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Modeling Onset of Hourly Nesting Activity in a Freshwater Turtle Using Abiotic Variables and Physiological Capacity

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ABSTRACT.—**Nesting is an essential, yet variable, reproductive behavior in most oviparous organisms. Although many factors conceivably influence nesting behaviors, it is unclear which factors strongly influence terrestrial nest timing in aquatic nonavian reptiles. As climate is changing rapidly, understanding the relative influences of biotic and abiotic factors on nesting behaviors may yield important information on future changes in daily and seasonal nesting activity. We collected hourly data to examine the significance of local weather conditions to the timing of within-season nesting activity in a large population of Painted Turtles (*Chrysemys picta*). We quantified nesting activity as the ratio of females who nested to all females who could nest in each hour, adjusting the size of the denominator to include the time required to shell a subsequent egg clutch. We then used zero-inflated models to identify potential weather predictors of presence/absence of nesting activity and strength of nesting responses (i.e., the fraction of turtles nesting that could nest). Higher temperatures and rainfall predicted stronger nesting responses, whereas lower temperatures and no rainfall predicted the absence of nesting activity, indicating that both temperature and rainfall are important cues in within-season nesting phenology. Our study enhances our understanding of abiotic influences on the terrestrial nesting behavior of aquatic organisms.**

The timing of reproductive events is essential to organismal fitness. Survival of offspring is conditional upon successful synchrony of reproductive events with environmental factors, such as resource availability or temperature (Weatherhead, 2005; McKinnon et al., 2012; Shiao et al., 2015). Thus, environmental conditions can influence timing of reproductive events (Schaper et al., 2001; Cresswell and Mccleery, 2003; Visser and Both, 2005). For example, photoperiod affects reproductive seasons in spotted antbirds (Wikelski et al., 2000), and rain stimulates breeding patterns in several species of Darwin's finches in the Galápagos (Boag and Grant, 1984) as well as timing of reproductive seasons in scincid lizards and Keelback Snakes (James, 1991; Brown and Shine, 2006). Some sea turtles seem to adjust daily nesting behavior to avoid lethally high temperatures (Spotila et al., 2017). Therefore, the timing of nesting is conceivably under strong selection. Identifying the factors that influence such timing is thereby important for understanding patterns of reproductive behavior in oviparous species.

Potential abiotic influences on onset of nesting seasons and daily nesting activity are numerous but unclear in their degree of impact. Many empirical studies suggest that bird fecundity changes with latitude as a function of changes in resource availability during breeding seasons, accompanying seasonality differences (Ashmole, 1963; Pincheira-Donoso and Hunt, 2017; but see Rose and Lyon, 2013). Fall temperatures experienced by Painted Turtles correlate with clutch frequency in following summers, as females can allocate energy to follicles over successive seasons (Congdon and Tinkle, 1982), suggesting reproductive output is tied to heat balance (Rollinson and Brooks, 2007). In northern climates in particular, selection may exert pressure for earlier nesting seasons in the spring to ensure sufficient incubation time before winter (Obbard and Brooks, 1981). Temperature is important for nesting across ectothermic species. Sufficient thermal energy is required to finish nesting (Christens and Bider, 1987; Congdon et al., 1987; Bowen et al., 2005), and high temperatures can decrease nest construction time (Christens and Bider, 1987; Frye et al., 2017).

Reports about the effects of rainfall on nesting vary across taxa. Rainfall is often correlated with temperature (Shukla and Misra, 1977; Nicholson and Entekhabi, 1987). Changes in rainfall could potentially affect temperature cues for organisms. High-intensity rainfall events stimulate nesting initiation in some bird species and in Collared Iguanas (Grant and Grant, 1989; Lloyd, 1999; Randriamahazo and Mori, 2001). Nesting during or after rainfall offers benefits for terrestrially nesting aquatic reptiles in particular, as it minimizes evaporative water loss (Wilson et al., 1999), potentially optimizes locomotion over softened substrate (Pike, 2008), and may reduce predation risk (Czaja et al., 2018). However, excessive rainfall can inhibit embryonic development of offspring during the incubation period (Bodensteiner et al., 2015), or even drown nests (Kraemer and Bell, 1980; Campos, 1993). Reports regarding the effects of rainfall on nesting among turtles conflict; some studies conclude rainfall is a cue for nesting (Burke et al., 1994; Pike, 2008; Espinoza et al., 2018; Petrov et al., 2018), whereas others do not (Tucker, 1997; Bowen et al., 2005; Geller, 2012). Consequently, the influence of rainfall on nesting activity and success remains unclear for aquatic reptiles, and may be highly context specific.

Physiology plays a role in timing of nesting initiation as well. Freshwater turtles and larger tortoises often lay multiple clutches within a single nesting season and must take time to shell their new clutch of eggs before they can nest again (Iverson and Smith, 1993; Ernst and Lovich, 2009), limiting the period when they can renest. Appropriate abiotic conditions may occur during this shelling period. Further, females may not necessarily nest immediately when their eggs are shelled. Variation in internesting intervals, as well as in timing of nesting events, exists within and among individuals (Iverson and Smith, 1993). Therefore, biotic factors, in addition to abiotic ones, could play a role in determining when an individual female emerges to construct a nest. We are unaware of studies that quantitatively account for this physiological component in evaluating the relationships of abiotic cues to nesting activity.

