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Minimal shift of eastern wild turkey nesting phenology associated with projected climate change

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ABSTRACT

Climate change may induce mismatches between wildlife reproductive phenology and temporal occurrence of resources necessary for reproductive success. Verifying and elucidating the causal mechanisms behind potential mismatches requires large-scale, longer-duration data. We used eastern wild turkey (*Meleagris gallopavo silvestris*) nesting data collected across the southeastern U.S. over eight years to investigate potential climatic drivers of variation in nest initiation dates. We investigated climactic relationships with two datasets, one inclusive of successful and unsuccessful nests (full dataset) and another of just successful nests (successfully hatched dataset), to determine whether successfully hatched nests responded differently to weather changes than all nests did. In the full dataset, each 10 cm increase in January precipitation was associated with nesting occurring 0.46–0.66 days earlier, and each 10 cm increase in precipitation during the 30 days preceding nesting was associated with nesting occurring 0.17–0.21 days later. In the successfully hatched dataset, a 10 cm increase in March precipitation was associated with nesting occurring 0.67–0.74 days earlier, and an increase of one unit of variation in February maximum temperature was associated with nesting occurring 0.02 days later. We combined the results of these modeled relationships with multiple climate scenarios to understand potential implications of future climate change on wild turkey nesting phenology; results indicated that mean nest initiation date is projected to change by <0.1 day by 2040–2060. Wild turkey nesting phenology did not track changes in spring green-up timing, which could result in phenological mismatch between the timing of nesting and the availability of resources critical for successful reproduction.

Climate change is contributing to shifts in the reproductive phenology of wildlife populations [18] and the availability of resources required for successful reproduction [55,60]. However, study of the relationships between climate change and wildlife often are of limited geographic scope [20,34] or short duration [8,39,80]. Local-scale, shorter-term studies are subject to spurious correlations, may miss long-term ecological trends, and lack generalizability [23,54]. Broad-scale long-term research is more capable of elucidating relationships between climate change and wildlife reproductive phenology [46,64], readily informs management and conservation actions across greater spatial scales [65,92], and contributes substantively to broader understanding of ecological processes and unifying principles [4,11].

Wildlife reproductive phenology is subject to modification due to climate change [62,94]. Shifts in one species' phenology may not track the phenology of primary producers, specifically green-up (caribou [*Rangifer tarandus*], [60]; roe deer [*Capreolus capreolus*], [58]), or prey species (great tits [*Parus major*], [63]), resulting in phenological mismatch. Due to warming trends associated with climate change, some wildlife now reproduce when food is not sufficiently available, decreasing offspring survival [58,60,93]. Species with prolonged gestation periods must make breeding decisions months in advance when spring conditions are unknown, resulting in limited capacity to

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prevent phenological mismatches [10]. Species with short time spans between breeding and offspring birth or egg laying purportedly are more capable of shifting breeding phenology to match resource availability. However, climate change-induced phenological mismatch may even affect these more-flexible species (e.g., great tits, [91]).

Climate change is expected to change weather patterns globally [3, 79]. Aside from rising temperatures, temperature variability is expected to change, with some regions becoming more variable and others less variable [3]. Increased temperature variability is associated with decreased wildlife fitness (ostrich [*Struthio camelus*] fertility, [74]) and increased metabolic demands (e.g., water acquisition for evaporative cooling, [66]). During breeding periods, increased temperature variability is associated with reduced breeding success (southern yellow-billed hornbill [*Tockus leucomelas*], [86]) and offspring survival (southern pied babbler [*Turdoides bicolor*], [9]), but how or whether it influences breeding phenology is understudied. Likewise, rainfall patterns are expected to shift globally with individual storm rainfall totals generally expected to increase because of the greater moisture content of warmer air [79]. Increased rainfall is associated with modified foraging success (magnificent frigatebird [*Fregata magnificens*], [56]), predation rates (bank voles [*Myodes glareolus*] predated by pygmy owls [*Glaucidium passerinum*], [83]), and perceived predation risk (redshanks [*Tringa totanus*], [31]). Increased rainfall, particularly during cold weather, increases metabolic demands of endotherms, which can reduce adult and offspring survival (northern wheatears [*Oenanthe oenanthe*], [53]). Greater precipitation has also been associated with increased offspring mortality (common buzzard [*Buteo buteo*], [40]; Magellanic penguin (*Spheniscus magellanicus*), [7]) and changes in timing of wildlife reproduction (insectivorous bats [*Myotis* spp.], [27]; Kirtland's warbler [*Setophaga kirtlandii*], [69]). Conversely, greater precipitation can spur vegetation flushes that provide additional forage, potentially having a positive influence on reproduction (common degu [*Octodon degus*], [49]). Without unifying principles, understanding how climate change influences wildlife phenology requires species-specific inquiry.

We sought to determine how climate change may influence breeding phenology of the eastern wild turkey (*M. gallopavo silvestris*). One of the most economically and socially important wildlife species, the wild turkey is broadly-distributed throughout North America [14,15,50,78, 81]. Having been extirpated from much of its previous range due to unregulated harvest and habitat loss [37], substantial intervention, including the end of market hunting and reintroduction, made wild turkey restoration one of North American's greatest conservation success stories [22]. Now a highly sought-after game species, wild turkey hunters contributed an estimated $1.8 billion to the U.S. economy in 2003, which spurred $4.4 billion in total economic activity ($7.08 billion in 2022 dollars when accounting for inflation; [78]). However, southern populations of the eastern wild turkey are in decline [24,81]. Attempting to reverse wild turkey declines, some state management agencies have reduced hunting season duration and bag limits [14,44]. However, the cause of these declines remains unknown, so shifts in hunting season structure may not resolve perceived problems.

