






## RESEARCH ARTICLE

# Robust assessment of associations between weather and eastern wild turkey nest success

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## Abstract

Temperature and precipitation have been identified as factors that potentially influence eastern wild turkey (*Meleagris gallopavo silvestris*) reproduction, but robust analyses testing the relationship between weather parameters and turkey nest success are lacking. Therefore, we assessed how weather influenced turkey daily nest survival using 8 years of data collected from 715 nests across the southeastern United States. We also conducted exploratory analyses investigating if weather conditions during or prior to nesting best predicted nest success. We then assessed the possible implications of climate change through 2041–2060 for future eastern wild turkey daily nest survival and nest success for variables determined significant in analyses. During incubation, positive anomalies of minimum daily temperature were associated with greater daily nest survival. Precipitation during nesting was not a good predictor of daily nest survival. Exploratory analyses unexpectedly indicated that weather conditions in January prior to incubation were more important to nest success than weather conditions during incubation. In January, negative anomalies of minimum temperature and greater average daily precipitation were associated with greater nest success. Projections of future nest success or daily nest survival based on these relationships with the predictive covariates, and informed by climate models, suggest that nest success may increase as January precipitation

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increases and that daily nest survival may increase as temperature during incubation increases. These positive associations could be offset by a negative association between nest success and the expected increases in January minimum average temperature. Additional research is needed to investigate causes of these relationships and assess the implications of climate change for eastern wild turkey poult survival.

#### KEYWORDS

climate change, Galliformes, *Meleagris gallopavo*, Phasianidae, precipitation, temperature, wet hen hypothesis

Eastern wild turkey (*Meleagris gallopavo silvestris*; wild turkey) nest success may be influenced by a variety of factors, including vegetation structure and composition, precipitation, temperature, and nest initiation timing (Roberts and Porter 1998, Kilburg et al. 2014, Keever et al. 2023). Weather, the short-term conditions that determine climate when summarized over decades, influences avian nest success (Webb et al. 2012, Grudinskaya et al. 2022, Kämpfer et al. 2022), indicating climate change is likely to underlie change in nest success for some avian species. Climatic measures that differ from historical conditions (i.e., anomalies; warmer temperatures that are expected under future climate change scenarios) can influence avian nest success positively (Becker and Weisberg 2015) or negatively (Oswald et al. 2020). Warmer temperatures, especially in spring, in principle could reduce metabolic stress on incubating female wild turkeys, whereas warmer temperatures in summer could increase female metabolic stress or impede their ability to regulate egg temperature. Extreme precipitation events, which are expected to become more pronounced and common under future climate change scenarios (Fischer and Knutti 2016, Tabari 2020), cause inundation and failure of nests (Thompson and Furness 1991, Fisher et al. 2015, Mwangi et al. 2018), including wild turkey nests (Byrne and Chamberlain 2013). Weather conditions may augment predator-prey relationships by changing activity patterns (Benson et al. 2019), changing foraging duration (van de Ven et al. 2019), or modifying predator efficacy (Rubolini et al. 2003). For instance, the wet hen hypothesis states that female wild turkeys that remain wet for prolonged periods are harassed or killed by predators at elevated rates, leading to nest abandonment and failure (Roberts et al. 1995, Roberts and Porter 1998, Lowrey et al. 2000). Hence, increased precipitation resulting from climate change could plausibly increase the rate of nest abandonment and female predation during nesting.

Precipitation and temperature prior to the nesting season could indirectly influence wild turkey nest success by augmenting conditions around the nest or influencing adult female body condition. Wetter, warmer conditions in January–March may foster a more robust flush of vegetation during spring green-up in April, whereas dry conditions preceding green-up delay leaf emergence (Seyednasrollah et al. 2018), and sustained droughts reduce leaf biomass (Klos et al. 2009). Likewise, extreme cold weather or late freezes can damage or kill overwintering buds or new growth, thereby reducing leaf biomass. Reductions in plant biomass decrease the concealment of nests, possibly increasing predation risk (Kilburg et al. 2014). Greater leaf biomass could also increase substrate that supports arthropod abundance as an important food source for poults and adult wild turkeys (Hurst and Stringer 1975, Healy 1985, Iglay et al. 2005, McCord et al. 2014, Kilburg et al. 2015). Alternatively, weather conditions preceding nesting could affect nest success by influencing female wild turkey physiological condition. Avian maternal body condition and food availability, both of which can be influenced by temperature and precipitation (McCloy and Grace 2023), can affect nest success (Milenkaya et al. 2015). Female condition is also associated with rates of nest abandonment in avian species (Yorio and Boersma 1994).