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Further, several studies have sought to understand environmental cues relating to the onset of nesting seasons (Congdon et al., 1983; Obbard and Brooks, 1987; Mazaris et al., 2009; Janzen et al., 2018), yet few have attempted to investigate the role of such cues in daily nesting activity. Some studies report diel nesting activity of various turtle species (Petokas and Alexander, 1980; Christens and Bider, 1987; Congdon and Gatten, 1989), but do not specifically address the possible mechanisms behind the distribution of nesting times. Organisms experience environmental conditions on a much finer temporal scale than is typically investigated (but see Frye et al., 2017). Given the sensitive role that weather conditions could play, analyzing nesting behavior on a finer temporal scale can provide a clearer lens to dissect the reproductive behavior of oviparous organisms. We investigated relationships of abiotic factors to hourly nesting behavior in Painted Turtles, while accounting for physiological limits on nesting ability, and introduce a new way to quantify nesting responses by weighting the counts of nesting turtles against the pool of females putatively able to nest at that time. We employ this method to test the prediction that both higher temperatures (Frye et al., 2017) and presence of rainfall (Bowen and Janzen, 2005) at the onset of an hour would elicit stronger nesting responses.

MATERIALS AND METHODS

Study Site.—We conducted our study at the Thomson Causeway Recreation Area (TCRA) near Thomson, Illinois, USA (41°57′N, 90°07′W) in May–June 2017. The TCRA is an island in the Mississippi River, approximately 450 × 900 m, with a 200-m-wide slough between the east side and the Illinois shoreline. Most turtles emerge from the slough to enter the nesting area, but it is also accessible from the west (see Kolbe and Janzen, 2002).

Study Species.—Painted Turtles provide an excellent study system for evaluating biotic and abiotic influences on nesting initiation because they are affected by both physiological constraints to nesting and variable abiotic conditions. Common and widespread, Painted Turtles occur across much of the United States and southern Canada (Ernst and Lovich, 2009). The nesting season for Painted Turtles ranges from mid-May to late June at the TCRA (Schwanz et al., 2010), during which females oviposit almost exclusively during daylight hours (Tinkle et al., 1981; Congdon and Gatten, 1989; Frye et al., 2017), initiating nesting between 0500 and 2200 h (Bowen et al., 2005).

Data Collection.—We set up a weather station (Onset HOBO USB U30-NRC-SYS-C data logger with additional sensors) in the main nesting area to record hourly measurements of air temperature at 1.2 m and relative humidity (12-bit Temperature/RH S-THB-M002; +/− 0.21°C/+/− 2.5%), soil temperature at 10 cm (12-bit Temperature Smart Sensor S-TMB-M002; +/− 0.21°C), and rainfall (Davis 0.01-in. Smart Rain Gauge; +/− 4.0 mm). We placed the soil sensor in sandy loam below a grass-covered surface under partial shade cover. Additionally, we deployed a data logger (HOBO Pro v2 U22-001; +/− 0.21°C) approximately 10 m from the southeastern shore of our study site to record hourly, near-surface water temperature in the slough.

We monitored the area daily for nesting Painted Turtles by walking transects on an hourly schedule between 0500 and 2200 h. Turtles in our population are individually marked, so we were able to track whether a female was laying her first, second, or third clutch of the season, based on previous captures. We recorded the number of Painted Turtles observed initiating nesting each hour and which clutch each turtle was laying (first, second, or third). For analysis, we only used data from forays where a turtle successfully oviposited. We also assume that we detected every individual female nesting throughout the season, as we surveyed our study site during all hours of known Painted Turtle activity (Bowen et al., 2005) and conducted our surveys at an interval slightly less than the average time nesting females take to nest at similar latitudes (Frye et al., 2017), ensuring that we observed every nesting attempt of the season. We also did not detect any nests that were laid at the site without us present, and any such instances of females nesting undetected have been very rare in the 30 yr of surveys conducted at the TCRA. Because adult Painted Turtles experience low levels of predation across their range (Spencer and Janzen, 2010), we assume that the probability of female survival was essentially equal to one (sensu Warner et al., 2016). Additionally, detection of turtles through visual transects was not limited by any of our weather variables, as we surveyed in all weather conditions, including very heavy rains. Thus, we are confident our detection methods do not confound our abiotic covariates. We collected data from 19 May to 25 June 2017, reflecting the timing and duration of a typical nesting season at the TCRA (Janzen et al., 2018).

Data Analysis.—We used zero-inflated models to parse nesting and nonnesting conditions into two discrete groups and identified separate sets of predictor variables for nesting and nonnesting conditions. The count component built a negative binomial-distributed model of the count sections of the response distribution (where the number of nesting turtles is greater than zero) and estimated abiotic predictors related to the strength of a nesting response (the total number of nesting turtles in a given hour). The zeros component of the model assembled a second set of predictors for only the sections of the response distribution consisting of many zeros (at least 5–6 consecutive responses equal to 0) and estimated abiotic predictors related to the presence or absence of a nesting response in a given hour.

To control for the time required to shell a subsequent clutch of eggs following completion of a prior nesting event, we removed a female from the pool of turtles available to nest for 219 hours following each of her nesting events, corresponding to the shortest internesting interval observed in this population during the 2017 season. We used the shortest internesting interval instead of the longest to ensure that females were returned to the pool of available nesting turtles as soon as it was possible for another nesting attempt to occur, thus minimizing the chance of overestimating the response variable. Any female not within the 219-h internesting interval following a nesting event was assumed to be physiologically capable of nesting, including those females who had yet to be observed nesting. We transformed each hourly count of nesting turtles into a weighted nesting response, based on the ratio of females who nested in a given hour to females who were physiologically capable of nesting in that hour.

$$p_n = p_{n-1} - e_{n-1} + e_{n-219},$$

$$r_n = \text{nint}\left(1,000 \cdot \frac{e_n}{p_n}\right).$$

We calculated the response variable for a given hour (r_n) by dividing the number of nesting events in the given hour (e_n) by the pool of females who were capable of nesting in that hour (p_n). We calculated the pool of females capable of nesting in a given hour by subtracting the number of nesting events from

TABLE 1. List of temperature variables tested during the modeling process. For each temperature variable or set of temperature variables (left column), a model was constructed using the given temperature variable, relative humidity, rainfall, and rainfall 1 h prior to a given hour.