One potential cause of eastern wild turkey population declines is reduced nest success resulting from a mismatch between resource availability and the timing of nesting because of climate change. Spring green-up produces a pulse of nutrient-rich foliage that harbors invertebrates, which are a vital food resource for turkey adults and young poults [32,33,48]. A mismatch between resources associated with green-up and the timing of turkey reproduction should negatively influence nest success and poult survival, and possibly female body condition during the breeding season. Climate change induced shifts in temperature may be inversely influencing the timing of turkey nesting; for example, warmer temperatures in late winter and early spring may cause nesting to occur earlier. Additionally, timing of spring green-up has already shifted earlier throughout much of the southeastern U.S. [57,75]. Although overall green-up trends have become progressively earlier, the timing of turkey nesting may not precisely parallel temporal changes in green-up. If the timing of green-up and turkey nesting is mismatched, sufficient cover and food may not be available to support sustainable reproduction. Temperatures are expected to become more variable across most of the planet. Increased temperature variability during spring has been anecdotally associated with delayed turkey nesting [87], but quantitative analysis is needed to assess whether data support this anecdotal assertion.

Anecdotal evidence indicated turkeys modify nesting phenology to align with wet periods and avoid dry periods [73], which may be done to target resource pulses. Wet weather facilitates plant growth, which provides vegetative forage and harbors invertebrates as food for reproductive females [29,51]. Increased plant growth also provides cover for females and their nests [42,43,51]. However, whether rainfall immediately prior to nesting is most important in determining the timing of nesting, or whether a lag effect results from the time it takes plants to respond to rainfall, is unknown. The southeastern U.S. is expected to experience shifts in rainfall distribution and intensity under climate change projections [12,79], so shifts in the timing of turkey nesting would be expected.

We used relatively long-term (eight years) and large-scale (five states across the southeastern U.S.) wild turkey nesting data to investigate purported connections between climate change and turkey nest initiation date (the date when incubation began). Our objective was to determine whether spring green-up timing, temperature and temperature variability prior to nesting, or rainfall prior to nesting explained turkey nest initiation date. We predicted that (1) nest initiation date would track the onset of warmer spring temperatures but not spring green-up, (2) increased rainfall immediately prior to nesting would result in later nest initiation, and (3) increased temperature variability would result in later nest initiation.

Materials and methods

Study sites

We used data collected from 13 study sites, including publicly and privately-owned properties, distributed across five states in the southeastern U.S. (Fig. 1). Data collection spanned 2014 to 2021, but research duration at individual sites varied from 1 to 7 years. Descriptions of the 13 study sites follow:

- The southern management section of Angelina National Forest (ANF; research year: 2017) in east Texas was 18,751-ha. The site was dominated by longleaf pine (*Pinus palustris*) forests with <5% of the forest composed of open land cover types (e.g., pasture, hay fields), and prescribed fire was applied on a 2–3 year burn interval.
- The 105,545-ha Fort Polk Wildlife Management Area (FPO; research year: 2020) in west-central Louisiana was jointly owned by the U.S. Department of Defense and the U.S. Forest Service (Kisatchie National Forest) and managed by the Louisiana Department of Wildlife and Fisheries. The site was dominated by longleaf pine, loblolly pine (*P. taeda*), shoftleaf pine (*P. echinata*), slash pine (*P. elliottii*), and mixed-oak (*Quercus* spp.) forests, bottomland hardwoods, and forest openings [97]. Prescribed fire was applied to pine-dominated uplands on a 3–5 year return interval.
- Within Kisatchie National Forest (KNF; research years: 2014–2015, 2017–2020) in west-central Louisiana we monitored turkeys in the Catahoula, Kisatchie, and Winn Ranger Districts; three of the five disjunct districts that compose KNF. These districts spanned 158,030-ha of U.S. Forest Service property. The site was dominated by longleaf pine, bluejack oak (*Q. incana*), blackjack oak (*Q. marilandica*), and post oak (*Q. stellata*) in upland areas, loblolly pine and mixed-oak (*Quercus* spp.) forests, bottomland hardwoods, and forest openings. Prescribed fire was applied to pine-dominated uplands on a 3–5 year return interval.

Fig. 1. Location of eastern wild turkey (*Meleagris gallopavo silvestris*) study sites and study areas across the southeastern U.S. We grouped study sites into study areas to account for spatial clustering of data.

- The 30,071-ha Peason Ridge Wildlife Management Area (PRI; research years: 2016–2018) in west-central Louisiana was owned by the U.S. Department of Defense and managed by the Louisiana Department of Wildlife and Fisheries. The dominant species were longleaf pine, loblolly pine, and shortleaf pine interspersed with bluejack oak, blackjack oak, and post oak. Open, early-successional areas were common. Prescribed fire was applied to pine-dominated uplands on a 3–5 year return interval.
- Florida Parishes (FLP; research years: 2020–2021) in southeastern Louisiana was composed of private lands and the 1496-ha Sandy Hollow Wildlife Management Area, which were dominated by loblolly pine, longleaf pine, bottomland hardwood, and mixed pine-hardwood forests, hay fields, and cattle pastures. Prescribed fire was applied in longleaf pine-dominant areas on a 3–5 year return interval.
- The 3723-ha Silver Lake Wildlife Management Area (SLA; research years: 2015–2016) in southwest Georgia was owned and managed by the Georgia Department of Natural Resources. The site was dominated by longleaf, loblolly, and slash pines (*Pinus elliottii*) and lowland oak forests [95]. Prescribed fire was applied on a 2–3 year return interval.
- The 4613-ha B. F. Grant Wildlife Management Area (BFG; research years: 2017–2020) in central Georgia was co-managed by the Georgia Department of Natural Resources – Wildlife Resources Division and the Warnell School of Forestry and Natural Resources at the University of Georgia. The site was dominated by loblolly pine, mixed hardwood, and mixed pine forests and hay fields. Prescribed fire was not routinely applied.
- The 15,873-ha Cedar Creek Wildlife Management Area (CCR; research years: 2017–2020) in central Georgia was co-managed by the Georgia Department of Natural Resources and the U.S. Forest Service. The site was dominated by loblolly pine, mixed pine, mixed hardwood, and bottomland hardwood forests. Prescribed fire was applied on a 3–5 year return interval.
- The 25,900-ha Webb Wildlife Management Area Complex (WEB; composed of Hamilton Ridge, Palachucola, and Webb Wildlife Management Areas; research years: 2015–2018) was managed by the South Carolina Department of Natural Resources. The site was dominated by longleaf, loblolly, and slash pine forests, and bottomland hardwoods. Prescribed fire was applied on a 3–5 year return interval.
- The 78,000-ha Savannah River Site (SRS; research year: 2021) in southern South Carolina along the Savannah River was a U.S. Department of Energy National Environmental Research Park. The SRS received the least hunting pressure of any site, permitting 24 hunters for a one-day fall hunt. The site was dominated by longleaf, loblolly, and slash pine, bottomland hardwood, and cypress (*Taxodium distichum*)-tupelo (*Nyssa aquatic* and *N. sylvatica* var. *biflora*) forests [5]. Prescribed fire was applied on a 3–10 year return interval.
- The North Carolina mountains (NCM; research years: 2020–2021) study site included 83 private properties in Mitchell, Avery, Madison, Yancey, and McDowell counties and had the most variable elevation of any study site (500–1800 m). Land cover predominantly was pine-hardwood forest with dense understory of mountain laurel (*Kalmia latifolia*) and great rhododendron (*Rhododendron maximum*), and cool-season grass pastures.
- The North Carolina Piedmont (NCP; research years: 2020–2021) study site included 63 private properties in Moore County and land cover was pine plantations, mixed hardwood forest, row-crop agriculture, and poultry and swine production facilities.
- The North Carolina coastal plain (NCC; research years: 2020–2021) study site included 52 private properties in Sampson, Duplin, and Bladen counties and land cover was mixed hardwood-pine forest, poultry and swine production, row-crop agriculture, and warm-season grass pastures.