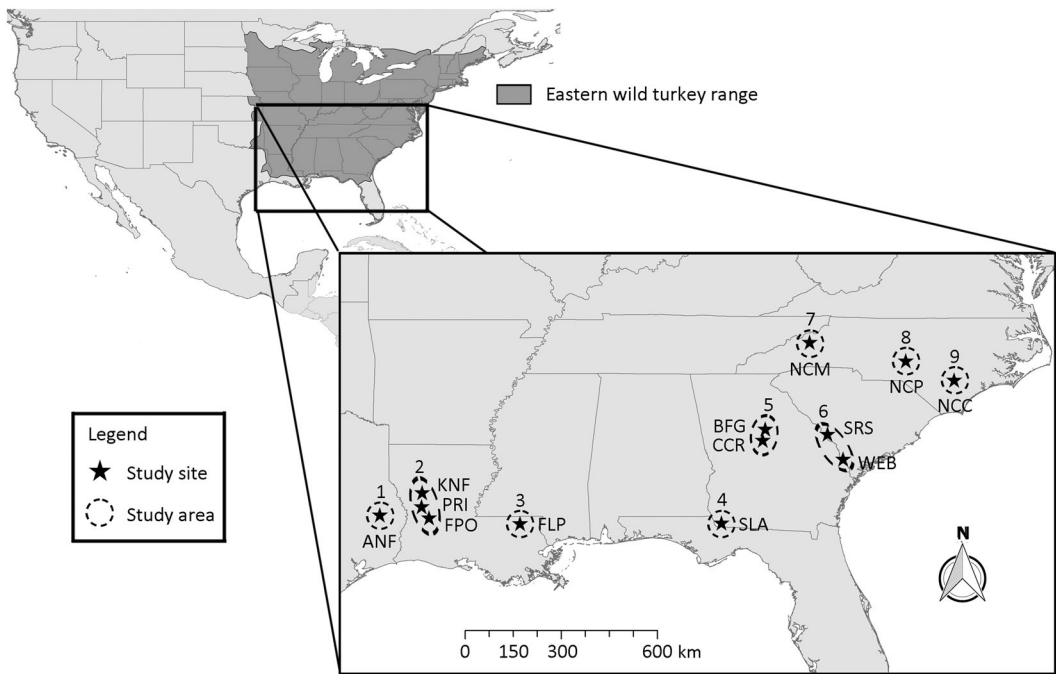
Understanding how weather conditions, nest-concealing vegetation, nest timing, and nest age are associated with nest success is of particular importance given recent declines in eastern wild turkey populations throughout

much of their range (Ericksen et al. 2015, Chamberlain et al. 2022). Wild turkeys are a socio-economically important species, and turkey hunting contributed \$4.4 billion to the United States economy in 2003 (\$7.08 billion in 2022 dollars; Southwick Associates 2003). Inferring future consequences of climate change for wild turkeys will enable managers to plan for climate-induced population change. Although weather conditions and climate are not manageable factors, knowing how abiotic factors may affect productivity, the primary factor influencing turkey populations (Vangilder 1992, Roberts et al. 1995), is important to management agencies for long-term conservation efforts.

We used 8 years of nesting data collected from 5 states in the southeastern United States to investigate how weather conditions were associated with wild turkey nest success. Our primary objective was to understand associations between weather and daily nest survival during incubation. We predicted that positive daily minimum temperature anomalies would increase daily nest survival, 48-hour accumulated precipitation would be negatively associated with daily nest survival, and greater nest age (count of days the nest had been active) would not influence daily nest survival. We then calculated how significant relationships could affect wild turkey daily nest survival by 2041–2060. Our secondary objective was to perform exploratory analyses investigating whether temperature anomalies and precipitation best predicted nest success during or prior to incubation. We also investigated whether nest-site vegetation and incubation timing influenced nest success. We predicted that weather conditions during incubation would be a better predictor of nest success than weather conditions prior to incubation, greater average daily precipitation during incubation would decrease nest success, and warmer minimum temperatures during incubation would increase nest success. Finally, we calculated how statistically significant relationships could influence wild turkey nest success by 2041–2060.

## STUDY AREA

We used data collected from 13 study sites, including publicly and privately owned properties, distributed across 5 states in the southeastern United States (Figure 1). Data collection spanned 8 years from 2014 to 2021, but research duration at individual sites varied from 1–7 years. Study sites included Angelina National Forest (ANF; 18,751 ha) in east Texas; Fort Polk Wildlife Management Area (FPO; 105,545 ha), Kisatchie National Forest (KNF; 158,030 ha), Peason Ridge Wildlife Management Area (PRI; 30,071 ha), and Florida Parishes (FLP; 1,496 ha) in Louisiana; Silver Lake Wildlife Management Area (SLA; 3,723 ha), B. F. Grant Wildlife Management Area (BFG; 4,613 ha), and Cedar Creek Wildlife Management Area (CCR; 15,873 ha) in Georgia; Webb Wildlife Management Area Complex (WEB; 25,900 ha) and the Savannah River Site (SRS; 78,000 ha) in South Carolina; and private lands in the mountain (NCM; 83 private properties), Piedmont (NCP; 63 private properties), and coastal plain (NCC; 77 private properties) ecoregions of North Carolina in the United States. Elevation at all study sites was <200 m, except NCM where elevation ranged from 500 m to 1,800 m. Timber production was the dominant land use across most study sites, excluding NCC where poultry and swine production, row crops, and pastures were the dominant land uses. Pastures were also dominant in the privately owned valleys of NCM, while forests were dominant on the federally owned (U.S. Forest Service) mountains. Longleaf pine (*Pinus palustris*), loblolly pine (*P. taeda*), slash pine (*P. elliottii*), and mixed hardwood forests were dominant in uplands with fields intermixed and lowlands dominated by hardwood forests. Climate throughout the study area was classified as humid subtropical (Beck et al. 2018). Our study occurred in the northern hemisphere where 1 December to 28 February was winter, 1 March to 31 May was spring, 1 June to 31 August was summer, and 1 September to 30 November was fall. We summarized weather data using the gridMET 4-km resolution dataset (Abatzoglou 2013) for each nest location. Annual average low temperatures observed at study sites during the study ranged from 6.92°C (NCM) to 14.78°C (ANF). Annual average high temperatures ranged from 18.93°C (NCM) to 27.03°C (SLA). Annual total precipitation ranged from 124.80 cm (SRS) to 212.40 cm (FPO). Potential nest predators included American crows (*Corvus brachyrhynchos*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), feral hogs (*Sus scrofa*), nine-banded armadillos (*Dasyops*



