Modeling the Effects of Climate Change–Induced Shifts in Reproductive Phenology on Temperature-Dependent Traits

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Abstract
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Keywords
temperature-dependent sex determination, constant temperature equivalent (CTE), development, Chrysemys picta

Disciplines
Ecology and Evolutionary Biology | Evolution | Population Biology | Terrestrial and Aquatic Ecology

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Modeling the Effects of Climate Change–Induced Shifts in Reproductive Phenology on Temperature-Dependent Traits

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ABSTRACT: By altering phenology, organisms have the potential to match life-history events with suitable environmental conditions. Because of this, phenological plasticity has been proposed as a mechanism whereby populations might buffer themselves from climate change. We examine the potential buffering power of advancing one aspect of phenology, nesting date, on sex ratio in painted turtles (Chrysemys picta), a species with temperature-dependent sex determination. We developed a modified constant temperature equivalent model that accounts for the effect of the interaction among climate change, oviposition date, and seasonal thermal pattern on temperature during sexual differentiation and thus on offspring sex ratio. Our results suggest that females will not be able to buffer their progeny from the negative consequences of climate change by adjusting nesting date alone. Not only are offspring sex ratios predicted to become 100% female, but our model suggests that many nests will fail. Because the seasonal thermal trends that we consider are experienced by most temperate species, our result that adjusting spring phenology alone will be insufficient to counter the effects of directional climate change may be broadly applicable.

Keywords: temperature-dependent sex determination, constant temperature equivalent (CTE), development, Chrysemys picta.

Introduction

The most commonly observed biotic response to climate change is a shift in phenology (i.e., timing of life-history events; Visser and Both 2005; Parmesan 2006; Moser et al. 2009). Examples include advances in flowering date, tree bud burst, arrival of migrant birds and butterflies, frog breeding, and nesting in birds and reptiles (e.g., Beebee 1995; Menzel and Fabian 1999; Forister and Shapiro 2003; Visser et al. 2004; Both et al. 2006; Telemeco et al. 2009). These temporal shifts in response to climate change presumably result from individuals using thermal cues to time life-history events (Parmesan 2006; van Asch and Visser 2007), an important consequence of which is that temperatures at the onset of these events remain relatively stable from year to year. Plasticity in phenology therefore has been proposed as a mechanism whereby individuals might buffer themselves from the impacts of climate change (Visser and Both 2005; Schwanz and Janzen 2008; Telemeco et al. 2009).

Shifting phenology, however, only allows individuals control of conditions at the onset of life-history events. Because temperature trajectories during the growing season are roughly parabolic (increasing from spring to summer and then decreasing), if organisms respond to increasing average temperatures by starting their spring phenological cycles earlier, they will face steeper seasonal temperature changes. Thus, even though temperatures at the onset of life-history events could be held constant by adjusting phenology, temperatures over the periods that follow might still increase (fig. 1). This shift could be particularly important for oviparous organisms that lack parental care, such as many ectotherms (Vitt and Caldwell 2009), because environmental temperatures during embryogenesis affect survivorship and phenotype (Du et al. 2003; Shine 2005; Booth 2006). Even if these species advance their phenology such that temperatures at nesting are constant, temperatures during embryogenesis might still increase. Thus, many species might be unable to compensate for the effects of warming climates on their developing offspring by advancing phenology.

We explored the power of advancing phenology to buffer populations from climate change using painted turtles (Chrysemys picta), a species with temperature-dependent sex determination (TSD; Bull 1980). Temperature during development directly determines the sex of individuals with TSD (Bull 1980; Godfrey et al. 2003; Warner and Shine 2008). In painted turtles, warm temperatures produce females and cool temperatures produce males (Janzen and Paukstis 1991). Species with TSD provide a unique opportunity for studying the biological impacts of shifting phenology in response to climate change because temperature directly affects a key trait without additional
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Figure 1: Hypothetical seasonal temperatures in spring, summer, and autumn before (solid line) and after (dotted line) a homogeneous increase in temperature. As females advance the nesting date in response to climate warming, the slope of temperature change during the period when offspring sex is labile (thermosensitive period [TSP]; horizontal boxes and corresponding lines) will increase. As a result, advancing the nesting date in response to climate change such that temperature at the time of oviposition remains constant from year to year may be insufficient to keep the TSP from warming and sex ratios from becoming biased.