Nesting phenology

We used rocket nets to capture female wild turkeys January-March 2014–2021. We radio-tagged captured turkeys with very high frequency (VHF) backpack global positioning system (GPS) transmitters [28] produced by Biotrack (Wareham, Dorset, United Kingdom). From 1 March to 1 September, transmitters collected one location per night at 23:59 and hourly locations each day from 0500 to 2000 until the battery died or the transmitter was recovered [17]. We released turkeys at the point of capture following processing. Trapping and handling procedures were approved by the Institutional Animal Care and Use Committees at the University of Georgia (protocols A2014 06-008-Y1-A0 and A3437-01), Louisiana State University (protocol A2014-013, A2015-07, A2018-13, and A2021-14) and North Carolina State University (protocol 19-739-O).

We downloaded the GPS data for each female ≥1 time per week and determined when locations became focused around a single point, which was an indicator of nest incubation initiation [96,97], We were able to identify termination of incubation behavior when the female's GPS locations no longer were clustered at the nest site. Once the female quit incubating or the nest reached the end of the 28-day incubation period, we inspected the nest site to determine if eggs hatched [19,96,97). We classified a nest as failed when no eggs hatched, there were signs of crushed eggshells, or there were no eggshells present; a successful hatch was indicated by the presence of pipped eggshells [13]. Because we were interested in how weather and spring green-up influenced nest initiation timing, we only included each individual's first nesting attempt in a given year.

Weather and plant phenology

We used weather data available for 2014–2021 to determine whether annual variation in spring temperature, rainfall, and spring green-up influenced turkey nest initiation date. We obtained gridded daily high and low temperature and total rainfall data with a 4-km resolution, the finest scale available for the spatial and temporal extent of the project, from gridMET [1]. We calculated average maximum temperature and total precipitation for January, February, and March of the nesting year for each nest location. We then calculated the variance of monthly maximum temperatures using the var function in program R (version 4.1.2; [61]). Finally, we calculated the total precipitation in the 30 days prior to incubation initiation.

We used the start of growing season attribute from the C6 Eastern CONUS eMODIS RSP dataset as a surrogate for spring green-up for 2014–2020 [77]. These data are a derived product of the Aqua MODIS C6 NDVI data with 250-m resolution [85]. We used the start of growing season attribute from the Earth Resources Observation and Science (EROS) Visible Infrared Imaging Radiometer Suite (eVIIRS) remotely sensed phenology dataset with 375-m resolution for 2021 because it replaced the C6 Eastern CONUS eMODIS RSP dataset, which was discontinued at the end of 2020. We used bilinear interpolation to rescale the 250-m resolution 2014–2020 data to 375-m resolution, which matched the resolution of the 2021 data. We extracted the start of the growing season date associated with each nest location.

Statistical analysis

Effects of weather on nesting phenology

We investigated associations between temperature, rainfall, and spring green-up and turkey nest initiation date using Cox proportional hazards models [21]. Proportional hazards models have been used to investigate time-to-event scenarios including changes in reproductive phenology [6,45,91]. To determine if weather and green-up influenced successful nests differently than all nests, we created a subset of only successful nests (successfully hatched dataset).

Average daily maximum January temperature was excessively correlated (absolute Pearson correlation coefficient > 0.6) with average daily maximum temperature in February and March for both the full and successfully hatched datasets, and therefore could not be included in the same model. To avoid including the two correlated variables in the same model, we built two semi-global models for each dataset, one containing all 11 fixed effect variables (Table 1) except average daily maximum January temperature and the other containing all 11 fixed effect variables except average daily maximum February and March temperatures. We calculated the Variance Inflation Factor (VIF) for each model to assess multicollinearity and determined that VIF was below the threshold of 5, above which excessive collinearity exists [47]. We then fit the two semi-global Cox proportional hazards models for each dataset. We ran Cox proportional hazards models in the survival package (version 3.2–13) in program R via RStudio [70]. The Cox proportional hazards model enabled us to account for spatial non-independence of nests by using a frailty model, a commonly used approach to handle random effects [16,41,88]. In a frailty model, the random effect is assumed to have a multiplicative effect on the baseline hazard function. We used this approach as a way to capture similarities among nests initiated at the same study area (i.e., spatial random effect; Fig. 1) that were not explained by our measured covariates. We considered variables with 95% confidence intervals (CIs) that did not overlap zero to be significant predictors of turkey nest initiation date. The full dataset model containing average daily maximum January temperature failed to converge except when the variance of daily maximum temperature in February variable was removed. Therefore, we removed variance of daily maximum temperature in February from this single model and reran the model.