**FIGURE 1** The location of eastern wild turkey study sites in the southeastern United States and the study areas we grouped them into when accounting for spatial autocorrelation. Cumulatively, we monitored 715 nests across these study sites between 2014 and 2021. We adapted the eastern wild turkey range from Ericksen et al. (2015). Study sites included Angelina National Forest (ANF) in east Texas; Fort Polk Wildlife Management Area (FPO), Kisatchie National Forest (KNF), Peason Ridge Wildlife Management Area (PRI), and Florida Parishes (FLP) in Louisiana; Silver Lake Wildlife Management Area (SLA), B. F. Grant Wildlife Management Area (BFG), and Cedar Creek Wildlife Management Area (CCR) in Georgia; Webb Wildlife Management Area Complex (WEB) and the Savannah River Site (SRS) in South Carolina; and private lands in the mountain (NCM), Piedmont (NCP), and coastal plain (NCC) ecoregions of North Carolina.

*novemcinctus*), raccoons (*Procyon lotor*), ratsnakes (*Pantherophis* spp.), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*; Melville et al. 2014, Yeldell 2016, Sanders et al. 2020, Crawford et al. 2021, Boone and Johnson 2023).

## METHODS

### Reproduction data

We captured female wild turkeys using rocket nets January–March from 2014 to 2021. We placed very high frequency (VHF) backpack global positioning system (GPS) transmitters (Guthrie et al. 2011) produced by Biotrack (Wareham, Dorset, United Kingdom) on each captured turkey. Beginning 1 March transmitters collected  $\geq 9$  locations from 0500–2000 and 1 location each night at 2359 until the battery died or the transmitter was recovered after a mortality event or during recapture the following year (Cohen et al. 2018). We released turkeys at the point of capture following processing.

We located each turkey  $\geq 2$  times each week to monitor survival and nesting activity. We downloaded the GPS data  $\geq 1$  time/week and visually assessed female locations to determine when movements became localized to a

small area, suggesting nest initiation (Yeldell et al. 2017a, b). We denoted nest incubation initiation date as the first day when the female spent that night at the nest site (Bakner et al. 2019). We denoted nesting as complete when the female quit returning to the nest. We then inspected the inactive nest to determine if eggs hatched (Conley et al. 2016, Yeldell et al. 2017a, b). When no eggs hatched, eggshells were crushed, or no eggshells remained, we classified the nest as failed, whereas we classified a nest as successfully hatched when pipped eggshells were present (Chamberlain et al. 2020). Because first nests contribute the most to recruitment (Little et al. 2014, Yeldell et al. 2017a), we only included each individual's first nesting attempt in a given year (i.e., we omitted 242 second, third, and fourth nesting attempts).

## Vegetation and weather data

To determine whether visual obstruction associated with vegetation influenced nest success, we sampled vegetation within a 15-m radius of each nest following methods outlined by Keever et al. (2023). Using a Robel pole (Robel et al. 1970), we measured the height of visual obstruction (cm) between the center of the nest and 15 m in each cardinal direction. We then averaged these 4 values to create a single metric of visual obstruction for each nest. We collected these measurements <3 days following hatch date or nest failure to minimize post-nesting vegetation growth (McConnell et al. 2017).

We obtained weather data from 2014–2021 to investigate effects of temperature or precipitation on wild turkey nest success. We extracted daily low temperature and daily precipitation for each nest location (4-km resolution) from gridMET (Abatzoglou 2013). For each individual nest location, we calculated average precipitation and average minimum temperature separately for January, February, March, 30 days prior to incubation initiation, and during incubation for each individual nest. We selected 30 days prior because breeding behaviors occur during this period (Wakefield et al. 2020). We calculated anomalies as the difference between the observed average minimum temperature and the average minimum temperature from 1981–2010 for each nest location in January, February, March, 30 days prior to incubation initiation, and during incubation for each individual nest (using the same ordinal dates for the 1981–2010 average and the nesting temporal period being investigated). We used anomalies from the mean rather than simply using the observed minimum average temperature to account for seasonal temperature change; for example, a low of 15°C in March would be uncharacteristically warm, but it would not be as anomalous in May. We did not include high temperatures in analyses because they were correlated with minimum temperatures ( $r$  range = 0.83–0.94), and because spring high temperatures are unlikely to reach thermal limits for a species that renests into the summer.

## Statistical analysis

Our first objective was to understand associations between weather conditions and daily nest survival during incubation. We investigated how the daily minimum temperature anomaly, 48-hour precipitation, and the number of days a nest had been active (count of days since incubation began) influenced daily nest survival. We chose a 48-hour precipitation window to ensure it included the time immediately prior to nest success or failure because nests often fail in the early morning (e.g., if a nest fails at 0100, the precipitation amount for the day of failure is likely less relevant than the precipitation amount from the day before). We included the number of days the nest was active because nests closer to hatching presumably received greater maternal effort over the longer duration and therefore may have been more vigilantly protected. We evaluated variable collinearity and no absolute correlation coefficient was  $\geq 0.7$  (Dormann et al. 2013). We used a generalized linear mixed-effects model with an inverse-link function in program R (version 4.1.2; R Core Team 2022) using the lme4 package (Bates et al. 2015) to assess associations between weather conditions and daily nest survival. This approach allows for the inclusion of random