Temperature variable	Description
A_n	Air temperature value at the onset of a given hour n
A_{n-1}	Air temperature value 1 h prior to a given hour n
A_{n-2}	Air temperature value 2 h prior to a given hour n
A_{n-3}	Air temperature value 3 h prior to a given hour n
A_{n-6}	Air temperature value 6 h prior to a given hour n
A_{n-12}	Air temperature value 12 h prior to a given hour n
W_n	Water temperature value at the onset of a given hour n
W_{n-1}	Water temperature value 1 h prior to a given hour n
W_{n-6}	Water temperature value 6 h prior to a given hour n
W_{n-12}	Water temperature value 12 h prior to a given hour n
S_n	Soil temperature value at the onset of a given hour n
S_{n-1}	Soil temperature value 1 h prior to a given hour n
S_{n-6}	Soil temperature value 6 h prior to a given hour n
S_{n-12}	Soil temperature value 12 h prior to a given hour n
$A_n + S_n + A_n \times S_n$	Air and soil temperature at the onset of a given hour n, plus their interaction term
$A_n + W_n + A_n \times W_n$	Air and water temperature at the onset of a given hour n, plus their interaction term
$W_n + S_n + W_n \times S_n$	Water and soil temperature at the onset of a given hour n, plus their interaction term
$A_n + W_n + S_n + (A_n \times W_n) + (A_n \times S_n) + (W_n \times S_n)$	Air, water, and soil temperature at the onset of a given hour n, plus all possible interaction terms
$A_{n-1} + S_{n-1} + A_{n-1} \times S_{n-1}$	Air and soil temperature 1 h prior to a given hour n, plus their interaction term
$A_{n-1} + W_{n-1} + A_{n-1} \times W_{n-1}$	Air and water temperature at the onset of a given hour n, plus their interaction term
$W_{n-1} + S_{n-1} + W_{n-1} \times S_{n-1}$	Water and soil temperature 1 h prior to a given hour n, plus their interaction term
$A_{n-1} + W_{n-1} + S_{n-1} + (A_{n-1} \times W_{n-1}) + (A_{n-1} \times S_{n-1}) + (W_{n-1} \times S_{n-1})$	Air, water, and soil temperature 1 h prior to a given hour n, plus all possible interaction terms
$S_n + S_n \times R$	Soil temperature at the onset of a given hour n, plus an interaction between soil temperature and rainfall at the onset of a given hour n
T_{avg}	Mean air temperature value over the past 24 h prior to a given hour n
$T_{\max}$	The highest air temperature value over the past 24 h prior to a given hour n
$T_{\min}$	The lowest air temperature value over the past 24 h prior to a given hour n

the previous hour (e_{n-1}) from the pool of nesting turtles in the previous hour (p_{n-1}) plus females that were completing their internesting interval upon entering the current hour, a value corresponding to the number of nesting events that occurred 219 h before the current hour (e_{n-219}). The initial value of the total pool of females capable of nesting at the beginning of the nesting season (p_0) was 216, corresponding to the number of females who were observed nesting at the TCRA in the 2017 nesting season. We then multiplied the resulting ratio of nesting turtles to those available to nest in a given hour by 1,000 and rounded to the nearest integer, generating a distribution of transformed counts usable as the response in a zero-inflated negative binomial model.

We included all weather variables in models as predictors in both the count and zeros distribution. Temperatures at various time intervals are potential predictors of nesting activity (Bowen et al., 2005). We tested hourly air, water, and soil temperatures, sliding windows of single-value temperature measurements (taken from the sensors) at 1, 6, and 12 h prior to a given hour, and average, maximum, and minimum temperatures over the prior 24 h. For temperature measurements at the onset of an hour and at 1 h prior, we also tested several interaction terms (Table 1). For each temperature measurement in Table 1, we built a full model containing that temperature measurement, rain at the onset of an hour, rain 1 h prior to the onset of an hour, and relative humidity. We then compared these models, using the Akaike information criterion (AIC) as an optimality criterion (Akaike, 1974). We also calculated the pseudo R-squared value for each model as a measure of relative model fit, by squaring the Pearson's correlation coefficient between observed values and predicted values from each of the models.

We evaluated our predictor variables for cocorrelation to avoid encountering high collinearity among multiple temperature predictor variables in models. Relative humidity was moderately correlated with some temperature variables, but during the modeling process had consistently very low estimates. There were no high correlations between rain and other predictor variables. We have deposited correlation matrices that illustrate these data on figshare (https://doi.org/10.6084/m9.figshare.10260692). We quantified rainfall as a binary variable with states presence of rainfall and absence of rainfall at the onset of a given hour. Difficulty in analyzing rain effects has been noted in the past as a potential reason why reports conflict on impacts of rainfall on nesting (Tucker, 1997). Discretizing rainfall to a binary state allows a precise analysis of rain effects amidst zero saturation in the data distribution. All analyses were performed using R version 3.5.1 (R Core Team, 2018), with the pscl (Zeileis et al., 2008) and mpath (Wang et al., 2015) packages.