Table 1
Description and abbreviation of variables included in Cox proportional hazards models used to investigate how weather, vegetation, and spring green-up were associated with incubation timing of 717 eastern wild turkey (*Meleagris gallopavo silvestris*) nests in the southeastern United States between 2014 and 2021.

Variable Abbreviation	Description
Max Avg Temp Jan	Average daily maximum January temperature. Spatial resolution: 4 km.
Max Avg Temp Feb	Average daily maximum February temperature. Spatial resolution: 4 km.
Max Avg Temp March	Average daily maximum March temperature. Spatial resolution: 4 km.
Max Temp Var Jan	Variance of daily maximum January temperature. Spatial resolution: 4 km.
Max Temp Var Feb	Variance of daily maximum February temperature. Spatial resolution: 4 km.
Max Temp Var March	Variance of daily maximum March temperature. Spatial resolution: 4 km.
Precip Jan	Total January precipitation. Spatial resolution: 4 km.
Precip Feb	Total February precipitation. Spatial resolution: 4 km.
Precip March	Total March precipitation. Spatial resolution: 4 km.
Precip Total 30 Prior	Total precipitation in 30 days prior to nest initiation. Spatial resolution: 4 km.
Spring Green-up	Ordinal date of the start of the growing season. Spatial resolution: 375 m.
Study Area	Grouping of study sites based on close proximity.

Future implications of climate change for turkey nesting phenology

To understand potential implications of future climate change projections for eastern wild turkey nesting phenology, we projected changes in nest initiation date as a function of changes in climate for each of the four models. For each of the two semi-global full dataset models and the two semi-global successfully hatched dataset models, we investigated two greenhouse gas forcing scenarios (Representative Concentration Pathway [RCP] 4.5 and RCP 8.5) that bounded a wide range of possible outcomes [35]. We obtained climate projection data from the 20 models in the Multivariate Adaptive Constructed Analogs (MACA) Coupled Model Inter-Comparison Project Phase Five (CMIP5) ensemble [1,30, 82] for variables revealed to be significant by the Cox proportional hazards models (January precipitation, March precipitation, total precipitation in the 30 days prior to nest initiation, and variance of daily maximum temperature in February). We selected the MACA CMIP5 dataset because it was trained using the gridMET data we used in the Cox proportional hazards models, which eliminates issues caused by incorporating datasets created using different methodologies. We obtained RCP 4.5 and RCP 8.5 projection data with a 4-km resolution for each year 2041–2060 at each nest site. We focused on the significant variables because there was not climate projection data available for all of the variables we used in the original analysis. Although it would be ideal to have projected climate data for every variable in our analysis, we believe this has limited effect on our projections since the effect sizes were small and the uncertainty was large for the non-significant variables. For each of the four datasets and models (2 semi-global models for full dataset and successfully hatched dataset), we projected nest initiation date using the fitted model and under the two climate scenarios (RCP 4.5 and RCP 8.5) wherein non-significant variables were held at their observed mean. For ease of interpretation, we present results from the projections in terms of the number of days earlier or later turkey nesting would shift for each climate scenario and for the full dataset and the successfully hatched dataset.

Results

Effects of weather on nesting phenology

The full dataset included 717 nests and the successfully hatched dataset included 186 nests. The timing of nesting and spring green-up varied among years in the dataset (Fig. 2). In the full dataset, the first nest occurred on ordinal day 71, the last nest occurred on ordinal day 186, and the mean date was ordinal day 110 (Fig. 3). Analysis of the full dataset revealed two statistically significant relationships that were present in both semi-global models. Greater total January rainfall was associated with earlier nesting (full dataset Model 1: $\widehat{\beta} = 0.007$, 95% CI $= 0.004$ to 0.009; Model 2: $\widehat{\beta} = 0.007$, 95% CI $= 0.003$ to 0.011; Table 2). Each 10 cm increase in January rainfall was associated with nesting occurring 0.67 to 0.69 days earlier (full dataset Model 1 and 2, respectively; Table 2). Greater total precipitation in the 30 days prior to nest initiation was associated with later nesting (full dataset Model 1: $\widehat{\beta} = -0.002$, 95% CI $= -0.003$ to -0.0005; Model 2: $\widehat{\beta} = -0.002$, 95% CI $= -0.004$ to -0.001). Each 10 cm increase in precipitation was associated with nesting occurring 0.17 to 0.24 days later (full dataset Model 1 and 2, respectively; Table 2). No other variable, including spring green-up, was a significant predictor of turkey nest initiation date in the full dataset.

Analysis of the successfully hatched dataset revealed two statistically significant relationships that were present in both semi-global models. Greater daily maximum temperature variance in February was associated with later nesting (successfully hatched dataset Model 1: $\widehat{\beta} = -0.022$, 95% CI $= -0.039$ to -0.005; Model 2: $\widehat{\beta} = -0.019$, 95% CI $= -0.037$ to -0.001; Table 3). Each one unit of variance increase was associated with nesting occurring 0.02 days later (results were consistent for successfully hatched dataset Model 1 and 2; Table 3). Greater total March rainfall was associated with earlier nesting (successfully hatched dataset Model 1: $\widehat{\beta} = 0.007$, 95% CI $= 0.003$ to 0.011; Model 2: $\widehat{\beta} = 0.006$, 95% CI $= 0.002$ to 0.010; Table 3). Each 10 cm increase in March rainfall was associated with nesting occurring 0.62 to 0.68 days earlier (successfully hatched dataset Model 2 and 1, respectively; Table 3). No other variable included in semi-global models, including spring green-up, was a significant predictor of nest initiation date in the successfully hatched dataset.

Future implications of climate change for turkey nesting phenology

Average observed January precipitation was 13.16 cm. Average projected January precipitation for 2041–2060 for RCP 4.5 was 11.86 cm and for RCP 8.5 was 12.27 cm (minimum single-year average: 10.67 cm; maximum single-year average: 14.73 cm). Based on the full dataset models and projected future changes in January precipitation for 2041–2060 (Fig. 4), nest initiation could shift later by 0.09 days (independent estimate for both semi-global models) under RCP 4.5 or later by 0.06 days (independent estimate for both semi-global models) under RCP 8.5.