effects, enabling us to include study area as a random intercept to account for possible spatial autocorrelation caused by non-random sampling. We calculated the variance inflation factor of each variable included in the global model to assess multicollinearity and determined that no variance inflation factor exceeded the threshold of 5 (McClave and Sincich 2003). We tested all possible combinations of the 3 fixed effect variables, plus pairwise interactions between these variables (13 models). We ranked models using Akaike's Information Criterion accounting for small sample size ( $AIC_c$ ) and conservatively considered those with  $\Delta AIC_c < 4$  to be competing models (Akaike 1973, Burnham and Anderson 2002). We conducted full model averaging of all competing models (Burnham and Anderson 2002). We considered variables with 95% confidence intervals that did not overlap zero to be significant predictors of daily nest survival.

To assess possible implications of climate change for future eastern wild turkey daily nest survival, we used climate model projections of future warming from the coupled model intercomparison project (CMIP6; Almazroui et al. 2021). We extracted averaged values for 2041–2060 for variables determined significant in the final model averaged model. We extracted these values for 3 greenhouse gas forcing scenarios referred to as shared socioeconomic pathways (SSPs 1-2.5, 2-4.5, and 5-8.5; O'Neill et al. 2014) summarized for eastern North America (Almazroui et al. 2021). These 3 SSPs represent a range of future greenhouse gas concentration pathways (and associated climate forcings) ranging from a stabilized amount of warming of approximately 2°C relative to pre-industrial conditions (SSP 1-2.5) to continued rapid warming throughout the twenty-first century (SSP5-8.5). The projected warming amounts for each SSP were based on an ensemble of 31 global climate models. We extracted the projected future annual average, upper 66% confidence interval, and lower 66% confidence interval for each SSP. We used 66% confidence intervals because these were the data that were available (Haensler et al. 2013, Almazroui et al. 2021). We then projected each significant relationship using model-averaged estimates from significant variables, with non-significant variables fixed at their observed mean. By using these 3 scenarios and their 66% confidence intervals, we provided a robust projection of how temperature and precipitation changes could influence eastern wild turkey daily nest survival. Because these are projections of annual temperature and precipitation change across eastern North America, there are likely to be differences between the values used and the projected changes for the specific months and locations of interest in this study. Broadly, we expected the direction and magnitude of change to be consistent. The overall approach to using climate change projections in this way is analogous to the use of global warming levels (Tebaldi et al. 2021) to assess relative changes at specific amounts of global warming, regardless of the timeframe over which it occurs. We were interested in making comparisons between our projected estimates of nest success and estimated nest survival under future climate conditions, so we calculated the expected incubation period nest survival by raising our daily nest survival rates to the average incubation length for a nest to hatch (28 days; Harper and Exum 1999) and compared those to our estimates of nest success. This allowed for approximate comparisons between this and the following analysis.

Our second objective was to perform exploratory analyses investigating whether temperature anomalies and precipitation best predicted nest success during or prior to incubation. We started by determining if weather conditions in January, February, March, 30 days prior to incubation initiation, or during incubation were more important to nest success (binary measure of whether or not a nest hatched). We built 5 models, 1 for each of the aforementioned time periods that included weather variables (minimum average temperature anomaly and average daily precipitation) plus incubation initiation date, visual obstruction, and year. We included an interaction between average daily precipitation and minimum average temperature anomaly in all 5 models to assess whether precipitation influenced nest success more during cold conditions than during warm conditions. We included an interaction between incubation initiation date and minimum average temperature anomaly in the during incubation model to assess whether temperature anomalies during earlier nests were more or less important than temperature anomalies during later nests. Weather variables included in these models were averages throughout the period, which provided insight into how longer-term weather trends influenced nest success. We checked variable collinearity using the Pearson correlation coefficient and determined that no absolute correlation coefficient was  $\geq 0.7$  (Dormann et al. 2013). We ran generalized linear mixed-effects models with a logit-link function in program R

(version 4.1.2; R Core Team 2022) using the lme4 package (Bates et al. 2015). Generalized linear mixed-effects models enabled us to include random effects and we included study area (Figure 1) as a random intercept to account for possible spatial autocorrelation caused by non-random sampling. We calculated the variance inflation factor for each model to assess multicollinearity and determined that the variance inflation factor was below the threshold of 5, above which excessive collinearity exists (McClave and Sincich 2003), for all 5 models. To assess which time period(s) may have been most important in determining nest success, we ranked these 5 models by AICc and considered models with  $\Delta AICc < 4$  to be competing models (Akaike 1973, Burnham and Anderson 2002). We conducted full model averaging of all competing models (Burnham and Anderson 2002). We considered variables with 95% confidence intervals that did not overlap zero to be significant predictors of wild turkey nest success. We then applied the previously described approach for projecting climate change effects on daily nest survival to project the effects on eastern wild turkey nest success.

## RESULTS

We monitored 715 first nests initiated by 682 individual female turkeys during the 2014–2021 breeding seasons. Of 17 turkeys monitored multiple years, we monitored 16 individuals for 2 years and 1 individual for 3 years. Overall hatch rate was 26% (186 nests) and failure rate was 74% (529 nests). Annual hatch rate ranged from 14.9% in 2017 to 37.3% in 2015 (Table 1). Study area hatch rate ranged from 0% (out of 4 nests) in ANF to 42.6% (out of 61 nests) in FLP (Table 2). Incubation of the earliest nest started 12 March, the latest initial nest being incubated failed on 14 July, and mean incubation initiation date was 19 April (non-leap year).

