matthews et al. 2011), our analyses indicated time of year (ordinal date) was an important predictor of brood survival to 2 weeks post-hatch (Tables 1, 2; Figure 2). The probability of a brood surviving to 2 weeks post-hatch peaked when nests hatched in mid-May, and then precipitously declined thereafter (Figure 2). Fields et al. (2006) and Matthews et al. (2011) also observed declining survival for prairie-chicken broods as the season progressed, and has been observed for other Galliformes including grey partridge *Perdix perdix* (Panek 1992) and ring-necked pheasant *Phasianus colchicus* (Riley et al. 1998). It is likely that time-of-year effects are confounded with the influence of other factors including insect availability, habitat quality, temperature, precipitation patterns, and hen condition (Riley et al. 1998; Flanders-Wanner et al. 2004; Fields et al. 2006; Matthews et al. 2011).

Various aspects of weather are known to influence brood survival for Galliformes (e.g., Lehmann 1941; Moss 1985; Panek 1992; Riley et al. 1998). For example, previous studies have highlighted the importance of rainfall received during the early brooding period on survival of young prairie-chickens, with extremes in both directions being potentially detrimental to survival (e.g., Lehmann 1941; Jurries 1979; Morrow et al. 1996; Schole et al. 2011). Temperature effects have also been reported for survival of galliform broods including gray partridge (Panek 1992), ring-necked pheasants (Riley et al. 1998), and sharp-tailed grouse (Flanders-Wanner et al. 2004). Although our first-stage analyses indicated support for some weather parameters (rain, KBDI, temperature) in predicting 2-week brood survival, these variables were not supported in combined stage two models (Table 1). Fields et al. (2006) also failed to find support for weather variables in predicting brood survival for greater and lesser prairie-chickens.

The lack of support we observed for weather variables in predicting survival of the brood unit to 2 weeks post-hatch should not imply that these variables are unimportant to chick survival. We observed the highest number of 6-week old chicks per brood when KBDI was at intermediate levels during the first 2 weeks after hatch. The Keetch-Byram Drought Index is determined by local rainfall and temperatures (Alexander 1990). Additionally, ordinal date was important in predicting 2-week brood survival, and it is highly correlated with temperature. Rather, our findings suggest that some chicks within a brood likely perish during extreme values of KBDI during the first 2 weeks resulting in fewer chicks per brood at 6 weeks, but food as indicated by invertebrate abundance and fire ant treatment determines whether the brood unit collectively survives to 2 weeks.

Even though our candidate models included weather metrics for 0–6 weeks post-hatch, the number of chicks per brood at 6 weeks post-hatch was best predicted by the mean KBDI from 0–2 weeks post-hatch (Table 2; Figure 3). This finding emphasizes the importance of the first 2 weeks post-hatch for galliform chicks (Newell et al. 1987; Panek 1992; Hannon and Martin 2006; Schole et al. 2011). The Keetch-Byram Drought Index ranges from 0 (no moisture deficiency), to 800 (severe drought). Each KBDI unit represents 0.25 mm of soil moisture depletion (Keetch and Byram 1968). Therefore, values of KBDI from 200–400, at which our most supported final model predicts maximum chicks per brood (Table 2; Figure 3), represents 50–100 mm of precipitation needed to fully saturate soil. Our findings are consistent with those of Lehmann (1941:33) who concluded: (1) rainfall in May is of greater significance than other months because most Attwater's prairie-chicken chicks hatch in May, and (2) production of chicks is highest when May rainfall is approximately 3.8 cm below average. Values for KBDI are inversely related to precipitation received (Keetch and Byram 1968; Alexander 1990). Therefore, our finding of maximized brood survival at moderate KBDI values and that reported by Lehmann (1941) under conditions of slightly below average rainfall likely reflects a "happy medium" for newly hatched chicks, whereby danger is low from both precipitation and flooding, or desiccation due to dry conditions.

Intrinsic differences among brood hens may also contribute to post-hatch survival of chicks (e.g., Moss et al. 1981; Fields et al. 2006; Buner et al. 2011). A potential difference among hens in our study of particular interest was whether they had been reared in the wild by Attwater's prairie-chicken hens or had been hand-raised in captivity. Poor breeding success in the wild is a commonly reported malady for captive-bred animals (e.g., Parish and Sotherton 2007; Buner et al. 2011; Rymesova et al. 2013). However, we did not find evidence for any of the hen characteristics we hypothesized might predict Attwater's prairie-chicken brood survival (Tables 1, S2). Small sample sizes for some variables may have limited our ability to detect differences in brood survival among hen traits that we evaluated (Table S1). This was especially the case for captive-reared (*n* = 124) vs. wild (*n* = 14) status, but consistent with our findings, Buner et al. (2011:599) concluded regarding captive-bred grey partridge: "…once the released hens successfully hatch chicks, their chick-rearing behavior is normal. It also indicates that despite many generations of captive breeding, released stock with a game farm background maintains its natural breeding potential." Our observations suggest this may be the case for captive-reared Attwater's prairie-chickens as well. Despite relatively large sample sizes of SY (*n* = 85) and ASY (*n* = 53) Attwater's prairie-chicken hens in our dataset, hen age class was not competitive in predicting 2-week brood survival, consistent with observations by McNew et al. (2012) for greater prairie-chickens and Riley et al. (1998) for ring-necked pheasants. In contrast, Fields et al. (2006) found that broods reared by ASY prairie-chickens were 9.8× more likely to survive to 60 days post-hatch than those reared by SY hens, and Hannon and Martin (2006) stated that older female ptarmigan *Lagopus* spp. raised more chicks to independence than first- or second-time breeders.

Management Implications

We examined a comprehensive list of variables hypothesized to influence Attwater's prairie-chicken brood survival and identified five that were important in predicting survival through 6 weeks post-hatch. Invertebrate abundance (dry mass), treatment for red imported fire ants, ordinal date, and maximum NDVI were most important for predicting survival of the brood unit to 2 weeks of age. Management actions with demonstrated efficacy for increasing invertebrate abundance include fire ant suppression (Morrow et al. 2015), soil disturbance to encourage forbs which support insects (Jones 1963), and patch burning (Engle et al. 2008). Maintenance of high quality nesting habitat (e.g., USFWS 2010; Starns et al. 2020) and predator management, including the use of predator-deterrent fences (Morrow and Toepfer 2020) are actions that managers can take to increase success of early nests and mitigate for the reductions in survival we observed for late season broods (Figure 2). Finally, we observed the highest number of chicks at 6 weeks post-hatch when KBDI values were intermediate (not too dry, not too wet) during the 2 weeks after hatch. While management cannot control precipitation patterns in the short-term, actions can be taken to ensure that runoff efficiently drains from brood habitat. In the long-term, climate predictions for Texas indicate “unprecedented” drought risk resulting from climate change driven by greenhouse gas emissions (Cook et al. 2015). Our data suggest that increases in frequencies of severe droughts will lead to substantially fewer Attwater’s prairie-chicken chicks surviving to independence, and may further complicate recovery of this species.