Average observed total precipitation in the 30 days prior to nest initiation was 12.46 cm. Average projected total precipitation in the 30 days prior to nest initiation for 2041–2060 for RCP 4.5 was 11.02 cm (minimum single-year average: 8.78 cm; maximum single-year average: 13.47 cm) and for RCP 8.5 was 10.91 cm (minimum single-year average: 9.28 cm; maximum single-year average: 13.61 cm). Based on the full dataset models and projected future changes in total precipitation in the 30 days prior to nest initiation for 2041–2060 (Fig. 4), nest initiation could shift earlier by 0.02 to 0.03 days (range of semi-global models) under RCP 4.5 or earlier by 0.03 to 0.04 days (range of semi-global models) under RCP 8.5. Cumulatively, the two predictors of nest initiation date using the full dataset indicate nest initiation could occur 0.06 to 0.07 days later (range of semi-global models) under RCP 4.5 or 0.02 to 0.03 days later (range of semi-global models) under RCP 8.5 during 2041–2060.

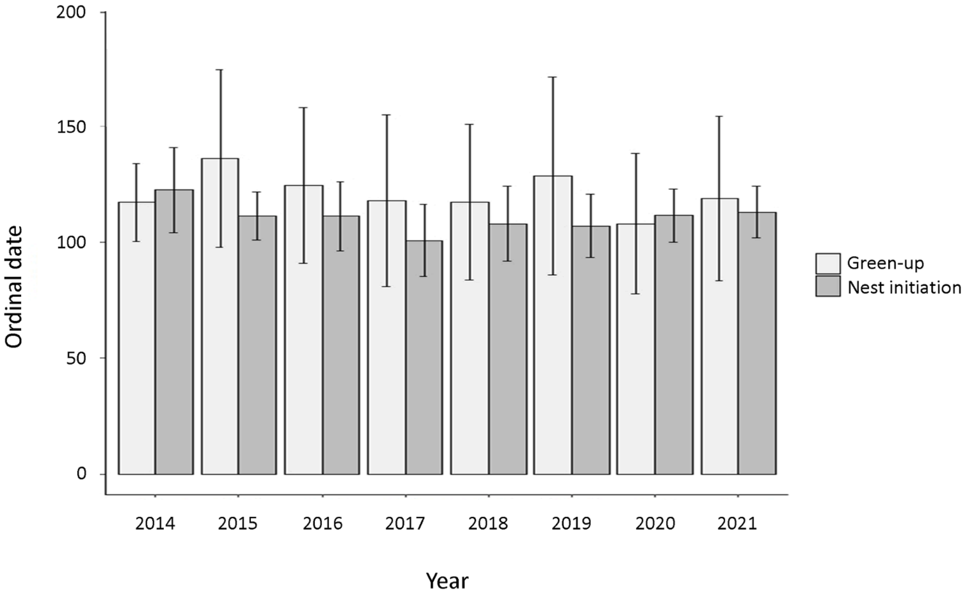

Fig. 2. Variation in eastern wild turkey nest initiation date (the date when incubation began) and spring green-up date at each nesting site for 717 nests monitored 2014–2021. Bars depict means and black vertical lines depict 95% confidence intervals.

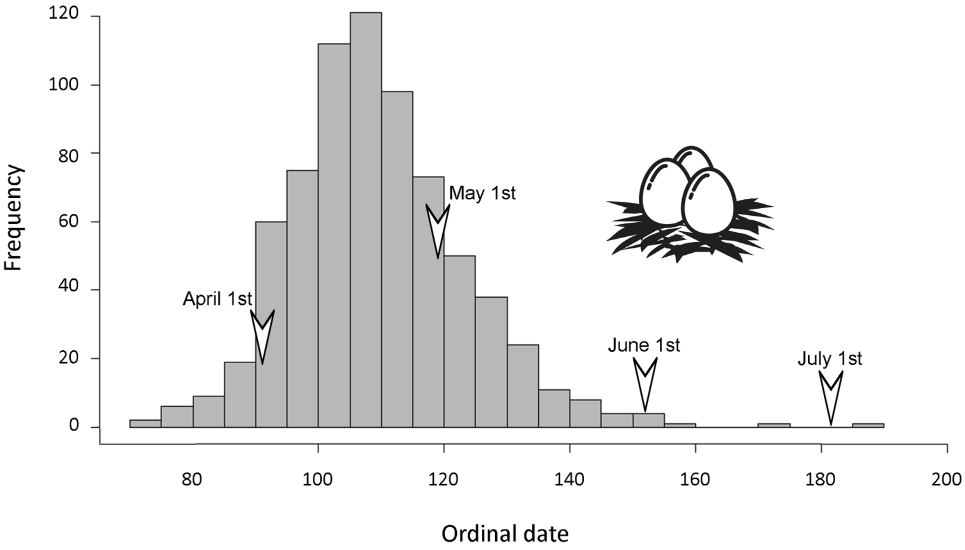

Fig. 3. Distribution of eastern wild turkey nest initiation dates (date when incubation began) in the dataset of 717 nests monitored 2014–2021. The first nest occurred on ordinal day 71, the last nest occurred on ordinal day 186, and the mean date was ordinal day 110.

Table 2

. Beta estimates ($\widehat{\beta}$) and 95% confidence intervals (95% CI) for variables included in the two semi-global models used to investigate how weather, vegetation, and spring green-up were associated with incubation timing in 717 eastern wild turkey (*Meleagris gallopavo silvestris*) nests in the southeastern United States between 2014 and 2021. Significant associations are in bold. Detailed variable descriptions are in Table 1.