Analyses pertaining to the primary objective (i.e., understanding associations between weather conditions during incubation and daily nest survival) produced 6 competing models (Table 3). Model averaging of competing models revealed 1 significant predictor of daily nest survival. As observed daily minimum temperature anomalies went from negative to positive relative to the historical average, daily nest survival increased ( $\beta = 0.07$ , CI = 0.05–0.09; Figure 2) with daily nest survival increasing from 94.50% (CI = 93.29–95.50%) to 97.15% (CI = 96.41–97.74%) as temperature anomaly increased from 5°C below average to 5°C above average. The 4 other variables included in competing models were not significant predictors of daily nest survival (Table 4). Based on results of the top model, using the projected temperature increases through 2041–2060 relative to nest survival at the observed mean temperature, eastern wild turkey daily nest survival would be expected to increase by 0.40%

**TABLE 1** Number of eastern wild turkey nests monitored, cumulative percent of nests that survived to hatching for each year of the study (2014–2021), and the minimum and maximum percent that survived across the 9 study sites in each year. Cumulatively, we monitored 715 nests in the southeastern United States (Texas, Louisiana, Georgia, South Carolina, and North Carolina).

Year	Number of nests	Success (%)	Minimum (%)	Maximum (%)
2014	28	28.6	13.0	100.0
2015	51	37.3	25.0	46.7
2016	69	30.4	0.0	40.6
2017	87	14.9	0.0	50.0
2018	89	21.3	11.1	37.0
2019	57	19.3	0.0	26.1
2020	141	29.1	16.7	51.5
2021	193	30.0	0.0	42.9



**TABLE 2** Geographic location, number of eastern wild turkey nests monitored, and the percent of nests that survived to hatching for each study area (Figure 1). Cumulatively, we monitored 715 nests in the southeastern United States (Texas, Louisiana, Georgia, South Carolina, and North Carolina) between 2014 and 2021.

Study area	Study sites <sup>a</sup>	Geographic location	Number of nests	Success (%)
1	ANF	East Texas	4	0.0
2	FPO, KNF, PRI	West-central Louisiana	206	13.1
3	FLP	Southeastern Louisiana	61	42.6
4	SLA	Southwestern Georgia	41	39.0
5	BFG, CCR	Central Georgia	154	21.4
6	SRS, WEB	Southwestern South Carolina	87	41.4
7	NCM	North Carolina mountains	62	24.2
8	NCP	North Carolina Piedmont	54	33.3
9	NCC	North Carolina coastal plain	46	32.6

<sup>a</sup>Study sites included Angelina National Forest (ANF), Fort Polk Wildlife Management Area (FPO), Kisatchie National Forest (KNF), Peason Ridge Wildlife Management Area (PRI), Florida Parishes (FLP), Silver Lake Wildlife Management Area (SLA), B. F. Grant Wildlife Management Area (BFG), Cedar Creek Wildlife Management Area (CCR), Webb Wildlife Management Area Complex (WEB), the Savannah River Site (SRS), and private lands in the mountain (NCM), Piedmont (NCP), and coastal plain (NCC) ecoregions of North Carolina.

(66% CI = 0.33–0.54%) from 96.03% to 96.42% under SSP1-2.5, 0.51% (66% CI = 0.42–0.62%) from 96.03% to 96.52% under SSP2-4.5, and 0.66% (66% CI = 0.53–0.78%) from 96.03% to 96.66% under SSP5-8.5. When looking at expected nest survival cumulatively for the incubation period, relative to nest survival at the observed mean temperature, eastern wild turkey nest survival could increase by up to 11.28% (66% CI = 9.16–15.23%) under SSP1-2.5, 14.28% (66% CI = 11.76–17.42%) under SSP2-4.5, and 18.54% (66% CI = 14.81–21.73%) under SSP5-8.5.

Analyses pertaining to the secondary objective (i.e., investigating whether temperature anomalies and precipitation best predicted nest success during or prior to incubation) indicated that weather conditions in January preceding nesting were the best predictor of nest success. There were no other competing models (Table 5), so model averaging was not necessary. Greater average daily precipitation in January was associated with greater nest success ( $\beta = 0.43$ , CI = 0.11–0.75; Figure 3A) with a 1-mm increase in average daily rainfall above the mean observed in this study (4.24 mm/day) associated with a 19.14% increase in nest success from 30.18% to 35.96%. Warmer minimum January temperatures were associated with decreased nest success ( $\beta = -0.50$ , CI = -0.82 to -0.19; Figure 3B) with a 1°C increase in temperature anomalies associated with a 13.48% relative decrease in nest success; absolute values of 35.02% nest success for mean conditions declined to 30.30% for every 1°C increase in temperature. As the nesting season progressed, nest success declined ( $\beta = -0.02$ , CI = -0.04 to -0.01; Figure 3C) with every additional day that a nest was initiated after mean nest initiation date associated with a 0.50% decrease in nest success. Visual obstruction by nest-site vegetation was not a significant predictor of nest success (Table 6).