RESULTS

We recorded 294 Painted Turtle nesting events made by 216 individuals at the TCRA during the 38-d study period, with the first nest constructed on 28 May. Of these 216 individuals, 137 females were observed nesting once and 79 females were observed nesting twice. No females were observed nesting three times in this season. The pool of available nesting turtles changed throughout the nesting season, falling after days of high nesting activity and rising in days of lower nesting activity (Fig. 1). We observed two peaks in nesting activity, roughly 10 d apart (Fig. 1). Our transformed counts showed nesting

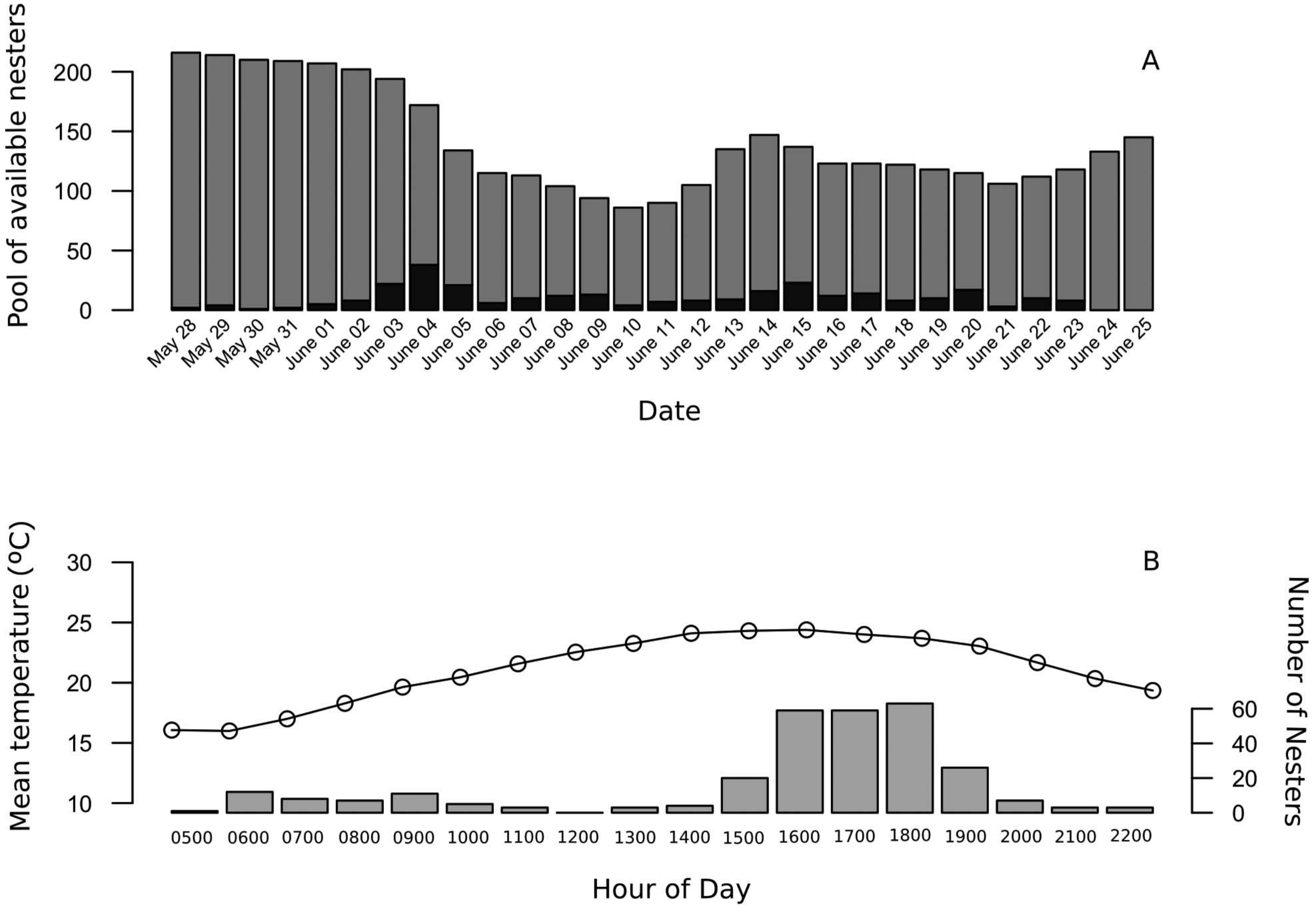

FIG. 1. Raw daily counts of nesting Painted Turtles at the TCRA. (A) Raw counts are compared to counts of adult females that did not nest, beginning at the onset of the nesting season on 28 May 2017. The combined height of the gray and black bars for each date corresponds to the total number of females capable of nesting that day. Changes in the height of the gray bars correspond to changes in the number of available nesting turtles, accounting for the obligate 219-h internesting interval following a prior nesting event. (B) Average hourly air temperature over the course of the nesting season is shown above bars representing total counts of daily nesting turtles at each hour over the course of the nesting season.

responses between the first and second peaks were more similar than that shown by raw counts of nesting females (Fig. 2), indicating a similar percentage of turtles nesting at both peaks out of the total number of females capable of nesting. In other words, the first peak was likely similar in magnitude to the second peak given physiological constraint, rather than greater in magnitude as the raw counts would suggest. Both peaks in nesting activity also coincided with a gradual increase in temperature in the days leading to peak activity (Fig. 3).

Hourly nesting was highest from 1500 to 1800 h (68.4% of total nesting turtles), concurrent with the highest mean hourly temperatures (Fig. 1) and the lowest mean hourly relative humidity. Nesting activity was also higher in early morning from 0500 to 0900 h (mean air temperature = 19.3°C) than midday from 1000 to 1400 h (mean air temperature = 25.3°C). Late evening, from 1900 to 2200 h, had moderate levels of nesting activity (13.3% of total nesting turtles; mean air temperature = 23.4°C). After the onset of the nesting season, 60% of rainfall events were accompanied by nesting activity in the same hour. Each time nesting accompanied a rainfall event, 1–5 more Painted Turtles (mean = 2.67) nested in that hour compared with the previous hour of no rainfall (Fig. 4).

Different abiotic variables had different estimate values in the count versus zeros component of the model (Table 2). The count component had positive temperature and rainfall estimates in every model, whereas temperature and rainfall had negative estimates in every model for the zeros component (Table 3). In other words, hours with higher temperatures and presence of rainfall accorded with higher levels of nesting activity. Relative humidity estimates were always negative when in the count component and positive when in the zeros component (Table 3), meaning higher relative humidity levels were associated with lower nesting activity. Our best model using AIC as an optimality criterion used soil and water temperature with an interaction term as the temperature measurement (Table 3). By contrast, our model with the highest pseudo R squared used air temperature 3 h prior to the onset of the nesting event (Table 2). Models incorporating interactions between air and water temperature suffered from high correlation between those two variables (r = 0.86), resulting in uninterpretable output, and were removed from analysis.