complicating factors. Moreover, species with TSD might be at risk of climate change–induced extinction because directional changes in temperature could skew sex ratios (Janzen 1994a; Tellemco et al. 2009; Wapstra et al. 2009). By advancing the nesting date (observed in numerous TSD species, e.g., Doody et al. 2006; Schwanz and Janzen 2008; Tellemco et al. 2009), females might control the temperatures to which their developing offspring are exposed and counter these negative effects. However, sex in species with TSD is generally determined during the middle third of development (termed the thermosensitive period [TSP]; Janzen and Paukstis 1991; Georges et al. 2005; Shine et al. 2007), which in turtles begins a month or more after oviposition and continues for another month (Janzen and Paukstis 1991; Georges et al. 2005; Shine et al. 2007). Early nesting will buffer progeny from sex ratio shifts induced by climate change only if temperature at oviposition predicts temperature during the TSP (Tellemco et al. 2009; fig. 1).

Generally, laboratory trials involving temperature assess the effects of constant temperature treatments. While informative, such studies poorly replicate natural conditions where temperatures fluctuate daily and seasonally (Ackerman and Lott 2004; Angilletta 2009). Methods are therefore needed to translate results from constant temperature experiments such that they make accurate predictions about organisms exposed to natural conditions. One such method is the constant temperature equivalent (CTE) model (Georges 1989), which condenses diel thermal variation from natural nests into a single number (the CTE) that can be used to predict the sex ratios of species with TSD (Georges 1989; Georges et al. 1994). The CTE model accurately predicts sex ratios in many species (e.g., Les et al. 2007; Delmas et al. 2008; Mitchell et al. 2008), although it is not universally applicable (Warner and Shine 2011).

We developed a modified CTE model that accounts for the effects of nesting date and seasonal increases in temperature on offspring sex ratio. We then applied our modified CTE model to a population of painted turtles to examine whether advances in the nesting date could buffer
populations of species with TSD from biased sex ratios induced by climate change.

The Model

The CTE model calculates the temperature above and below which half of development occurs, or the temperature associated with the median developmental rate (Georges 1989). We briefly present the original CTE model (for further details, see Georges 1989; Georges et al. 2004) and then describe our modifications.

The original CTE model assumes that developmental rate \( ds/dt \) increases linearly with temperature \( T \):

\[
\frac{ds}{dt} = \begin{cases} 
A(T - T_o), & T > T_o; \\
0, & T < T_o,
\end{cases}
\]

where \( A > 0 \) is the rate of increase and \( T_o \) is the critical thermal minimum below which no significant development occurs. Temperature varies daily in a simple, periodic fashion around a constant mean \( M \) with a daily range equal to 2\( R \):

\[
T = R \cos t + M, \quad 0 \leq R < M.
\]

Time \( t \) is scaled so that 1 day = 2\( \pi \) units. In natural nests, the daily range frequently varies, and an average \( R \) can be estimated using the statistical thermal variance \( (\sigma')^2 \); L. Harmon, unpublished data): \( R = (2(\sigma')^2)^{1/2} \). The amount of development \( s \) that takes place from time 0 to time \( t \) is \( \int_0^t (ds/dt)dt \). Because the cosine function is symmetrical, the entire period of development can be characterized by considering only the half-day interval \( (0, \pi) \). During this period, there is a time \( t' \) that divides the half-day cycle into two intervals in which total development is exactly equal. The temperature associated with this time is the CTE. We can find \( t' \) by solving

\[
\int_0^{t'} \frac{ds}{dt}dt = \int_{t'}^{\pi} \frac{ds}{dt}dt
\]

and then the CTE (termed \( T' \) in Georges 1989) by solving

\[
\text{CTE} = R \cos t' + M.
\]

Sex ratios can be predicted by comparing the CTE value from natural nests to the temperature that results in a 1:1 sex ratio under constant incubation conditions (pivotal temperature \( T_{\text{inv}} \)).