Over 2041–2060, annual precipitation is projected to increase in eastern North America by 3.86% (66% CI = 2.04–6.78%) under SSP1-2.5, 5.22% (66% CI = 2.41–7.39%) under SSP2-4.5, and 5.65% (66% CI = 2.81–8.70%) under SSP5-8.5. Based on results of the top model because model averaging was not necessary, assuming similar changes in future January precipitation relative to the annual mean, such increases would also increase eastern wild turkey nest success by 2.77% (66% CI = 1.32–5.11%) from 30.18% to 31.02% under SSP1-2.5, 3.86% (66% CI = 1.62–5.60%) from 30.18% to 31.34% under SSP2-4.5, and 4.20% (66% CI = 1.93–6.67%) from 30.18% to 31.45% under SSP5-8.5. Over the same mid-century period, annual temperatures in eastern North America are projected to increase by 1.55°C (66% CI = 1.25–2.13°C) under SSP1-2.5, 1.99°C (66% CI = 1.62–2.46°C) under



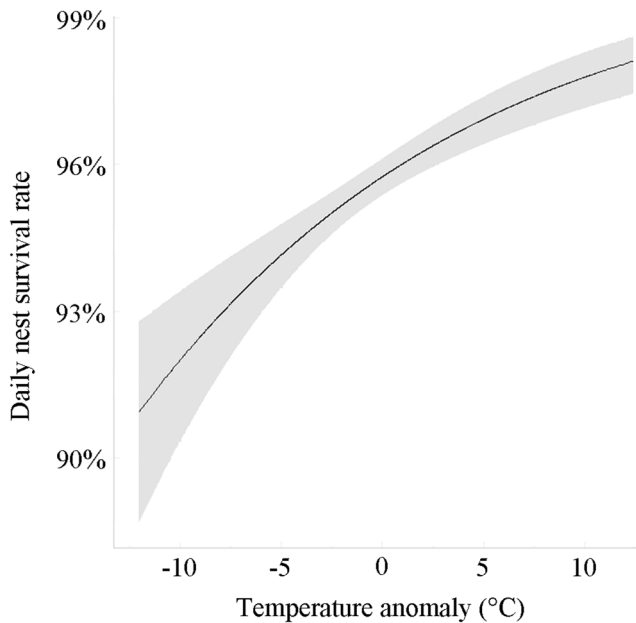
**TABLE 3** Akaike's Information Criterion accounting for small sample size ( $AIC_c$ ) values comparing models describing the effects of weather and maternal investment on daily nest survival for 715 eastern wild turkey nests in the southeastern United States (Texas, Louisiana, Georgia, South Carolina, and North Carolina) between 2014 and 2021. We also present the difference between each model's  $AIC_c$  and the best model's  $AIC_c$  ( $\Delta AIC_c$ ),  $AIC_c$  weight, cumulative model weight (Cum. Wt), and log likelihood (LL) for 13 generalized linear mixed-effects models. Temperature anomaly was the only variable with a significant association based on 95% confidence intervals of the coefficients. Variables included observed daily minimum temperature anomaly (compared to the 1981–2010 average), 48-hour precipitation total, and the number of days a nest had been active since incubation began as a proxy of maternal investment (day count). All models included study area as a random effect to account for spatially clustered sampling.

Model	$\Delta AIC_c$	Weight	Cum. Wt	LL
Temp anomaly (+)	0.00	0.41	0.41	-2,130.8
Temp anomaly (+) + precipitation	1.94	0.15	0.56	-2,130.7
Temp anomaly (+) + day count	1.99	0.15	0.71	-2,130.8
Temp anomaly (+) + precipitation + temp anomaly $\times$ precipitation	3.20	0.08	0.80	-2,130.4
Temp anomaly (+) + day count + temp anomaly $\times$ day count	3.71	0.06	0.86	-2,130.6
Temp anomaly (+) + precipitation + day count	3.93	0.06	0.92	-2,130.7
Temp anomaly (+) + precipitation + day count + temp anomaly $\times$ precipitation	5.20	0.03	0.95	-2,130.4
Temp anomaly (+) + precipitation + day count + precipitation $\times$ day count	5.34	0.03	0.98	-2,130.4
Temp anomaly (+) + precipitation + day count + temp anomaly $\times$ day count	5.66	0.02	1.00	-2,130.6
Day count	36.79	0.00	1.00	-2,149.2
Precipitation	38.05	0.00	1.00	-2,149.8
Precipitation + day count	38.27	0.00	1.00	-2,148.9
Precipitation + day count + precipitation $\times$ day count	39.31	0.00	1.00	-2,148.4

SSP2-4.5, and 2.63°C (66% CI = 2.07–3.13°C) under SSP5-8.5. Based on results of the top model, assuming future January temperature increases that are similar to the projected annual temperature change, eastern wild turkey nest success would decrease by 20.85% (66% CI = 16.80–27.47%) from 35.02% to 27.72% under SSP1-2.5, 25.67% (66% CI = 21.47–28.61%) from 35.02% to 26.03% under SSP2-4.5, and 34.01% (66% CI = 35.55–38.32%) from 35.02% to 23.11% under SSP5-8.5.