Supplemental Material

Data S1. Dataset used in the analysis of factors affecting Attwater’s prairie-chicken *Tympanuchus cupido attwateri* brood survival from 2009–2019 on the Attwater Prairie Chicken National Wildlife Refuge (APCNWR; Colorado County, Texas) and on private ranchlands in Goliad County, Texas.

Data S2. Description of variables in Data S1 used in the analysis of factors affecting Attwater’s prairie-chicken *Tympanuchus cupido attwateri* brood survival from 2009–2019 on the Attwater Prairie Chicken National Wildlife Refuge (Colorado County, Texas) and on private ranchlands in Goliad County, Texas.

Table S1. Variables hypothesized to affect Attwater’s prairie-chicken *Tympanuchus cupido attwateri* brood survival on the Attwater Prairie Chicken National Wildlife Refuge (Colorado

County, Texas) and on private ranchlands in Goliad County, Texas. Data were summarized by (1) whether the brood survived the first 2 weeks and (2) whether there were 1 or more chicks detected at 6 weeks for those broods that survived the first 2 weeks. For variables with missing values, the sample size is given in the row labeled *n*; otherwise, the sample size is given in the header row.

Table S2. Stage one candidate models for predicting Attwater's prairie-chicken *Tympanuchus cupido attwateri* 2-week brood survival and number of chicks per brood at 6 weeks post-hatch between 2009 and 2019 at the Attwater Prairie Chicken National Wildlife Refuge (Colorado County) and private ranchlands in Goliad County, Texas. Variables from best supported models in each category were selected for evaluation in subsequent stage two analyses.

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Figure 1

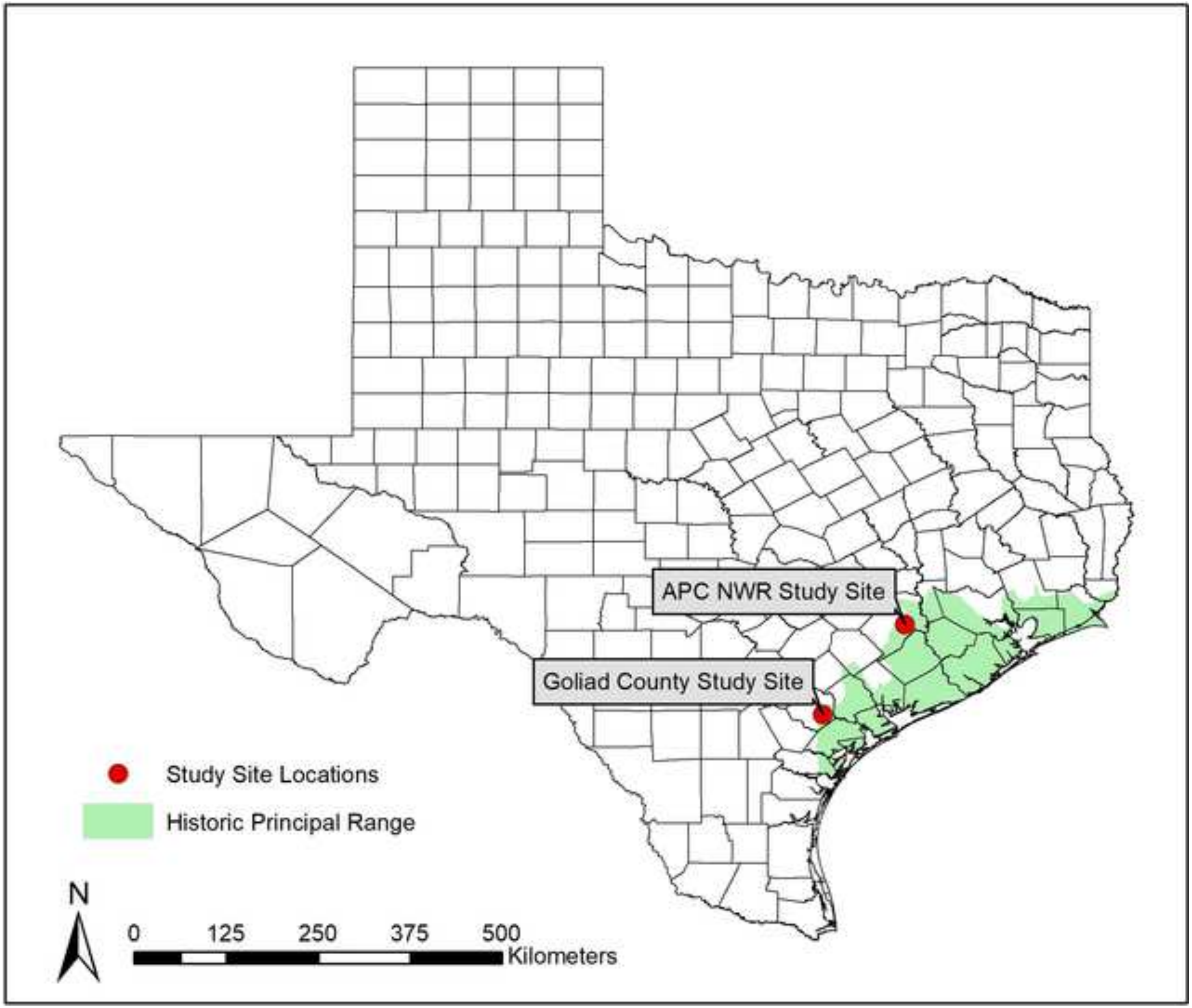

APC NWR Study Site
Goliad County Study Site
Study Site Locations
Historic Principal Range
N
0
125
250
375
500
Kilometers