Variable	$\widehat{\beta}$ (Model 1)	95% CI (Model 1)	$\widehat{\beta}$ (Model 2)	95% CI (Model 2)
Max Avg Temp Jan	−0.037	−0.099 – 0.024		
Max Avg Temp Feb			0.047	−0.025 – 0.119
Max Avg Temp March			−0.028	−0.099 – 0.043
Max Temp Var Jan	0.009	−0.002 – 0.020	0.002	−0.017 – 0.021
Max Temp Var Feb			0.009	−0.002 – 0.020
Max Temp Var March	−0.009	−0.020 – 0.003	−0.010	−0.025 – 0.006
Precip Jan	**0.007**	**0.004 – 0.009**	**0.007**	**0.003 – 0.011**
Precip Feb	−0.0008	−0.002 – 0.0004	−0.001	−0.002 – 0.0006
Precip March	−0.0007	−0.002 – 0.0008	−0.0004	−0.002 – 0.001
Precip Total 30 Prior	**−0.002**	**−0.003 – −0.0005**	**−0.002**	**−0.004 – −0.001**
Spring Green-up	0.0004	−0.002 – 0.003	0.0003	−0.002 – 0.003

Table 3

Beta estimates ($\widehat{\beta}$) and 95% confidence intervals (95% CI) for variables included in two semi-global models used to investigate how weather, vegetation, and spring green-up were associated with incubation timing in 186 successfully hatched eastern wild turkey (*Meleagris gallopavo silvestris*) nests in the southeastern United States between 2014 and 2021. Detailed variable descriptions are in Table 1.

Variable	$\widehat{\beta}$ (Model 1)	95% CI (Model 1)	$\widehat{\beta}$ (Model 2)	95% CI (Model 2)
Max Avg Temp Jan	0.067	−0.006 – 0.139		
Max Avg Temp Feb			0.046	−0.044 – 0.136
Max Avg Temp March			0.023	−0.064 – 0.110
Max Temp Var Jan	0.007	−0.009 – 0.023	0.002	−0.018 – 0.023
Max Temp Var Feb	**−0.022**	**−0.039 – −0.005**	**−0.019**	**−0.037 – −0.001**
Max Temp Var March	0.015	−0.005 – 0.035	0.018	−0.005 – 0.041
Precip Jan	0.002	−0.002 – 0.006	0.003	−0.001 – 0.007
Precip Feb	−0.001	−0.004 – 0.002	−0.001	−0.004 – 0.002
Precip March	**0.007**	**0.003 – 0.011**	**0.006**	**0.002 – 0.010**
Precip Total 30 Prior	−0.001	−0.004 – 0.001	−0.001	−0.003 – 0.001
Spring Green-up	0.003	−0.001 – 0.007	0.003	−0.001 – 0.007

Average observed March precipitation was 11.17 cm. Average projected March precipitation for 2041–2060 for RCP 4.5 was 12.05 cm (minimum single-year average: 8.57 cm; maximum single-year average: 14.55 cm) and for RCP 8.5 was 12.36 cm (minimum single-year average: 10.42 cm; maximum single-year average: 15.09 cm). Based on the successfully hatched dataset models and projected future changes in March precipitation for 2041–2060 (Fig. 5), initiation of successful nests could shift 0.05 to 0.06 days earlier (range of semi-global models) under RCP 4.5 or 0.07 to 0.08 days earlier (range of semi-global models) under RCP 8.5.

Average observed variance of daily maximum temperature in February was 27.59. Average projected variance of daily maximum temperature in February for 2041–2060 for RCP 4.5 was 28.45 (minimum single-year average: 25.38; maximum single-year average: 32.28) and for RCP 8.5 was 27.91 (minimum single-year average: 24.87; maximum single-year average: 34.82). Based on the successfully hatched models and projected future changes in variance of daily maximum temperature in February for 2041–2060 (Fig. 5), initiation of successful nests could shift 0.02 days later (independent estimate for both semi-global models) under RCP 4.5 or 0.06 to 0.07 days later (range of semi-global models) under RCP 8.5. Cumulatively, the two predictors of nest initiation date using the successfully hatched dataset indicate nest initiation could occur 0.03 to 0.04 days earlier (range of semi-global models) under RCP 4.5 or 0.00 to 0.02 days earlier (range of semi-global models) under RCP 8.5 during 2041–2060.