We elaborated Georges’s CTE model by adding two features: (1) a maximal temperature above which development is 0 and (2) a seasonal increase in daily mean temperature. As others have pointed out (e.g., Georges et al. 2005; Delmas et al. 2008), the assumption in equation (1) that developmental rate increases with temperature linearly to infinity is flawed. Within an optimal thermal range, a linear relationship is appropriate (Sharpe and DeMichele 1977; Georges et al. 2005), but the rate rapidly approaches 0 if temperatures rise above this range. Curvilinear approaches to modeling this relationship have been advanced (Georges et al. 2005; Neuwald and Valenzuela 2011), but each has many parameters that are difficult to estimate. In addition, the curvilinear models seem to perform similarly well, regardless of their complexity (Georges et al. 2005). We developed a simple alternative by adding a critical thermal maximum \( (T_{\text{MAX}}) \), above which no development occurs, to equation (1) (fig. S1A, available online in a zip file):

\[
\frac{ds}{dt} = \begin{cases} 
A(T - T_o) & \text{if } T_o < T < T_{\text{MAX}}, \\
0 & \text{if } T < T_o \text{ or if } T > T_{\text{MAX}}.
\end{cases}
\]

While this simplified approach has less resolution than curvilinear models within the thermal range where developmental rate decreases, that range is narrow (Georges et al. 2005), and embryos experience little development here. A model that allows the developmental rate to decrease more realistically at extreme high temperatures neither markedly outperforms this simple approach with our test data nor affects our qualitative results (described in the supplemental material, available online). The primary advantage of our approach is that \( T_{\text{MAX}} \) is relatively easy to estimate.

An important assumption of the original CTE model is constant mean temperature throughout the TSP (Georges 1989). Our second elaboration relaxes this assumption, allowing temperature to change linearly to reflect seasonal warming:

\[
T = R \cos t + M' + wt, \quad 0 \leq R < M',
\]

where \( M' \) is the mean temperature on the first day of the TSP and \( w \) is the rate of increase in mean daily temperature. By adjusting these two parameters, we can explicitly model the interaction between nesting date and seasonal thermal pattern on the CTE. Developmental rate, \( ds/dt \), is given by plugging equation (6) into equation (5). Georges (1989) exploits the fact that, because the temperature cycle is the same every day, the temperature associated with the median development rate over the whole TSP is also the temperature of median development during a single half-day cycle. We cannot use this shortcut because the temperature cycle changes from day to day, and we must instead examine development across the entire TSP to find the CTE. The CTE is therefore the temperature that makes the following equality true:

\[
\text{CTE} = R \cos t' + M' + wt'
\]
and our previous research (, , piv- and Janzen 1999; Warner et al. 2010). We estimated phys-
son), that has been extensively studied for the last 25 years
the historic thermal profile in nests (, ,
and Janzen 2008). For detailed methods, see the appendix,
(1) to describe the average nesting period (nest on June
M26.3C, R = 5.4C, w = 0.002C/2C; fig. A2, available online), and (3)
to confirm that the CTE model accurately predicts sex
ratios in this species. To estimate the parabolic shape of
the thermal trend over the reproductive season and how
temperature during the TSP (M' and w) will change with
warming and earlier nesting, we used historic records of
soil temperature measured at a nearby weather station
(figs. 2, 3).

For all simulations, we assumed that females advance
the nesting date such that soil temperature at nesting re-
mains constant. If hatching sex ratios are not buffered
under this scenario, it is unlikely that smaller shifts will
buffer progeny and larger shifts would likely result in eggs
being placed in nests too cool for development. We further
assumed that the TSP advances the same number of days
as the nesting date and that TSP length remains constant.
While these assumptions will not be fully accurate, adding
realistic variation minimally affects our results (see the
appendix). We simulated the effects of realistic changes in
slope during the TSP (w) and mean temperature at the
onset of the TSP (M') on CTE values given 0–6C warming
(fig. 3). For comparison, we also simulated the effects
of increased temperature on CTE values if females do not
alter their nesting phenology. This was done by holding
w at its historic value and increasing M' by the same
amount as the increase in environmental temperature (0–
6C).