Figure 2

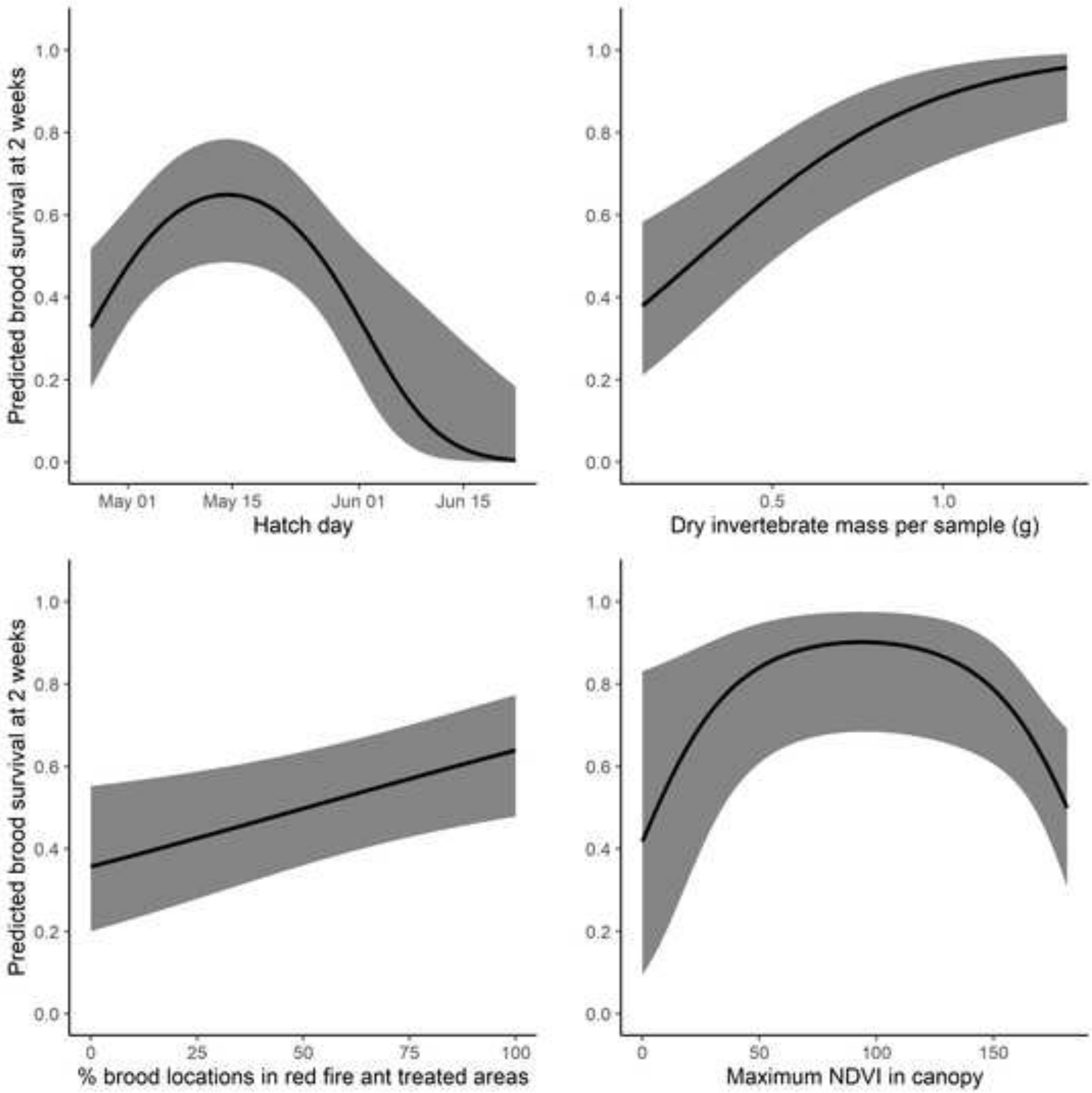
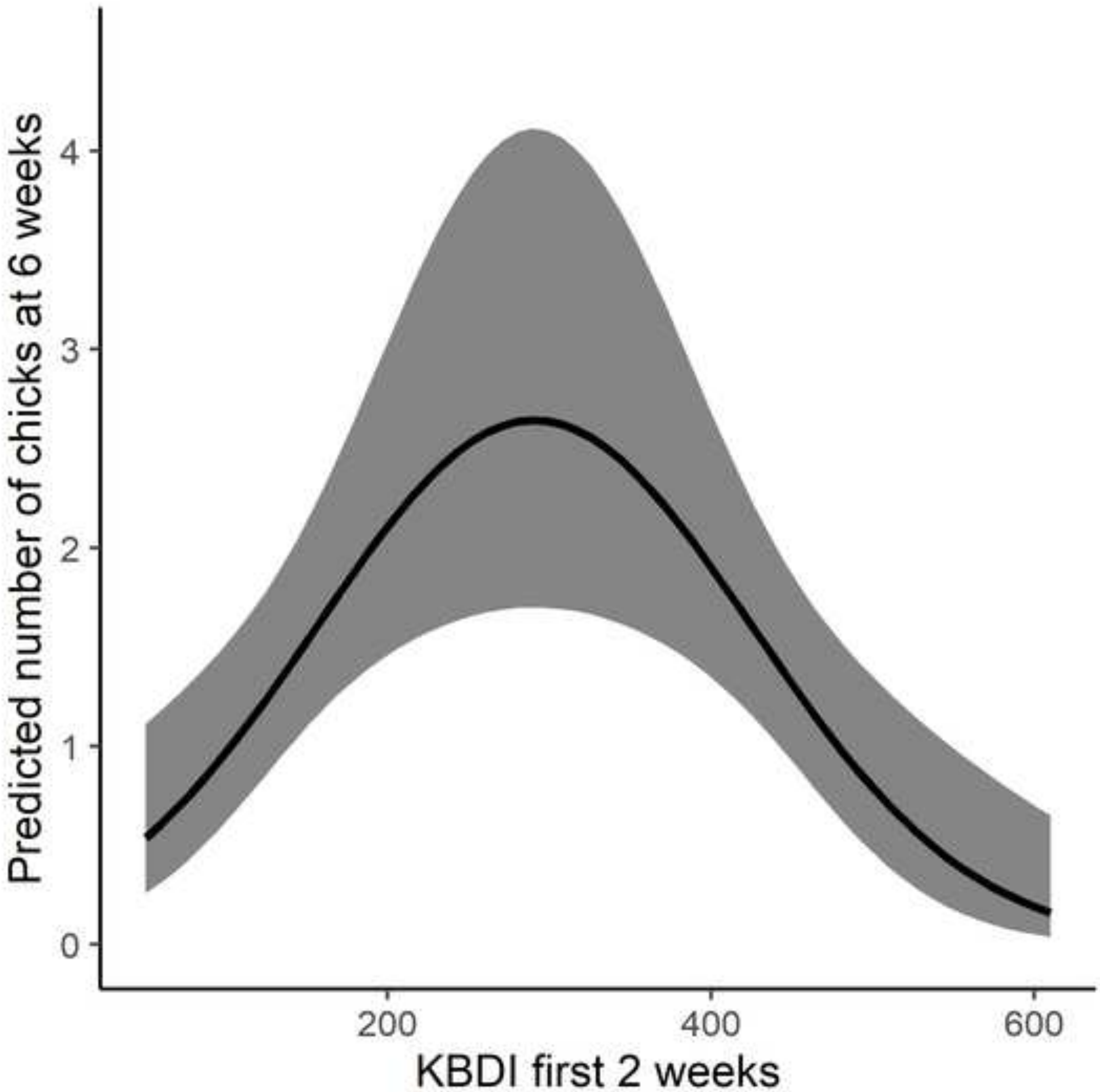