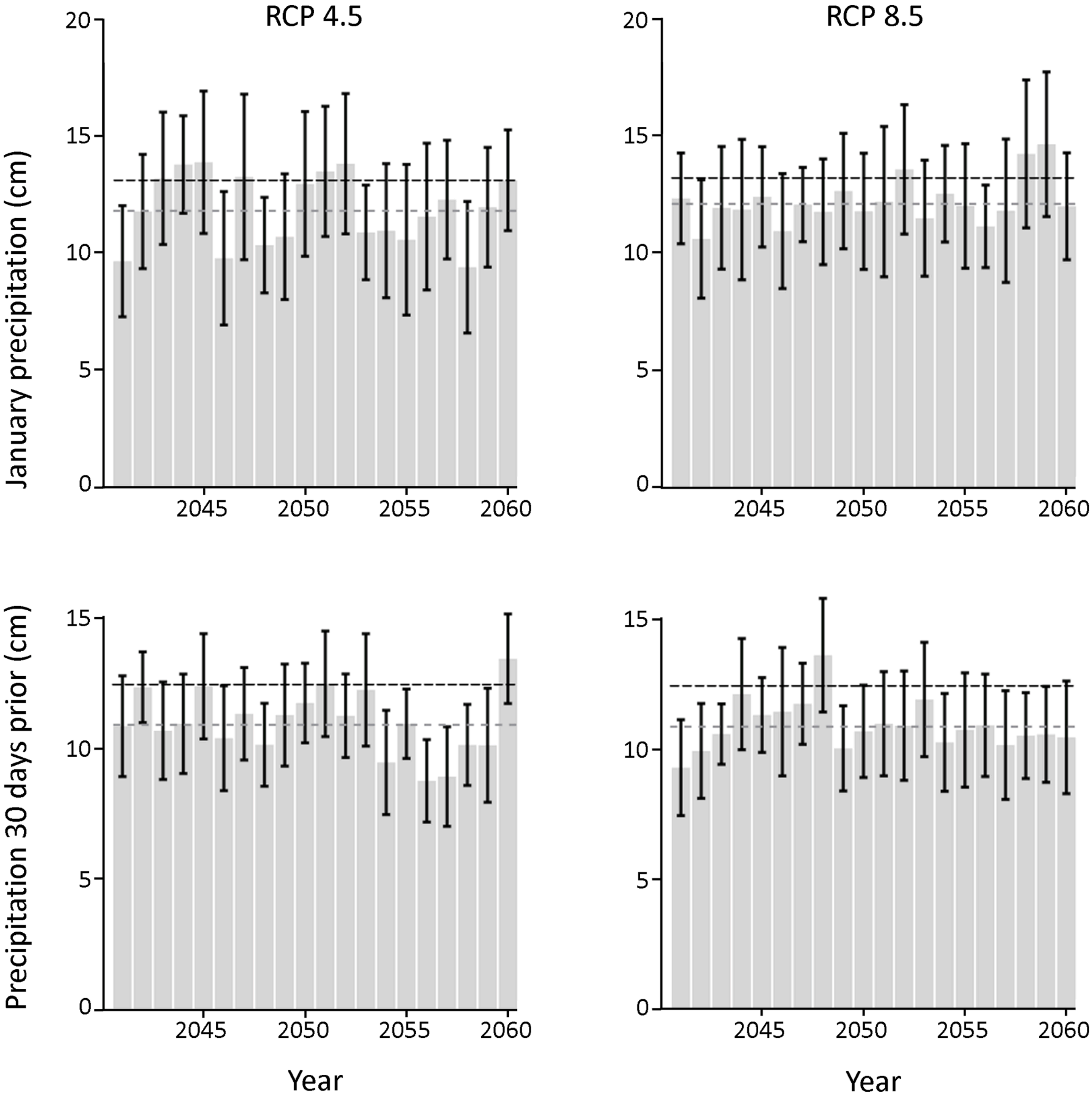

Fig. 4. Climate projection data from 2041 to 2060 obtained from the 20 models in the MACA CMIP5 ensemble for variables revealed to be significant (total January precipitation and total precipitation in the 30 days prior to nest initiation) in semi-global Cox proportional hazards models using the full dataset. We extracted climate data for each of the 717 nest locations included in the Cox proportional hazards models. Gray bars depict annual mean values, black vertical lines depict 95% confidence intervals, black dashed horizontal lines depict mean observed values the year each nest was monitored (2014–2021), and the gray dashed horizontal lines depict mean projected values across the 717 nest locations between 2041 and 2060.

Discussion

The influence of climate change on the reproductive phenology of wildlife has garnered substantial attention in recent years [72,90]. However, few studies have used long-term data gathered across large spatial scales, limiting their generalizability and power to inform management. Here, we used data collected over eight years from across the southeastern U.S. to investigate associations between climate change and eastern wild turkey nesting phenology. Although nest initiation date was variable among years, individual weather variables that predicted wild turkey nest initiation date accounted for less than one day of predicted change to nest initiation date between the data collection period (2014–2021) and the climate projection period (2041–2060). We perceive this to indicate that eastern wild turkey nest initiation date in the southeastern United States was relatively unresponsive to the investigated weather metrics and will also be relatively unresponsive to these metrics as they relate to climate change through 2060.

Counter to our prediction, nest initiation did not occur earlier in years or at locations with warmer temperatures preceding nesting. Conversely, in Virginia and West Virginia early onset of warm temperatures preceded nest initiation by ~30 days [52]. The disparity from our results may relate to snow, which was uncommon within our study area, but in Norman et al. [52] increased snow depth was associated with later nest initiation date. This indicates snow depth, not solely temperature, may have been the causal mechanism in Norman et al. [52]. Additionally, temperature may be less relevant to populations in temperate