## DISCUSSION

Using a robust region-wide 8-year dataset, we sought to determine how weather conditions influenced wild turkey daily nest survival and overall nest success. Contrary to our predictions, we did not document decreased daily nest survival associated with wet conditions during nesting, as postulated in the wet hen hypothesis (Roberts et al. 1995, Roberts and Porter 1998), which is widely referenced in peer-reviewed literature (Lopez et al. 1999, Lehman et al. 2008, Tyl et al. 2020). Wild turkeys have evolved to overcome heightened predation risk in wet conditions given the substantial predation pressure they experience and their purported persistence in the temperate eastern United States since the end of the Pleistocene (Brodkorb 1963). Although results from our study are incongruent with the wet hen hypothesis, assessment of how weather conditions influence all nest predation activity is needed to further assess the validity of the hypothesis more thoroughly. Additionally, how weather conditions influence



**FIGURE 2** Daily nest survival increased as the observed daily minimum temperature anomaly (compared to the 1981–2010 average) increased from  $-12.06^{\circ}\text{C}$  (minimum observed value) to  $12.44^{\circ}\text{C}$  (maximum observed value) for 715 first nests of eastern wild turkeys. Study sites spanned the southeastern United States (Texas, Louisiana, Georgia, South Carolina, and North Carolina) and data were collected between 2014 and 2021. The solid dark line depicts the estimated mean and the light gray shaded area depicts the 95% confidence interval.

**TABLE 4** Individual variable output from models investigating the effects of weather and maternal investment on daily nest survival for 715 eastern wild turkey nests in the southeastern United States (Texas, Louisiana, Georgia, South Carolina, and North Carolina) studied between 2014 and 2021. We present model-averaged beta estimates ( $\hat{\beta}$ ) and 95% confidence intervals (95% CI) for variables included in the 6 competing models. Variables included observed daily minimum temperature anomaly (compared to the 1981–2010 average), 48-hour precipitation total, and the number of days a nest had been active since incubation began as a proxy of maternal investment (day count).

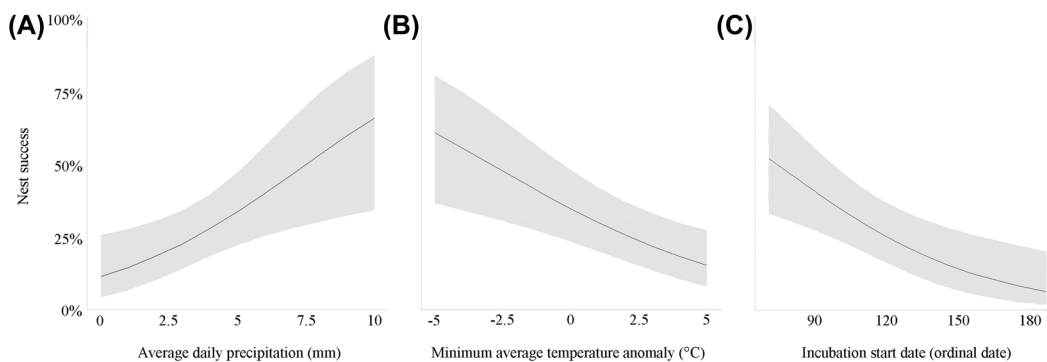
Variable	$\hat{\beta}$	95% CI
Temp anomaly	0.07	0.05–0.09
Day count	-0.0008	-0.01–0.01
Precipitation	-0.0008	-0.006–0.004
Temp anomaly $\times$ precipitation	-0.0006	-0.002–0.001
Temp anomaly $\times$ day count	-0.0007	-0.003–0.002

predation may vary throughout the wild turkey's range, requiring additional study of weather effects outside of the southeastern United States.

Warmer daily minimum temperatures during incubation were associated with greater nest survival, as has previously been reported (Vangilder and Kurzejeski 1995) or inferred (Rolley et al. 1998). Colder temperatures increase metabolic demands on incubating females, potentially requiring them to forage longer during incubation recesses. Increased incubation recess duration may lead to greater risk of nest failure (Lohr et al. 2020), possibly

**TABLE 5** Models investigating whether conditions during January, February, March, 30 days prior to incubation, or during incubation were the best predictor of nest success for 715 eastern wild turkey nests in the southeastern United States (Texas, Louisiana, Georgia, South Carolina, and North Carolina) between 2014 and 2021. Each model included an interaction between average daily precipitation and minimum average temperature anomaly. Non-weather variables were consistent across all 5 models and included year, start date (ordinal date when incubation began), and visual obstruction. Study area was included as a random effect in each model to account for spatially clustered sampling. The table includes the difference between each model's Akaike's Information Criterion accounting for small sample size ( $AIC_c$ ) value and the best model's  $AIC_c$  value ( $\Delta AIC_c$ ),  $AIC_c$  weight, cumulative model weight (Cum. Wt), and log likelihood (LL) for 5 generalized linear mixed-effects models investigating which time period and weather variables were more important to nest success (binary measure of hatch success).

Time period	$\Delta AIC_c$	Weight	Cum. Wt	LL
January	0.00	0.88	0.88	-383.9
During incubation	5.30	0.06	0.94	-385.5
February	6.53	0.03	0.98	-387.1
March	8.73	0.01	0.99	-388.2
Thirty days prior	8.76	0.01	1.00	-388.2



**FIGURE 3** The relationship between the percent of successful nests and A) average daily precipitation in January, B) minimum average temperature anomaly ( $^{\circ}C$ ) in January, and C) incubation initiation date for 715 first nests of eastern wild turkeys. Study sites spanned the southeastern United States (Texas, Louisiana, Georgia, South Carolina, and North Carolina) and data were collected between 2014 and 2021. The solid dark line depicts the estimated mean and the light gray shaded area depicts the 95% confidence interval.

accounting for the observed relationship between lower temperatures and increased nest failure in our study. Temperatures are expected to increase under future climate change projections (Almazroui et al. 2021). If eastern wild turkey reproductive timing remains static as was reported by Boone et al. (2023), nest survival could increase as temperatures increase.