Predicted brood survival at 2 weeks
1.0
0.8
0.6
0.4
0.2
0.0
May 01
May 15
Jun 01
Jun 15
Hatch day
0.5
1.0
Dry invertebrate mass per sample (g)
0
25
50
75
100
% brood locations in red fire ant treated areas
0
50
100
150
Maximum NDVI in canopy

Figure 3



Predicted number of chicks at 6 weeks
0
1
2
3
4
200
400
600
KBDI first 2 weeks

Figure 1. Location of the Attwater Prairie Chicken National Wildlife Refuge (APC NWR) and Goliad County, Texas study sites within the historic range of the Attwater's prairie-chicken *Tympanuchus cupido attwateri* as delineated by Lehmann (1941).

Figure 2. Relationship between date of hatch, percent of brood locations within areas treated to suppress invasive red imported fire ants *Solenopsis invicta*, median dry mass of invertebrates at brood sites, and maximum Normalized Difference Vegetation Index (NDVI) on Attwater's prairie-chicken *Tympanuchus cupido attwateri* brood survival from 0–2 weeks post-hatch between 2009 and 2019 at the Attwater Prairie Chicken National Wildlife Refuge (Colorado County) and private ranches in Goliad County, Texas. Shaded areas represent 95% confidence intervals.

Figure 3. Relationship between Keetch-Byram Drought Index (KBDI; Keetch and Byram 1968) during the first 2 weeks after hatching and the number of Attwater's prairie-chicken *Tympanuchus cupido attwateri* chicks per brood at 6 weeks post-hatch between 2009 and 2019 at the Attwater Prairie Chicken National Wildlife Refuge (Colorado County, Texas) and private ranches in Goliad County, Texas. Shaded areas represent 95% confidence intervals. The KBDI estimates soil moisture depletion and ranges from 0 (fully saturated soil) to 800 (maximum depletion).

Table 1. Two-stage model selection results for predicting Attwater's prairie-chicken *Tympanuchus cupido attwateri* 2-week brood survival between 2009 and 2019 at the Attwater Prairie Chicken National Wildlife Refuge (Colorado County) and private ranchlands in Goliad County, Texas. Variables from best supported models in each Type category (stage one) were combined for evaluation in subsequent stage two analyses (Type = Combined). Candidate models and variables are described in Table S2. Results for top models and the null are presented here. K = number of parameters estimated, **Δ** AIC_c = change in Akaike's Information Criterion corrected for small sample sizes, and w = model weight.

Table 2. Coefficients for the best supported combined models of 2-week brood survival and number of chicks per brood at 6 weeks for Attwater's prairie-chickens *Tympanuchus cupido attwateri* between 2009 and 2019 at the Attwater Prairie Chicken National Wildlife Refuge (Colorado County) and private ranchlands in Goliad County, Texas. Variables were standardized by subtracting the mean and dividing by the standard deviation.

Table 3. Two-stage model selection results for predicting the number of Attwater's prairie-chicken *Tympanuchus cupido attwateri* chicks per brood between 2009 and 2019 at the Attwater Prairie Chicken National Wildlife Refuge (Colorado County) and private ranchlands in Goliad County, Texas. Variables from best supported models in each Type category (stage one) were combined for evaluation in subsequent stage two analyses (Type = Combined). Candidate models and variables are described in Table S2. K = number of parameters estimated, **Δ** AIC_c = change in Akaike's Information Criterion corrected for small sample sizes, and w = model weight.

Table 1

Type	Model	K	AIC_c	ΔAIC_c	w
Weather and topography	KBDI + $temp^2$	3	175.19	0.00	0.20
	KBDI	2	176.42	1.23	0.11
	$KBDI^2$ + $temp^2$	3	176.67	1.48	0.10
	rain + $rain^2$	3	177.51	2.33	0.06
	$temp^2$	2	177.59	2.40	0.06
	$KBDI^2$	2	177.66	2.48	0.06
	rain	2	177.85	2.66	0.05
	null	1	177.94	2.76	0.05
Habitat	dry.mass + $dry.mass^2$ + rifa.trt	4	165.7	0.00	0.51
	dry.mass + $dry.mass^2$ + rifa.trt.hatch	4	166.63	0.93	0.32
	dry.mass + $dry.mass^2$	3	168.75	3.05	0.11
	dry.mass + rifa.trt	3	171.26	5.56	0.03
	dry.mass + rifa.trt.hatch	3	172.38	6.69	0.02
	dry.mass	2	176.13	10.43	0.00
	rifa.trt	2	176.61	10.92	0.00
	rifa.trt.hatch	2	177.53	11.83	0.00
	null	1	179.12	13.42	0.00
Phenology	maxn + $maxn^2$	3	171.1	0.00	0.22
	sosn + $sosn^2$	3	171.53	0.43	0.18
	null	1	171.89	0.79	0.15
Time and site	day^2	2	185.50	0.00	0.53
	day + day^2	3	187.37	1.86	0.21
	day	2	188.77	3.27	0.10
	null	1	189.82	4.31	0.06
Hen	null	1	177.94	0.00	0.32
Combined (stage 2 analyses)	dry.mass + day^2 + maxn + $maxn^2$ + rifa.trt	6	141.13	0.00	0.42
	dry.mass + day^2 + maxn + $maxn^2$ + rifa.trt.hatch	6	142.78	1.65	0.18