We more fully explored the model by allowing w and
M' to change independently within realistic limits. Since
diel thermal range might also change with future warming,
we considered a wide range of R values as well. For these
simulations, we calculated CTE values for all combinations
of w ranging from 0C/2C to 0.02C/2C (at intervals of
0.001C/2C), M' from 20C to 30C, and R from 1C to
10C (M' and R at intervals of 0.05C). By simulating the
effects of each realistic parameter value factorially, we ex-
amined (1) how sex ratios will likely respond to different
uniform warming scenarios and (2) what model param-
eters have the greatest effects on offspring sex ratio. Al-
though we identified TMAX = 34C as a reasonable esti-
mate, this is the parameter for which we have the least
direct information (see the appendix), so we repeated our
simulations with additional TMAX values (30C–40C at 2C
intervals).

To ground our exploration of the simulation results to
the natural history of painted turtles at Thomson, we as-
sumed historic, preclimate change parameter values of
w = 0C/2C, M' = 26C, R = 5C, and a 30-day TSP
(based on measurements at Thomson). Although we con-
sidered a range of possible temperature increases, we focus
on the effects of 4C warming because conservative pre-
dictions from climate models suggest that the midwestern
United States will experience temperature increases of this
magnitude or greater over the next century (Wuebbles and

\[
\sum_{i} \int_{a}^{b} \frac{ds}{dt} dt = \sum_{j} \int_{a}^{b} \frac{ds}{dt} dt, \tag{7}
\]

where the time intervals (a, b) are defined as all intervals
during the TSP for which temperatures are between T0
and the CTE and (a, b) are all time intervals with tem-
peratures between the CTE and TMAX (fig. A1, available
online). The left-hand side of equation (7) is the total
amount of development occurring below the CTE, and the
right-hand side is the total amount of development oc-
curring above the CTE. The temperature for which the
equality holds is, by definition, the CTE.

We developed a MATLAB (ver. R2009b; MathWorks, Ma-
tick, MA) algorithm to find the CTE in this model nu-
merically (code available in the supplemental material). The
algorithm takes a specified set of parameter values (M', R,
w, T0, TMAX and length of the TSP) and finds the CTE
associated with this parameter set. Any temperature between
T0 and TMAX is a viable candidate for the CTE; we considered
all candidate values at intervals of 0.01C within this range.
For each candidate CTE value, we solved equation (6) to
find all the times, t, at which temperature, Tt, was equal to
T0, the CTE, or TMAX. These times provide the limits of
integration in equation (7). The candidate CTE value that
best satisfied equation (7) was taken as the true CTE.