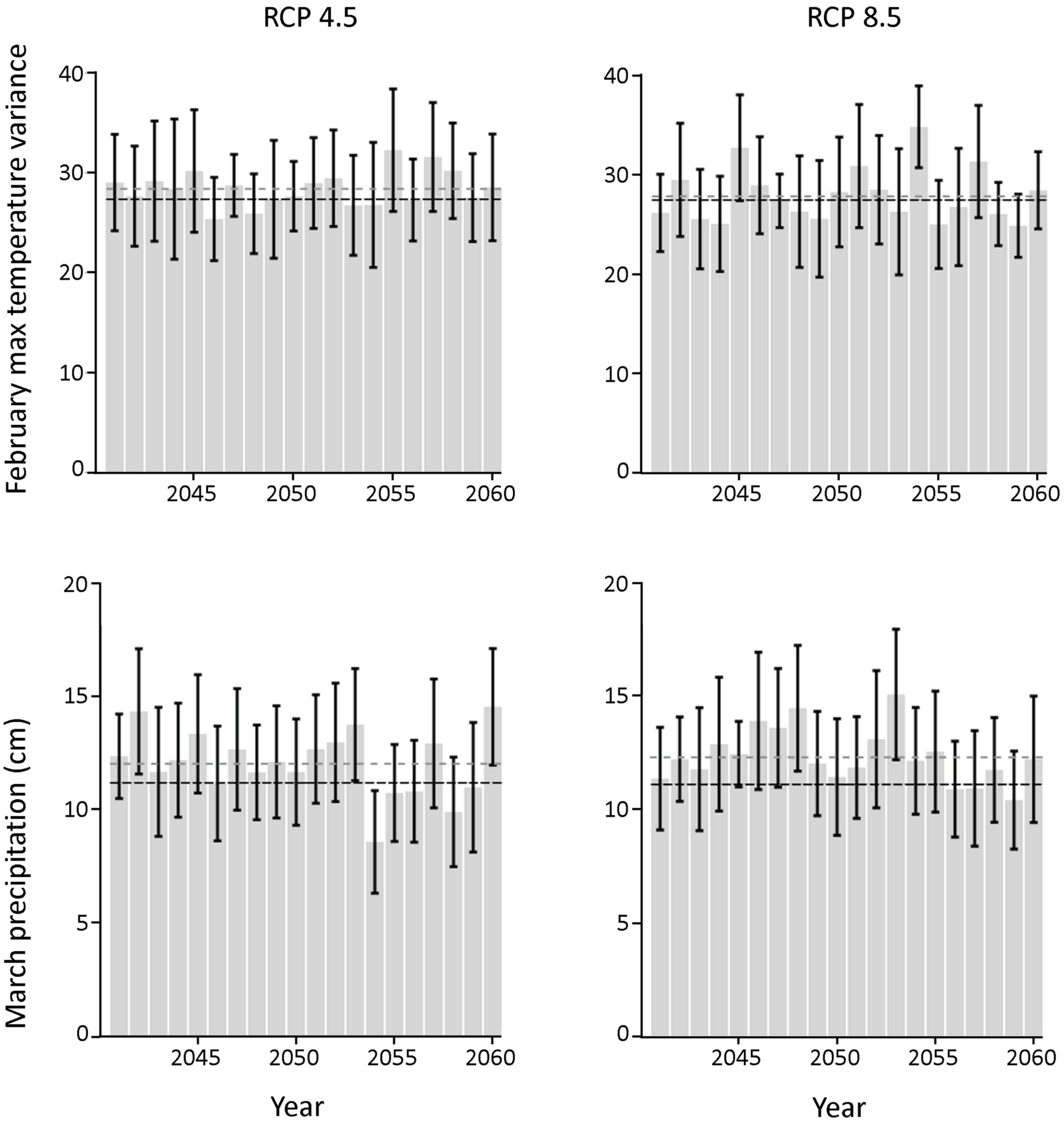

Fig. 5. Climate projection data from 2041 to 2060 obtained from the 20 models in the MACA CMIP5 ensemble for variables revealed to be significant (total March precipitation and variance of daily maximum temperature in February) in semi-global Cox proportional hazards models using the successfully hatched dataset. Climate data pertain to all 717 nest locations, not just the 186 successful nest locations, to increase the robustness of the sample. Gray bars depict annual mean values, black vertical lines depict 95% confidence intervals, black dashed horizontal lines depict mean observed values the year each nest was monitored (2014–2021), and the gray dashed horizontal lines depict mean projected values across the 186 successful nest locations between 2041 and 2060.

regions where spring temperatures are likely well within the thermal tolerance of turkeys, which range >1000 km farther north to central Maine [26] and whose close relative the Osceola turkey (*M. g. osceola*) occurs >350 km farther south in southern Florida [24].

The prediction that greater rainfall immediately prior to nesting would result in delayed nesting was supported. However, the relatively small effect size (0.17 – 0.21 day delay per 10 cm increase in total rainfall in the 30 days preceding nest initiation) indicated that even extreme rain events in the 30 days preceding nest initiation would minimally delay nest initiation date. Inability to delay nesting during periods of high rainfall could negatively affect recruitment given the suspected negative association between rainfall and wild turkey nest success. However, previous studies asserting a relationship between rainfall and nest success either reported a relationship that was not backed by their own analyses [68] or reported a relationship for a variable that was first introduced in the results and never described, making the study non-reproducible [67]. Inversely, in a drier, colder climate at the subspecies northwestern range limit, Tyl et al. [84] showed that daily nest survival was positively associated with increased rainfall. Additional investigation of the relationship between rainfall and nest success is needed. The projected rainfall data that we used indicated reduced future total rainfall during the breeding season, but climate projections indicate the intensity of future rainfall within individual rain events will likely increase even if total rainfall decreases [25,79], increasing the probability of nest failure if purported relationships between rainfall and nest success are valid.

Greater rainfall in the months prior to nesting, specifically January and March, was associated with earlier nesting. Elevated pre-nesting precipitation increases soil moisture, which could increase the magnitude of the resource pulse associated with spring green-up. This resource pulse includes vegetation that provides forage and cover and is associated with increased abundance of invertebrates, an important food source [29,32,33,48]. However, our study indicated that turkeys do not time nesting to align with spring green-up, and evidence linking invertebrate food availability to nest timing does not currently exist, so any potential relationship at present is speculative.

We documented support for the prediction that increased temperature variability would be associated with later turkey nesting. The increased physiological demands associated with more variable temperatures likely make these conditions less desirable for nesting. Increased future temperature variability in the projected dataset could lead to later timing of turkey nesting, but the implications for nest success are unknown. Extreme high temperatures associated with greater variance have caused offspring mortality in avian species inhabiting arid climates where desiccation is a threat [86], but desiccation-induced mortality is less likely in the southeastern U.S. where rainfall and surface water are more abundant. Extreme low temperatures associated with greater variance are a more plausible driver of potential nest failure, but this relationship requires further assessment for wild turkeys at the northern edge of their range.

Successfully hatched nests were most responsive to conditions in February. Specifically, greater maximum temperature variance was associated with later nest initiation date. Therefore, February maximum temperature variance but not rainfall appeared to have a greater impact on nesting phenology related to successfully hatched nests. Interestingly, temperature itself was not a good predictor of nest initiation date in either dataset. Instead, January rainfall and rainfall in the 30 days prior to nest initiation best accounted for variable nest initiation dates. These datasets included nest initiation date outliers which all produced failed nests, indicating rainfall may have been a more important factor for early and/or late nesters.

The breeding phenology of eastern wild turkeys across the southeastern United States varied considerably over the course of this study, as did spring green-up. However, nesting phenology did not track changes in timing of spring green-up, and the implications of this mismatch for turkey population recruitment are unknown. If the early-spring occurrence of turkey reproduction was historically timed to coincide with a resource pulse from green-up, this mismatch could already be negatively affecting offspring survival. Nest and poult survival are the greatest determinants of turkey population change [59], and therefore mismatch could be driving declines. In the absence of a known cause of the declines, agencies have taken measures to prevent or reverse future declines. Attempted strategies have included reducing bag limits, shortening hunting seasons, and shifting hunting seasons to later in the spring when hunting is less likely to disrupt breeding [14, 36].

Climate change has resulted in a mismatch between resource availability and arrival of offspring in numerous species across the globe [38], including close taxonomic relatives of turkeys (e.g., rock ptarmigan (*Lagopus muta*); [94]). Offspring mortality [63,76] and reduced offspring body condition [2,71] are products of breeding phenology that failed to track temporal changes in peak resource availability. However, relationships regarding mismatch between peak resource availability and offspring arrival are complex and mismatches do not inherently produce negative outcomes for offspring [89]. Understanding how or whether the eastern wild turkey's inelastic breeding phenology influences breeding success is vital to the management of this important game species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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