dry.mass + day^2 + rifa.trt	4	143.39	2.26	0.14
dry.mass + day^2 + maxn + maxn^2 + KBDI	6	144.64	3.51	0.07
dry.mass+ dry.mass^2 + day^2 + maxn + maxn^2 + KBDI	7	145.17	4.04	0.06
dry.mass + day^2 + maxn + maxn^2	5	145.47	4.34	0.05
dry.mass + day^2 + rifa.trt.hatch	4	145.48	4.36	0.05
dry.mass + day^2	3	147.49	6.36	0.02
dry.mass + maxn + maxn^2 + KBDI	5	150.22	9.09	0.00
dry.mass + maxn + maxn^2 + rifa.trt	5	150.63	9.50	0.00
dry.mass + maxn + maxn^2 + rifa.trt.hatch	5	151.69	10.56	0.00
dry.mass + maxn + maxn^2 + rain	5	152.51	11.38	0.00
dry.mass + rifa.trt	3	152.99	11.86	0.00
dry.mass + maxn + maxn^2	4	153.03	11.90	0.00
dry.mass + rifa.trt.hatch	3	154.50	13.37	0.00
dry.mass + rifa.trt.hatch + maxn^2 + sosn	5	154.73	13.60	0.00
day^2 + sosn + sosn^2 + rifa.trt	5	154.74	13.61	0.00
dry.mass	2	155.22	14.09	0.00
dry.mass + sosn + KBDI	4	155.27	14.15	0.00
null	1	165.31	24.18	0.00

Table 2

Model	Variable[a]	Coefficient	SE	95% CI Lower	95% CI Upper	*Z*	*P*
Brood survival 0–2 weeks:	(Intercept)	1.412	0.487	0.505	2.430	2.90	0.004
	dry.mass	1.341	0.361	0.680	2.109	3.71	<0.001
	day^2	-0.595	0.212	-1.067	-0.226	2.80	0.005
	maxn	-1.560	0.634	-2.877	-0.366	2.46	0.014
	maxn^2	-0.865	0.376	-1.653	-0.162	2.30	0.021
	rifa.trt	0.5704	0.231	0.131	1.043	2.47	0.014
Number of chicks per brood at six weeks:	(Intercept)	0.972	0.224	0.540	1.424	4.33	<0.001
	KBDI^2	-0.929	0.279	-1.508	-0.415	3.33	<0.001

[a]Model variables: dry.mass = median dry weight of invertebrates/sample collected at brood sites, day = ordinal date, maxn = maximum Normalized Difference Vegetation Index, rifa.trt = percent of brood observations within area treated to suppress red imported fire ants *Solenopsis invicta*, KBDI = Keetch-Byram Drought Index during first 2 weeks after hatch.

Table 3 Click here to access/download;Table;Table 3.doc

Type	**Model**[a]	***K***	**AIC$_c$**	**Δ AIC$_c$**	***w***
Time and site	null	2	191.75	0.00	0.37
Weather	KBDI^2 (2 week)	3	181.07	0.00	0.91
	KBDI^2 (6 week)	3	185.85	4.78	0.08
	null	2	191.75	10.67	0.00
Habitat	dry.mass^2	3	183.92	0.00	0.32
	null	2	184.94	1.02	0.19
Hen	null	2	191.75	0.00	0.30
Phenology	null	2	188.77	0.00	0.32
Combined (stage 2 analyses)	KBDI^2 (2 week)	3	175.18	0.00	0.90
	KBDI^2 (6 week)	3	180.1	4.92	0.08
	dry.mass^2	3	183.92	8.74	0.01
	null	2	184.94	9.76	0.01

[a]Model variables: KBDI = Keetch-Byram Drought Index, dry.mass = median dry mass of invertebrates/sample collected at brood sites.

Table S1. Variables hypothesized to affect Attwater's prairie-chicken *Tympanuchus cupido attwateri* brood survival on the Attwater Prairie Chicken National Wildlife Refuge (Colorado County, Texas) and on private ranchlands in Goliad County, Texas. Data were summarized by (1) whether the brood survived the first two weeks and (2) whether there were one or more chicks detected at six weeks for those broods that survived the first two weeks. For variables with missing values, the sample size is given in the row labeled *n*; otherwise, the sample size is given in the header row.

			Brood survived to two weeks			**One or more chicks alive at six weeks**		
Category	**Variable**	**Category/ metric**	**No (*n*=80)**	**Yes (*n*=58)**	**Total (*n*=138)**	**No (*n*=22)**	**Yes (*n*=32)**	**Total (*n*=54)**
Time and site	Year	2009	11 (13.8%)	5 (8.6%)	16 (11.6%)	3 (13.6%)	2 (6.2%)	5 (9.3%)
		2010	8 (10.0%)	11 (19.0%)	19 (13.8%)	1 (4.5%)	10 (31.2%)	11 (20.4%)
		2011	13 (16.2%)	2 (3.4%)	15 (10.9%)	2 (9.1%)	0 (0.0%)	2 (3.7%)
		2012	5 (6.2%)	8 (13.8%)	13 (9.4%)	3 (13.6%)	5 (15.6%)	8 (14.8%)
		2013	10 (12.5%)	3 (5.2%)	13 (9.4%)	0 (0.0%)	3 (9.4%)	3 (5.6%)
		2014	8 (10.0%)	12 (20.7%)	20 (14.5%)	7 (31.8%)	3 (9.4%)	10 (18.5%)
		2015	10 (12.5%)	8 (13.8%)	18 (13.0%)	4 (18.2%)	4 (12.5%)	8 (14.8%)
		2016	9 (11.2%)	2 (3.4%)	11 (8.0%)	1 (4.5%)	1 (3.1%)	2 (3.7%)
		2017	1 (1.2%)	1 (1.7%)	2 (1.4%)	0 (0.0%)	1 (3.1%)	1 (1.9%)
		2018	0	1	1	0	1	1