DISCUSSION

Aligning timing of reproduction with optimal environmental conditions is essential for enhancing organismal fitness. A variety of biotic and abiotic factors could influence the timing of nesting in oviparous organisms, with abiotic factors in particular holding potential to predict times of high nesting activity. We investigated

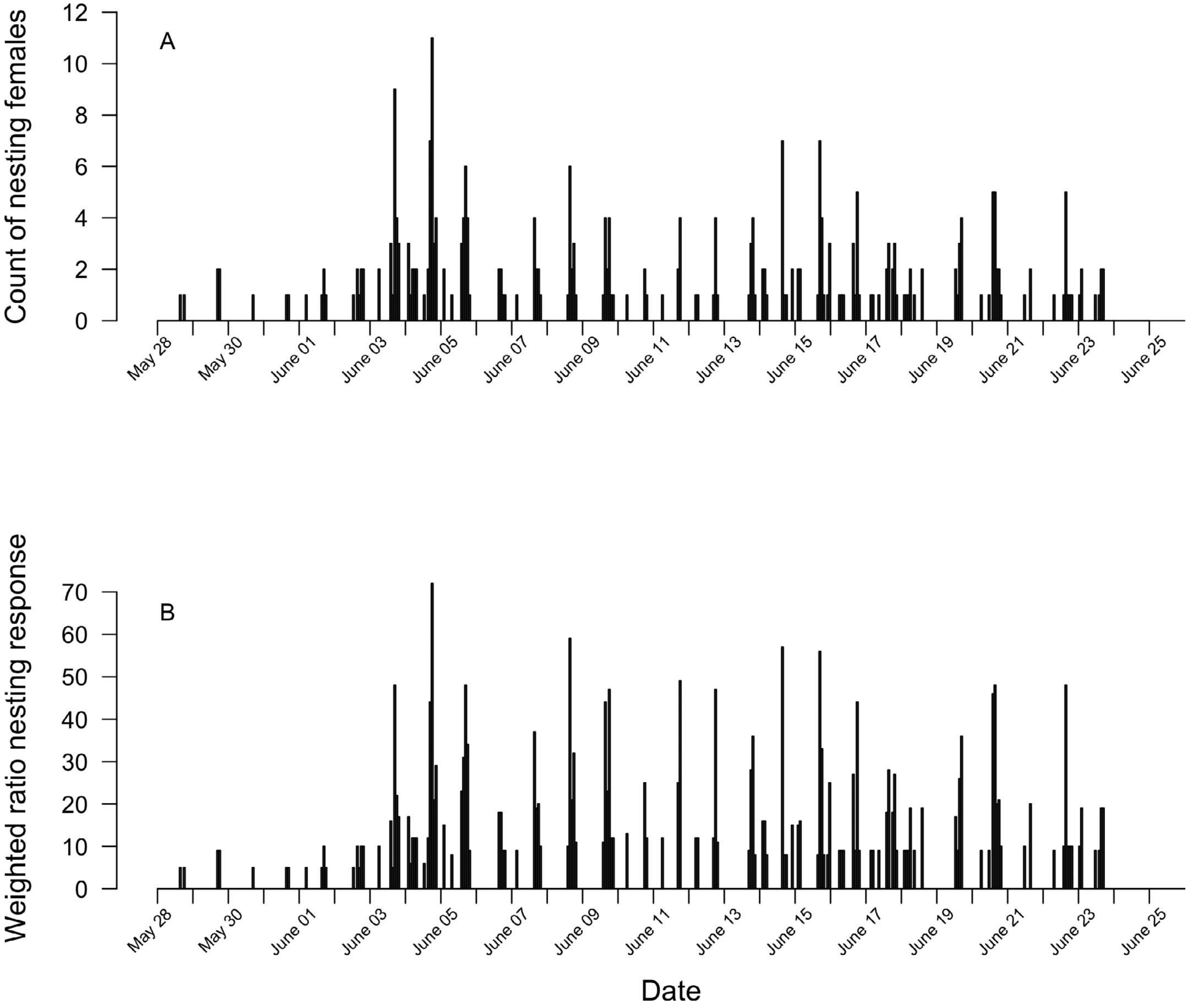

FIG. 2. Hourly nesting activity of Painted Turtles at the TCRA in the form of (A) counts of nesting turtles and (B) the weighted nesting ratio (see Methods). The charts are truncated to begin at 0500 h on 28 May (the first day of nesting) and end at 2200 h on 25 June (the end of the 2017 nesting season). Only the 18 h in which we recorded nesting activity are displayed for each date.

the relationships between weather variables and patterns of nesting activity within a single nesting season of Painted Turtles, using a novel transformed ratio of nesting turtles to those capable of nesting. Few studies of freshwater turtle phenology have attempted to evaluate these relationships on an hourly scale (e.g., Frye et al., 2017), and we are not aware of any studies that have controlled for physiological capacity in analysis of abiotic influences on nesting timing.