Unexpectedly, weather conditions during January prior to incubation were better predictors of wild turkey nest success than weather conditions during the other periods we tested, including during incubation. Although investigations of associations between turkey nest success and weather conditions prior to incubation are scant, our results match those from more northern populations where weather conditions prior to nesting were an important predictor of nest success (Delaware, USA [Ludwig 2012]; Manitoba, Canada [Kiss 2014]) but are counter to results from a southern population where conditions prior to nesting were not reported to be an important predictor of nest success (Mississippi, USA; Miller et al. 1998). Northern populations can experience prolonged

**TABLE 6** Individual variable output from the top model of associations between weather, vegetation, and incubation initiation date (start date) and nest success for 715 nests in the southeastern United States (Texas, Louisiana, Georgia, South Carolina, and North Carolina) studied between 2014 and 2021. We present beta estimates ( $\hat{\beta}$ ) and 95% confidence intervals (95% CI) for variables included in the top model. Weather variables included observed minimum average temperature anomaly (compared to the 1981–2010 average) and average daily precipitation. Non-weather variables included year, start date (ordinal date when incubation began), and visual obstruction.

Variable	$\hat{\beta}$	95% CI
Start date	-0.02	-0.04--0.01
Average precipitation	0.43	0.11--0.75
Temp anomaly	-0.50	-0.82--0.19
Year	-0.15	-0.44-0.14
Visual obstruction	0.10	-0.09-0.30
Average precipitation $\times$ temp anomaly	-0.04	-0.29-0.21

periods of snow cover, which has been linked to reduced female body condition (Porter et al. 1983) and postulated to result in reduced nest success (Ludwig 2012, Kiss 2014). Increased snowfall amounts compresses vegetation that conceals nests, and increased snow persistence delays the spring emergence of groundcover plants, potentially increasing predation and reducing nest success (Kiss 2014, Keever et al. 2023). Persistent snow cover was not a factor within our study area because of the geographic location of the study sites.

Increased precipitation in January prior to nesting was associated with increased nest success. Similarly, increased precipitation prior to nesting was positively associated with Merriam's wild turkey (*M. g. merriami*) nest success because it resulted in increased groundcover vegetation and better visual obstruction of nests (Lehman et al. 2008). Likewise, researchers that used a subset of the data analyzed in our study determined that an increase in a proxy metric of vegetation biomass (i.e., enhanced vegetation index) was associated with decreased daily hazard for wild turkey nests (Crawford et al. 2021). Increased rainfall in late winter is associated with faster and earlier vegetation growth (Seyednasrollah et al. 2018). Denser vegetation provides concealment for wild turkey nests, possibly decreasing predation (Kilburg et al. 2014). In our study the relationship between greater rainfall and greater nest success was not caused by an increase in concealing vegetation because visual obstruction was not a predictor of wild turkey nest success. Vegetation also provides forage for adult turkeys (Haegen et al. 1988, Decker et al. 1991), so greater vegetation biomass following wetter January weather could improve female wild turkey physiological condition at the beginning of the nesting season or decrease the amount of time required to forage during nesting. Reduced foraging duration is associated with reduced nest failure (Lohr et al. 2020), so increased January rainfall could decrease nest failure by decreasing foraging time.

Although weather conditions during nesting were expected to be a better predictor of nest success than conditions prior to nesting, the association between warmer January temperatures and decreased wild turkey nest success is plausible but requires further assessment. Warmer January temperatures may influence predator activity, predator metabolic demands, or predator abundance (e.g., by shifting predator reproduction to precede wild turkey nesting). Alternatively, warmer January temperatures could increase parasite load by enabling more parasites to survive the winter, as shown in other species (Heylen et al. 2013, Holand et al. 2019), thereby decreasing maternal body condition. We concede that these potential relationships are speculative. Future research is needed to investigate if warmer weather in the months preceding wild turkey nesting influences nest predator activity or metabolic demands or parasite loads for female wild turkeys.

## RESEARCH IMPLICATIONS

Most weather variables, including precipitation during nesting, were not important predictors of nest success. Moreover, analyses produced mixed results, with some relationships projected to increase future wild turkey nest success and others projected to decrease future wild turkey nest success. During incubation, positive minimum daily temperature anomalies were associated with greater daily nest survival. Unexpectedly, exploratory analyses indicated that weather conditions in January prior to incubation were more important to nest success than weather conditions during incubation. Negative January minimum temperature anomalies and greater average daily precipitation were associated with greater nest success. Research is needed to determine the mechanistic influence of associations between January weather conditions and wild turkey nest success, determine how the breeding phenology of predators of wild turkeys and wild turkey nests is associated with climate change, and evaluate how predator activity changes in response to short-term weather conditions and long-term climate change. Additionally, replication of this study in more northern latitudes would aid in determining the generalizability of these results throughout the entirety of the eastern wild turkey range. Finally, additional research is needed to determine the implications of climate change for poult survival and cumulative eastern wild turkey population recruitment.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## ETHICS STATEMENT

Trapping and handling procedures were approved by the Institutional Animal Care and Use Committees at North Carolina State University (protocol 19-739-O), Louisiana State University (protocol A2014-013, A2015-07, A2018-13, and A2021-14), and University of Georgia (protocols A2014 06-008-Y1-A0 and A3437-01).

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from relevant state agencies. Restrictions apply to the availability of these data, which were used under license for this study. Data may be obtained from the relevant state agencies, at their discretion.

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