Category	Variable	Category/ metric	Brood survived to two weeks No (*n*=80)	Yes (*n*=58)	Total (*n*=138)	One or more chicks alive at six weeks No (*n*=22)	Yes (*n*=32)	Total (*n*=54)
			(0.0%)	(1.7%)	(0.7%)	(0.0%)	(3.1%)	(1.9%)
		2019	5 (6.2%)	5 (8.6%)	10 (7.2%)	1 (4.5%)	2 (6.2%)	3 (5.6%)
	Site	APCNWR[a]	64 (80.0%)	51 (87.9%)	115 (83.3%)	19 (86.4%)	28 (87.5%)	47 (87.0%)
		Goliad	16 (20.0%)	7 (12.1%)	23 (16.7%)	3 (13.6%)	4 (12.5%)	7 (13.0%)
	Day	Mean	16-May	12-May	14-May	12-May	13-May	13-May
		Range	Apr 28–Jun 22	Apr 26–Jun 11	Apr 26–Jun 22	26 Apr–Jun 2	30 Apr–June 11	26 Apr–Jun 11
Weather and topography (0–2 weeks, 0–6 weeks)	Mean temp. (°C, 2 week average)	Mean (SD)	24.87 (2.21)	24.64 (1.86)	24.77 (2.06)	24.25 (1.96)	25.09 (1.70)	24.75 (1.84)
		Range	19.85–30.26	20.93–27.89	19.85–30.26	21.96–27.89	20.93–27.49	20.93–27.89
	Total rain (cm, 2 week)	Mean (SD)	6.64 (6.95)	8.11 (6.87)	7.26 (6.93)	8.62 (7.64)	7.41 (6.27)	7.90 (6.82)
		Range	0.00–33.96	0.00–33.96	0.00–33.96	0.03–22.89	0.00–33.96	0.00–33.96
	Days rain (2 week)	Mean (SD)	3.67 (2.15)	4.16 (2.08)	3.88 (2.13)	4.00 (2.35)	4.31 (1.99)	4.19 (2.13)
		Range	0.00–	0.00–	0.00–	1.00–	0.00–	0.00–

Category	Variable	Category/ metric	Brood survived to two weeks No (*n*=80)	Brood survived to two weeks Yes (*n*=58)	Brood survived to two weeks Total (*n*=138)	One or more chicks alive at six weeks No (*n*=22)	One or more chicks alive at six weeks Yes (*n*=32)	One or more chicks alive at six weeks Total (*n*=54)
			9.00	9.00	9.00	9.00	8.00	9.00
	Total wind (miles, 2 week)	Mean (SD) Range	1334.34 (1004.96) 353.70–4123.60	1154.40 (800.75) 471.90–4184.30	1258.71 (925.80) 353.70–4184.30	1216.02 (952.02) 525.50–4184.30	1122.96 (746.63) 471.90–3237.20	1160.87 (829.04) 471.90–4184.30
	Total evaporation (inches, 2 week)	Mean (SD) Range	3.36 (0.82) 1.92–5.32	3.23 (0.77) 1.92–4.74	3.31 (0.80) 1.92–5.32	3.24 (0.81) 1.92–4.74	3.30 (0.77) 2.01–4.69	3.27 (0.78) 1.92–4.74
	KBDI[b] (2 week)	Mean (SD) Range	315.40 (194.08) 26.00–631.93	256.67 (163.55) 28.40–629.67	290.72 (183.56) 26.00–631.93	254.01 (209.20) 28.40–629.67	276.83 (126.84) 79.40–566.27	267.53 (163.94) 28.40–629.67
	Mean temperature (°C, 6 week)	Mean (SD) Range	26.63 (1.43) 23.73–30.41	26.29 (1.10) 23.88–27.99	26.49 (1.31) 23.73–30.41	26.03 (0.93) 24.81–27.93	26.57 (1.16) 23.88–27.99	26.35 (1.10) 23.88–27.99
	Total rain (cm, 6 week)	Mean (SD) Range	15.96 (13.77) 1.14–50.60	21.25 (15.50) 2.44–50.60	18.18 (14.70) 1.14–50.60	22.40 (16.84) 2.44–50.60	19.48 (14.84) 2.44–50.60	20.67 (15.60) 2.44–50.60
	Days rain (6 week)	Mean (SD)	9.47 (4.87)	10.12 (3.84)	9.75 (4.47)	10.05 (4.28)	10.09 (3.78)	10.07 (3.95)

Category	Variable	Category/ metric	Brood survived to two weeks: No (*n*=80)	Yes (*n*=58)	Total (*n*=138)	One or more chicks alive at six weeks: No (*n*=22)	Yes (*n*=32)	Total (*n*=54)
		Range	2.00–20.00	3.00–19.00	2.00–20.00	3.00–18.00	4.00–19.00	3.00–19.00
	Total wind (miles, 6 week)	Mean (SD)	3634.04 (3136.81)	2960.09 (2439.88)	3350.78 (2874.40)	3068.85 (2734.18)	2952.35 (2411.78)	2999.81 (2523.42)
		Range	1092.10–11041.90	1432.20–10036.80	1092.10–11041.90	1449.40–10036.80	1432.20–9547.40	1432.20–10036.80
	Total evaporation (inches, 6 week)	Mean (SD)	10.27 (2.22)	10.29 (1.91)	10.28 (2.09)	10.35 (2.06)	10.33 (1.93)	10.34 (1.97)
		Range	6.97–14.96	6.97–14.12	6.97–14.96	7.31–14.12	6.97–13.17	6.97–14.12
	KBDI (6 week)	Mean (SD)	350.88 (203.13)	284.40 (165.75)	322.94 (190.55)	283.57 (196.55)	300.53 (147.87)	293.62 (167.83)
		Range	65.72–669.79	65.72–619.81	65.72–669.79	65.72–617.74	78.37–619.81	65.72–619.81
	TPI[c]	*n*	62	48	110	22	22	44
		Mean (SD)	3.04 (1.03)	2.88 (1.17)	2.97 (1.09)	2.96 (1.27)	2.74 (1.15)	2.85 (1.20)
		Range	-0.20–4.86	-0.24–4.81	-0.24–4.86	-0.13–4.81	-0.24–4.76	-0.24–4.81
	TPI.SD	*n*	62	48	110	22	22	44
		Mean (SD)	0.84 (1.04)	0.91 (1.22)	0.87 (1.12)	1.02 (1.29)	0.90 (1.25)	0.96 (1.26)
		Range	0.10–4.50	0.11–4.60	0.10–4.60	0.13–4.60	0.12–4.00	0.12–4.60