We found that temperature was an important cue for nesting activity for Painted Turtles, consistent with other studies (Bowen et al., 2005; Frye et al., 2017). Air and water temperature most likely serve as physiological cues for females preparing to emerge from the water to nest, given the importance of high body temperature for females to exert themselves physically on land during a nesting excursion (Congdon and Gatten, 1989; Krawchuk and Brooks, 1998). Changes in soil temperature likely reflect a lag in changes in air temperature (Geiger et al., 2009), as females deciding whether to emerge from the water have no direct means of sensing soil temperature. Our difference in which temperature variable generated the best model by AIC (soil and water temperature with an interaction term) and pseudo R squared (air temperature 3 h prior to the present hour) likely reflects this pattern. Our models suggest higher temperatures are correlated with elevated nesting activity, yet the pattern of diel activity does not appear to be directly associated with temperature. Nesting activity was highest in the late afternoon, comparable to other studies of Painted Turtles at northern latitudes (Christens and Bider, 1987; Congdon and Gatten, 1989; Rowe et al., 2005; Frye et al., 2017). Further, early morning hours had higher nesting activity than did the midday hours, but lower temperatures, suggesting higher temperature alone is unlikely to be the reason behind a temporal decrease in nesting activity around midday. One potential explanation could be avoidance of heat stress during midday temperatures (Frye et al., 2017). Females may be limited by high operative temperatures exceeding their preferred body temperatures (Rowe et al., 2014, 2017), preventing terrestrial movement and constraining their ability to nest in open areas. However, this is

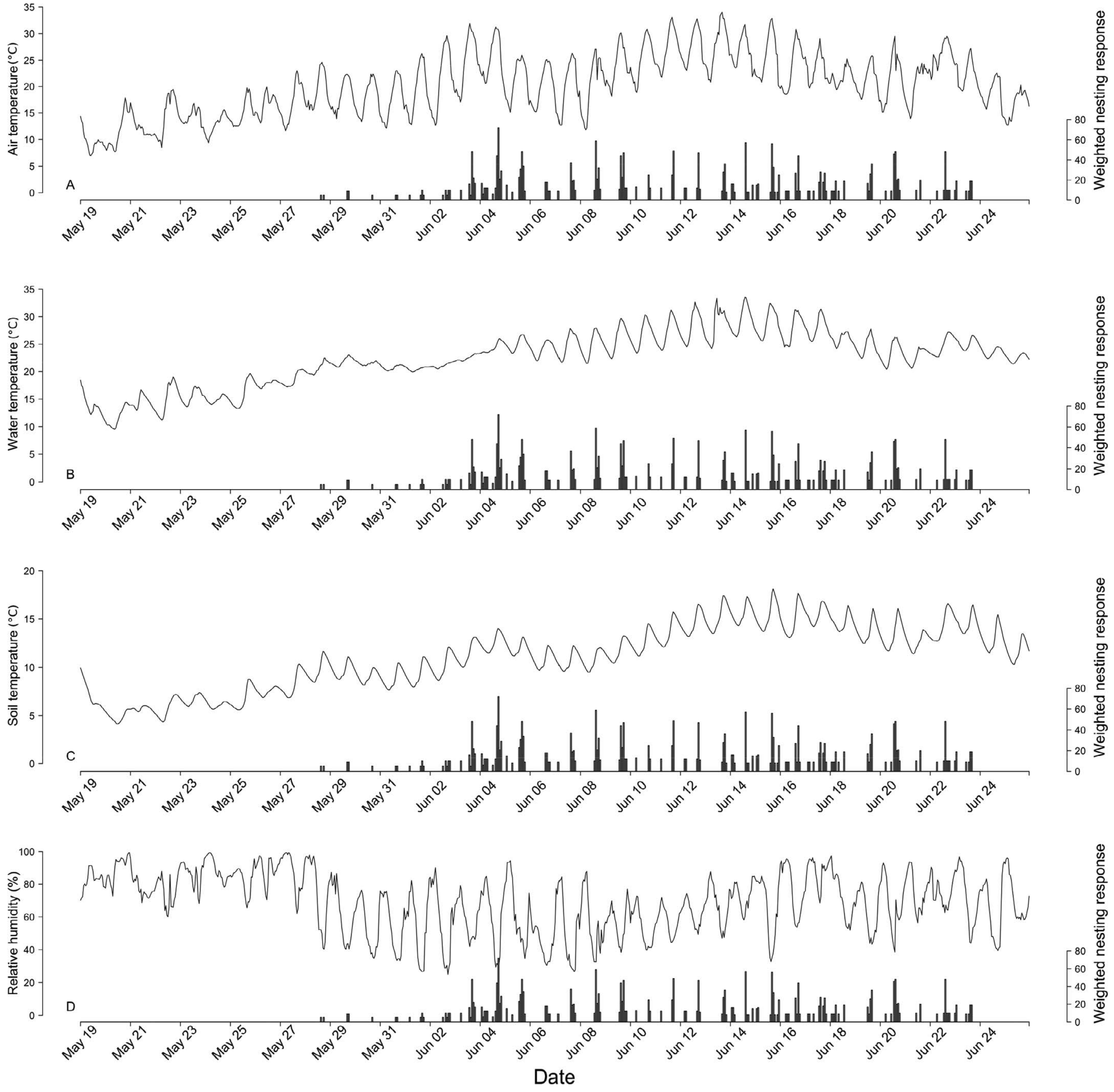

FIG. 3. Hourly measurements at the TCRA in 2017 for (A) air temperature at 1.2-m height, (B) water temperature at the surface, (C) soil temperature at 10-cm depth, (D) relative humidity, and (E) rainfall events. Measurements began at 0000 h on 19 May and ended at 2300 h on 25 June. The right axes correspond to the weighted nesting ratio for Painted Turtles (see Methods).

an unlikely issue at our site, as hours of highest nesting activity still had higher temperatures than did the midday period, and there are ample shade opportunities that allow females to avoid prolonged exposure to direct sunlight.