Estimation of Model Parameters and
Description of Simulations

We simulated our modified CTE model under varied re-
alistic conditions to examine the ability of painted turtles
(Chrysemys picta) to buffer the sex ratios of their progeny
from increasing environmental temperatures by advancing
the nesting date. Thermally induced shifts toward earlier
nesting have been documented in this species (Schwanz
and Janzen 2008). For detailed methods, see the appendix,
available online. Briefly, we focused on a population lo-
cated in the Thomson Causeway Recreation Area in Car-
roll County, Illinois (41°57'N, 90°07'W; hereafter, Thom-
son), that has been extensively studied for the last 25 years
(for detailed field methods, see Janzen 1994b; Weisrock
and Janzen 1999; Warner et al. 2010). We estimated phy-
ological model parameters using data from the literature
and our previous research (T0 = 14C, TMAX = 34C, piv-
otal temp [TPT] = 28C, transitional range of tempera-
tures [TRT; range that results in mixed-sex nests] = 26.65C–
29.35C). In addition, we used data from Thomson
(1) to describe the average nesting period (nest on June
1 and have a 30-day TSP beginning July 1), (2) to describe
the historic thermal profile in nests (M' = 26.3C, R = 5.4C, w = 0.002C/2C; fig. A2, available online), and (3)
Figure 2: Predicted effects of climate change on nest temperatures during the thermosensitive period (TSP) of *Chrysemys picta* at the Thomson Causeway Recreation Area. The thick black line shows mean daily 10-cm soil temperatures collected over 21 years at an Iowa City weather station, and the corresponding dashed lines show ±1 SE. The thick gray line depicts these data after transformation to match temperatures recorded in natural nests (see the appendix, available online), and the thick red line depicts predicted soil temperatures after a uniform 4.0°C temperature increase. The smoothed lines are quadratic functions fitted to these data (prior to transformation: temperature = $-3 \times 10^{-4} \text{time}^2 + 0.0515 \text{time} + 4.503$, with time in radians [day $\times 2\pi$]). The green arrow shows the average historic nesting date of *C. picta* (June 1), whereas the red arrow depicts when females would need to nest in order to nest at the same temperature before and after warming (May 11; 21-day shift). The green box and corresponding line depict temperatures during the historic TSP (approximately July), whereas the red box and corresponding black line depict predicted temperatures during the TSP after regional warming and shifted nesting. The inset depicts the gray (prewarming) and red (postwarming) nest temperature curves overlaid with days from oviposition on the X-axis.

Hayhoe 2004; IPCC 2007; Takle 2011). When not stated otherwise, parameters were held at their historic values for all simulations.

**Results**

**Effects of Climate Change and Earlier Nesting on TSP Temperature**

Even if females adjust their phenology such that they oviposit at the same soil temperature every year, temperatures during the TSP will rise as a result of climate change (figs. 2, 3). This results from increases in the slope of temperature change over the TSP ($w$) and the temperature at the onset of the TSP ($M'$; figs. 2, 3). Given uniform warming, a nest initiated at the historic oviposition temperature will gradually diverge from historic thermal conditions. Although average temperature during the pre-TSP period is predicted to increase only 0.81°C with 4°C warming (fig. 2, inset), temperature at the onset of the TSP ($M'$) should increase $\sim 2$°C. Slope during the TSP ($w$) should also increase with warming (from $\sim 0$ to 0.015°C/2πd), such that temperatures increase an additional $\sim 2.8$°C during the TSP (fig. 3; table A1, available online). Together, changes in $w$
Effects of regional warming and shifts in *Chrysemys picta* nesting date (no. of days advanced from the historic nesting date of June 1) at the Thomson Causeway Recreation Area on temperature at the onset of the thermosensitive period (TSP; $M'$) and the slope of temperature change during the TSP ($w$), both of which are predicted to increase. Highlighted points show the amount of warming that would be necessary for corresponding shifts, given the assumption that female *C. picta* nest at the same temperature annually. Values assume uniform increases in annual temperature.

and $M'$ result in the mean TSP temperature rising $\sim 3.2^\circ C$, even when females nest $\sim 3$ weeks early (figs. 2, 3).

Effects of Climate Change–Induced Shifts in Phenology on Sex Ratios

CTE values are predicted to rise out of the TRT (temperature range that results in a mixed-sex ratio) after $\sim 1.1^\circ C$ warming, resulting in a 100% female sex ratio and ultimately population extinction (fig. 4, solid line), even if female painted turtles advance nesting such that they oviposit at the same temperature each year. For comparison, if females fail to shift their nesting phenology and continue to nest on June 1, CTE values increase more rapidly and rise above the TRT after only $\sim 0.7^\circ C$ warming (fig. 4, dashed line). The CTE rises with nest temperature until $T_{MAX}$ is exceeded, at which point proportionately less development occurs at high temperatures and the CTE decreases (peaks in figs. 4 and 5 curves). When nests spend $>50\%$ of the TSP above $T_{MAX}$, however, the majority of development occurs at high temperatures just below $T_{MAX}$, and the CTE again rises. While embryos can survive minor excursions above $T_{MAX}$, extended periods or extreme spikes should be fatal (Du et al. 2003; Angilletta 2009; Neuwald and Valenzuela 2011); therefore, nests that spend more time above $T_{MAX}$ (right of the peaks in figs. 4 and 5) should experience high mortality.