Category	Variable	Category/ metric	Brood survived to two weeks: No (*n*=80)	Brood survived to two weeks: Yes (*n*=58)	Brood survived to two weeks: Total (*n*=138)	One or more chicks alive at six weeks: No (*n*=22)	One or more chicks alive at six weeks: Yes (*n*=32)	One or more chicks alive at six weeks: Total (*n*=54)
Habitat (0–2 weeks)	Median dry mass of invertebrates/ sample (g)	*n*	72	57	129	22	31	53
		Mean (SD)	0.53 (0.47)	0.71 (0.43)	0.61 (0.46)	0.69 (0.29)	0.76 (0.53)	0.73 (0.44)
		Range	0.03–2.62	0.21–2.42	0.03–2.62	0.24–1.17	0.21–2.42	0.21–2.42
	Median number of invertebrates/ sample	*n*	72	58	130	26	32	58
		Mean (SD)	125.62 (133.26)	142.21 (80.27)	133.02 (112.65)	159.41 (108.31)	129.44 (58.58)	141.65 (82.92)
		Range	17.50–1015.00	24.00–521.00	17.50–1015.00	51.00–521.00	24.00–245.00	24.00–521.00
	Mean effective vegetation height (cm)	*n*	67	56	123	21	31	52
		Mean (SD)	45.98 (18.72)	45.46 (14.00)	45.75 (16.67)	44.39 (14.88)	46.85 (14.04)	45.86 (14.29)
		Range	10.92–118.03	13.75–74.82	10.92–118.03	24.08–73.92	13.75–74.82	13.75–74.82
	Mean effective vegetation height CV (cm)	*n*	67	56	123	21	31	52
		Mean (SD)	47.94 (17.94)	45.79 (16.33)	46.96 (17.19)	49.30 (17.53)	43.79 (16.40)	46.02 (16.91)
		Range	20.50–120.83	23.80–96.01	20.50–120.83	28.60–96.01	23.80–90.40	23.80–96.01

Category	Variable	Category/ metric	Brood survived to two weeks No (*n*=80)	Brood survived to two weeks Yes (*n*=58)	Brood survived to two weeks Total (*n*=138)	One or more chicks alive at six weeks No (*n*=22)	One or more chicks alive at six weeks Yes (*n*=32)	One or more chicks alive at six weeks Total (*n*=54)
	Mean vegetation height (lidar, 9 m radius; cm)	*n*	57	42	99	19	19	38
		Mean (SD)	35.12 (3.50)	34.75 (1.62)	34.97 (2.85)	35.14 (1.72)	34.20 (1.38)	34.67 (1.61)
		Range	18.55–50.33	30.95–39.11	18.55–50.33	32.78–39.11	30.95–37.11	30.95–39.11
	Mean vegetation height (lidar, 21 m radius; cm)	*n*	57	42	99	19	19	38
		Mean (SD)	35.29 (2.89)	34.91 (1.73)	35.13 (2.46)	35.46 (2.11)	34.26 (1.13)	34.86 (1.77)
		Range	25.44–49.20	31.62–41.35	25.44–49.20	32.67–41.35	31.62–36.55	31.62–41.35
	Hatched within fire ant treated area	NO	40 (50.0%)	20 (34.5%)	60 (43.5%)	7 (31.8%)	13 (40.6%)	20 (37.0%)
		YES	40 (50.0%)	38 (65.5%)	78 (56.5%)	15 (68.2%)	19 (59.4%)	34 (63.0%)
	% locations within fire ant treated areas	*n*	79	58	137	22	32	54
		Mean (SD)	48.73 (49.98)	65.20 (46.80)	55.71 (49.17)	68.82 (46.81)	58.37 (48.26)	62.63 (47.51)
		Range	0.00–100.00	0.00–100.00	0.00–100.00	0.00–100.00	0.00–100.00	0.00–100.00
Hen	Hen age[d]	ASY	30 (37.5%)	23 (39.7%)	53 (38.4%)	8 (36.4%)	14 (43.8%)	22 (40.7%)
		SY	50 (62.5%)	35 (60.3%)	85 (61.6%)	14 (63.6%)	18 (56.2%)	32 (59.3%)

			Brood survived to two weeks			One or more chicks alive at six weeks		
Category	**Variable**	**Category/ metric**	**No (*n*=80)**	**Yes (*n*=58)**	**Total (*n*=138)**	**No (*n*=22)**	**Yes (*n*=32)**	**Total (*n*=54)**
	Hen fledged young previously	NO	75 (93.8%)	52 (89.7%)	127 (92.0%)	19 (86.4%)	29 (90.6%)	48 (88.9%)
		YES	5 (6.2%)	6 (10.3%)	11 (8.0%)	3 (13.6%)	3 (9.4%)	6 (11.1%)
	Hen nested previously	NO	64 (80.0%)	43 (74.1%)	107 (77.5%)	17 (77.3%)	23 (71.9%)	40 (74.1%)
		YES	16 (20.0%)	15 (25.9%)	31 (22.5%)	5 (22.7%)	9 (28.1%)	14 (25.9%)
	Hen source	CAPTIVE	73 (91.2%)	51 (87.9%)	124 (89.9%)	20 (90.9%)	27 (84.4%)	47 (87.0%)
		WILD	7 (8.8%)	7 (12.1%)	14 (10.1%)	2 (9.1%)	5 (15.6%)	7 (13.0%)
	Years out	Mean (SD)	1.35 (0.66)	1.40 (0.70)	1.37 (0.67)	1.32 (0.57)	1.47 (0.80)	1.41 (0.71)
		Range	1.00–4.00	1.00–4.00	1.00–4.00	1.00–3.00	1.00–4.00	1.00–4.00
	Total egg mass per brood (g)	*n*	79	58	137	22	32	54
		Mean (SD)	271.73 (58.55)	289.39 (52.31)	279.21 (56.48)	290.31 (37.05)	282.10 (58.26)	289.39 (52.31)
		Range	121.00–372.96	166.40–443.74	121.00–443.74	188.10–348.25	166.40–443.74	166.40–443.74
Plant phenology[e]	mean.amp	*n*	66	57	123	22	31	53
		Mean (SD)	21.80 (9.81)	22.50 (8.50)	22.13 (9.20)	22.97 (8.70)	21.90 (8.83)	22.35 (8.71)