Painted Turtles may prioritize the middle portion of the day for basking activity. Painted Turtles experience a gradual rise in body temperature in late morning, potentially connected to basking in sunlight or sitting in warm surface water (Rowe and Dalgarn, 2009). Basking is important for a wide variety of physiological processes in reptiles, such as growth, preparation for reproduction, thermoregulation, and ectoparasite removal (Boyer, 1965; Shine, 1980; Crawford et al., 1983). Females also bask longer and more frequently than males during the nesting season (Krawchuk and Brooks, 1998; but see Rowe et al., 2017) presumably because of the energetic demands of egg production (Carrière et al., 2008). By prioritizing the midday hours for basking, Painted Turtles may be capitalizing on such early-day basking time to provide energy to complete a nesting event shortly thereafter.

In contrast with Bowen et al. (2005), we found support for rainfall as a cue of nesting behavior within the Painted Turtle nesting season. Nesting during, or just after, a rain event has many potential benefits for a nesting turtle. Rain potentially renders digging more efficient by softening substrate (Seabrook, 1989), thereby speeding up nesting events and decreasing

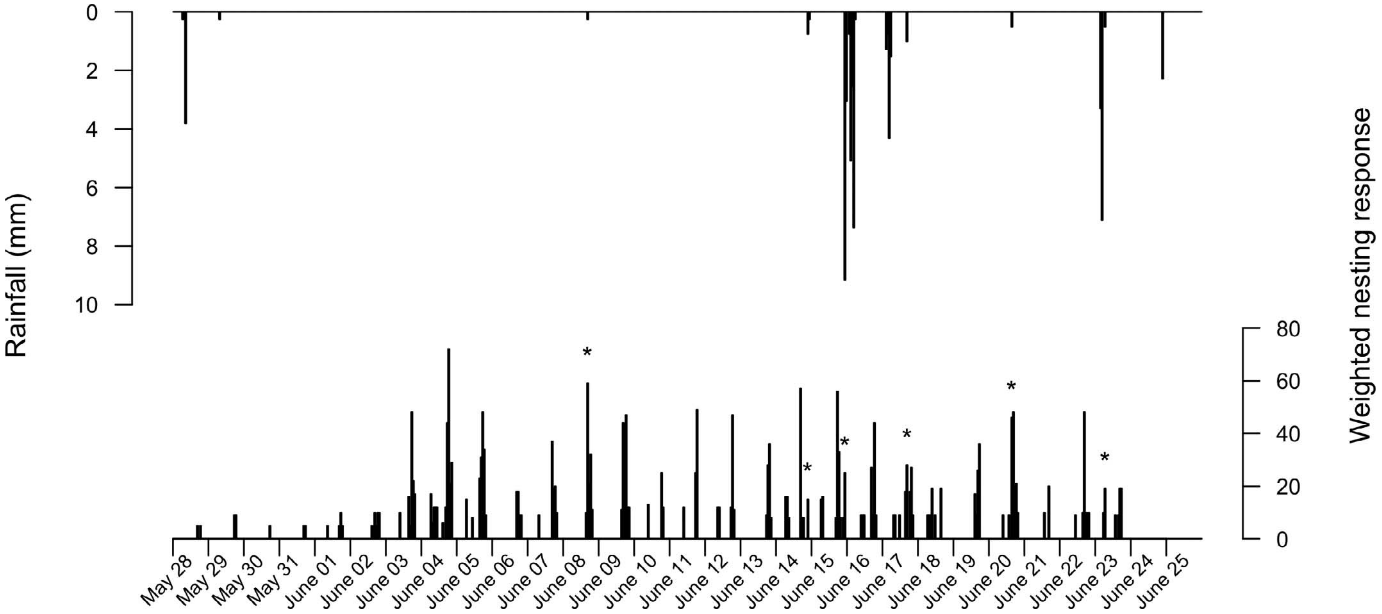

FIG. 4. Hourly rainfall events and Painted Turtle nesting activity at the TCRA in 2017. Hanging bars correspond to rainfall events. Measurements began at 0000 h on 28 May and ended at 2300 h on 25 June. Stars above bars in the nesting distribution indicate hours in which a rainfall event accompanied nesting. The right-hand axis corresponds to the weighted nesting ratio (see Methods).

predation risk for the mother. Rainfall may also erase predatory cues on nests, although this varies depending on the amount of rainfall (Bowen and Janzen, 2005; Czaja et al., 2018). The most obvious downside to nesting in rain is the possibility of heavy rain drowning nests. However, Painted Turtles will abandon nesting attempts during heavy rainfall if the nest cavity fills with water (Muell, unpubl. data), presumably avoiding embryo fatalities. If nesting turtles are detecting flooding risk during heavy rains, the benefits of nesting during a precipitation event may outweigh the risk of flooding.

In our study, we only considered turtles who successfully oviposited during nesting excursions. Incorporating unsuccessful nesting attempts may shed light on proximate weather effects on female emergence and attempts to nest, not just successful nesting forays, as environmental conditions may differ between completed and abandoned nesting attempts. In addition, the changing global climate is shifting daily nest timing and nesting seasons within and across taxa (Parmesan and Yohe, 2003; Thackeray et al., 2008; Benard, 2015; Janzen et al., 2018). To predict these shifts in daily timing and seasonal nesting periods, a detailed knowledge of abiotic cues for

TABLE 2. Comparison of zero-inflated negative binomial models generated for each temperature variable. The transformed nesting variable was used as a response. Each model used the given set of temperature variables, rainfall at the onset of the present hour, rainfall 1 h prior, and relative humidity at the onset of the present hour in both the count and zero distributions. Predictors for the count distribution correspond to variables important for predicting the number of nesting events (integers greater than zero), while predictors for the zero distribution correspond to variables important for predicting the lack of a nesting event.