Category	Variable	Category/ metric	Brood survived to two weeks: No (*n*=80)	Brood survived to two weeks: Yes (*n*=58)	Brood survived to two weeks: Total (*n*=138)	One or more chicks alive at six weeks: No (*n*=22)	One or more chicks alive at six weeks: Yes (*n*=32)	One or more chicks alive at six weeks: Total (*n*=54)
		Range	0.00–39.00	0.00–35.29	0.00–39.00	0.00–33.25	0.00–35.29	0.00–35.29
	mean.eosn	*n*	66	57	123	22	31	53
		Mean	137.71	137.40	137.57	137.75	135.59	136.48
		(SD)	(17.29)	(15.95)	(16.61)	(14.45)	(17.48)	(16.18)
		Range	100.00–157.14	100.00–153.62	100.00–157.14	100.00–153.62	100.00–153.57	100.00–153.62
	mean.maxn	*n*	66	57	123	22	31	53
		Mean	145.57	140.52	143.23	150.94	129.45	138.37
		(SD)	(56.09)	(53.35)	(54.67)	(46.17)	(59.21)	(54.75)
		Range	0.00–182.73	0.00–179.00	0.00–182.73	0.00–179.00	0.00–178.12	0.00–179.00
	mean.sosn	*n*	66	57	123	22	31	53
		Mean	142.69	140.41	141.64	141.59	138.64	139.87
		(SD)	(12.28)	(11.23)	(11.81)	(10.39)	(12.14)	(11.44)
		Range	100.00–165.00	107.33–153.20	100.00–165.00	107.50–149.71	107.33–153.20	107.33–153.20
	mean.tin	*n*	66	57	123	22	31	53
		Mean	18.65	20.65	19.58	17.74	22.92	20.77
		(SD)	(12.64)	(13.83)	(13.19)	(9.85)	(16.53)	(14.26)
		Range	0.00–58.00	0.00–60.00	0.00–60.00	0.00–33.12	0.00–60.00	0.00–60.00

[a]Attwater Prairie Chicken National Wildlife Refuge

[b]Keetch-Byram Drought Index (Keetch and Byram 1968).

[c]Topographic position index developed by Guisan et al. (1999).

[d]Hen age classes: second year (SY) or after second year (ASY)

[e]Variables include maximum increase in Normalized Difference Vegetation Index (NDVI) above the baseline (amp), NDVI at the end of photosynthesis (eosn), maximum level of NDVI (maxn), NDVI at the beginning of photosynthesis (sosn), and NDVI across the entire growing season (tin). These metrics were derived from time-series Collection 6 Aqua eMODIS NDVI data recorded at 250-m resolution (Jenkerson et al. 2020).

Type	Model	Model description
Weather and topography (0–2 weeks, 0-6 weeks)	days.rain	Linear relationship with number of days of rain
	days.rain + days.rain^2	Quadratic relationship with number of days of rain
	days.rain^2	Nonlinear relationship with number of days of rain
	rain + rain^2	Quadratic relationship with total rain
	rain + TPI.SD + rain*TPI.SD	Total rain with standard deviation of topographic position index and an interaction term.
	rain + TPI + rain*TPI	Total rain with topographic index and an interaction term.
	wind	Linear relationship with total wind
	wind + wind^2	Quadratic relationship with total wind
	wind^2	Nonlinear relationship with total wind
	evap	Linear relationship with total evaporation
	evap + evap^2	Quadratic relationship with total evaporation
	KBDI	Linear relationship with mean KBDI[a]
	KBDI + KBDI^2	Quadratic relationship with mean KBDI
	KBDI^2	Nonlinear relationship with mean KBDI

	rain	Linear relationship with total rain
	rain + rain^2	Quadratic relationship with total rain
	rain^2	Nonlinear relationship with total rain
	temp	Linear relationship with average temperature
	temp + temp^2	Quadratic relationship with average temperature
	temp^2	Nonlinear relationship with average temperature
	null	Constant brood survival
Habitat	dry.mass	Linear relationship with median dry mass of invertebrates
	dry.mass + dry.mass^2	Quadratic relationship with median dry mass of invertebrates
	mean.dry.mass * num.inverts	Mean dry mass per invertebrate plus median number of invertebrates with an interaction term
	mean.dry.mass + dry.mass	Mean dry mass per invertebrate plus median dry mass per sample
	num.inverts	Linear relationship with median number of invertebrates
	rifa.trt	Linear relationship with % of brood locations (0–2 weeks) within fire ant treated areas
	rifa.trt.hatch	Survival differs between broods hatched in fire ant treated vs untreated locations
	veg.ht[b]	Linear relationship with mean vegetation height
	veg.ht + veg.ht.cv	Linear relationship with mean vegetation height coefficient of

		variation
	veg.ht + veg.ht^2	Quadratic relationship with mean vegetation height
	veg.ht + veg.ht.cv^2	Quadratic relationship with mean vegetation height coefficient of variation
	veg.ht.cv^2	Nonlinear relationship with mean vegetation height coefficient of variation
	veg.ht^2	Nonlinear relationship with mean vegetation height
	null	Constant brood survival
Plant phenology	amp	Brood survival differs by maximum increase in Normalized Difference Vegetation Index (NDVI) above the baseline
	eosn	Brood survival differs by NDVI at the end of photosynthesis
	maxn	Brood survival differs by maximum NDVI
	sosn	Brood survival differs by NDVI at the beginning of photosynthesis
	tin	Brood survival differs by NDVI across the entire growing season
	null	Constant brood survival
Time and site	year	Brood survival differs by year
	site	Brood survival differs by site
	day + day^2	Brood survival has a quadratic relationship with ordinal date of hatch

	day^2	Brood survival has a non-linear relationship with ordinal date of hatch
	day	Brood survival has a linear relationship with ordinal date of hatch
	null	Constant brood survival
Hen	age	Brood survival differs by age of hen (second year or after second year)
	fledge.prev	Brood survival differs according to whether hen has fledged young previously
	nest.prev	Brood survival differs according to whether hen has nested previously
	source	Brood survival differs by source (wild-hatched, captive-reared) of hen
	years.out	Brood survival differs by number of years hen has been in the wild (i.e., time since release from captivity or since hatch for wild-hatched hens)
	total.egg.mass	Brood survival differs by total estimated fresh weight of clutch
	null	Constant brood survival

[a]Keetch-Byram Drought Index

[b]Models were run using both field measurements of effective vegetation height and remotely-sensed based estimates of vegetation height using LiDAR.

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