Temperature	Other predictors (both distributions)	ΔAIC	Akaike weight	Relative log-likelihood	Pseudo R-squared
$W_n + S_n + W_n \times S_n$	$R + R_{n-1} + \mathrm{RH}$	0	$9.07e^{-01}$	1.00	0.231
$W_{n-1} + S_{n-1} + W_{n-1} \times S_{n-1}$	$R + R_{n-1} + \mathrm{RH}$	5	$8.95e^{-02}$	$9.87e^{-02}$	0.219
$A_n + S_n + A_n \times S_n$	$R + R_{n-1} + \mathrm{RH}$	12	$2.30e^{-03}$	$2.54e^{-03}$	0.220
$A_{n-1} + S_{n-1} + A_{n-1} \times S_{n-1}$	$R + R_{n-1} + \mathrm{RH}$	14	$8.57e^{-04}$	$9.45e^{-04}$	0.238
$S_n + S_n \times R$	$R + R_{n-1} + \mathrm{RH}$	17	$1.47e^{-04}$	$1.62e^{-04}$	0.234
S_n	$R + R_{n-1} + \mathrm{RH}$	18	$1.07e^{-04}$	$1.18e^{-04}$	0.228
S_{n-1}	$R + R_{n-1} + \mathrm{RH}$	22	$1.62e^{-05}$	$1.79e^{-05}$	0.215
A_{n-3}	$R + R_{n-1} + \mathrm{RH}$	23	$9.07e^{-06}$	$1.00e^{-05}$	0.272
A_{n-2}	$R + R_{n-1} + \mathrm{RH}$	27	$1.28e^{-06}$	$1.42e^{-06}$	0.270
T_{max}	$R + R_{n-1} + \mathrm{RH}$	28	$6.81e^{-07}$	$7.51e^{-07}$	0.168
A_{n-1}	$R + R_{n-1} + \mathrm{RH}$	33	$6.61e^{-08}$	$7.29e^{-08}$	0.221
A_{n-6}	$R + R_{n-1} + \mathrm{RH}$	39	$3.93e^{-09}$	$4.34e^{-09}$	0.164
W_{n-1}	$R + R_{n-1} + \mathrm{RH}$	45	$1.72e^{-10}$	$1.90e^{-10}$	0.174
T_{avg}	$R + R_{n-1} + \mathrm{RH}$	48	$3.63e^{-11}$	$4.00e^{-11}$	0.116
A_n	$R + R_{n-1} + \mathrm{RH}$	50	$1.11e^{-11}$	$1.22e^{-11}$	0.153
W_n	$R + R_{n-1} + \mathrm{RH}$	52	$5.75e^{-12}$	$6.33e^{-12}$	0.147
S_{n-6}	$R + R_{n-1} + \mathrm{RH}$	69	$7.53e^{-16}$	$8.30e^{-16}$	0.095
T_{min}	$R + R_{n-1} + \mathrm{RH}$	70	$5.22e^{-16}$	$5.75e^{-16}$	0.113
S_{n-12}	$R + R_{n-1} + \mathrm{RH}$	89	$3.98e^{-20}$	$4.39e^{-20}$	0.097
W_{n-12}	$R + R_{n-1} + \mathrm{RH}$	109	$2.22e^{-24}$	$2.44e^{-24}$	0.081
A_{n-12}	$R + R_{n-1} + \mathrm{RH}$	123	$1.88e^{-27}$	$2.07e^{-27}$	0.081

TABLE 3. Breakdown of model statistics for the two models with the lowest AIC. Predictors for the count distribution correspond to variables important for predicting the number of nesting events (integers greater than zero), whereas predictors for the zero distribution correspond to variables important for predicting the lack of a nesting event. Patterns in the directions of the estimate for each predictor variable (+/−) were maintained across all models. The two models were separated by 5 AIC. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Model	Component	Predictor	Estimate	Standard error	Z-value
Lowest AIC model $W_n + S_n + W_n \times S_n + R + R_{n-1} + \text{RH}$	Count	Intercept	−8.17	3.40	−2.40*
		W_n	0.41	0.13	3.18**
		S_n	0.67	0.24	2.77**
		$W_n \times S_n$	−0.02	0.01	2.65**
		R	0.66	0.23	−2.83**
		R_{n-1}	0.63	0.38	1.64
		RH	−0.01	0.01	−3.47***
		Log(theta)	1.38	0.19	7.10***
	Zero	Intercept	9.79	4.99	1.96
		W_n	−0.19	0.21	−0.93
		S_n	−0.97	0.37	−2.62**
		$W_n \times S_n$	0.02	0.01	1.37
		R	−1.61	0.66	−2.42*
		R_{n-1}	0.64	0.87	0.73
		RH	0.03	0.01	4.68***
Second-lowest AIC model $S_{n-1} + W_{n-1} + S_{n-1} \times W_{n-1} + R + R_{n-1} + \text{RH}$	Count	Intercept	−7.99	−2.98	−2.68**
		W_{n-1}	0.41	0.11	3.58***
		S_{n-1}	0.67	0.22	3.11**
		$W_{n-1} \times S_{n-1}$	−0.02	0.01	−3.01**
		R	0.63	0.23	2.72**
		R_{n-1}	0.63	0.38	1.66
		RH	−0.01	0.00	−3.47***
		Log(theta)	1.39	0.18	7.54***
	Zero	Intercept	7.80	4.61	1.69
		W_{n-1}	−0.15	0.19	−0.77
		S_{n-1}	−0.75	0.35	−2.16*
		$W_{n-1} \times S_{n-1}$	−0.02	0.01	−3.01***
		R	0.63	0.23	2.72**
		R_{n-1}	−0.63	0.38	1.66
		RH	−0.01	0.01	−3.47***
		Log(theta)	1.39	0.18	7.54***

reproduction is required, and accounting for organismal physiology is crucial to delimit these cues accurately. We recommend continued collection of fine-scale data on potential abiotic correlates of phenology. Future avenues of study could also examine geographic variation in phenology within species (Edge et al., 2017; Janzen et al., 2018), shedding light on differential responses to climate change. Focusing research efforts in these directions will advance our understanding of the complicated interactions between biotic and abiotic factors in initiating essential reproductive behavior.

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