Figure 5 depicts results from the factorial simulations, showing the relationship between nest CTE and $w$ across a realistic range of $M'$ (fig. 5A), $R$ (fig. 5B), and $T_{MAX}$ (fig. 5C). It is helpful to examine predictions based on a single warming scenario to understand these results. We describe the biological effects of $4^\circ C$ warming. Because warming and shifts in phenology should directly affect only $w$ and $M'$, we hold all other parameters at their historical values ($T_0 = 14^\circ C$, $T_{MAX} = 34^\circ C$, $R = 5^\circ C$; fig. 5A). Assume for the moment that females can alter nesting such that TSP starting temperature remains stable over time at $26^\circ C$ and only slope increases. Following the line in figure 5A from the intercept ($w = 0$, $M' = 26^\circ C$ line in figure 5A from the intercept ($w = 0$, $M' = 26^\circ C$ line
Figure 4: Predicted effects of uniform increases in environmental temperature on constant temperature equivalent (CTE) values in painted turtle nests at the Thomson Causeway Recreation Area. The solid line depicts CTEs if females adjust their nesting date such that they always nest at the same temperature, whereas the dashed line depicts CTEs if females continue to nest on the average historic nesting date at Thomson (June 1). CTE values within the shaded transitional range of temperatures may result in either single- or mixed-sex nests, with TPIV representing the CTE that is predicted to result in a 1:1 sex ratio. To create the solid line, we simulated M′ and w values shifting in tandem according to predictions from figure 3. To create the dashed line, w was held at the historic predicted value at Thomson, while increases in environmental temperature were added to the historic M′ value. All other parameters were held at their historic mean values (Tₚ = 14.0°C, T_MAX = 34.0°C, R = 5.0°C, TSP length = 30 days).

as in the historical data) to the dotted line (w = 0.015, the value predicted for a 4°C increase in temperature) reveals that this would cause the CTE to rise from 28.5°C to 29.12°C. While this CTE results in female bias, it is within the TRT, and thus mixed-sex nests should occur. Moreover, if TSP starting temperature is slightly reduced (1°–2°C; e.g., M′ = 24°C line in fig. 5A), CTE values will remain very close to TPIV, and thus a 1:1 sex ratio could be maintained. If we return to our assumption that females advance their nesting date to track nesting temperature, both slope and TSP starting temperature will increase (fig. 3), resulting in a CTE of 29.78°C (fig. 5A; M′ = 28°C line at w = 0.015). This is concordant with the CTE value given at 4°C warming in figure 4 and should induce a 100% female sex ratio.

The predicted effects of other scenarios can be ascertained from figure 5 by examining additional parameter combinations. In general, CTE values increase with each parameter until nest temperatures exceed T_MAX, at which point CTE values begin to decrease. Slope (w) only exerts a minor effect on the CTE, whereas TSP starting temperature (M′) and diel thermal range (R) have more profound effects. The T_MAX value used did not affect the overall behavior of the model, except to affect the point at which CTE values began to decrease. This effect was minor for T_MAX values ≥34.0°C within realistic ranges for the other parameters.

Discussion

Power of Advancing the Nesting Date to Buffer Offspring from Climate Change

Even if female painted turtles alter their phenology to oviposit at the same temperature each year, temperatures
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during the TSP will increase if regional temperatures rise. While earlier nesting delays increases in TSP temperature, it cannot counter them. Soil temperature at oviposition fails to predict nest conditions later in development because of the parabolic shape of seasonal thermal progression. The two parameters that best describe this effect are temperature at the onset of the TSP (M′) and slope of temperature change during the TSP (w), both of which increase relative to oviposition temperature as the nesting date advances.

Our model predicts 100% female sex ratios given realistic values for changes in mean air temperature over the twenty-first century (Wuebbles and Hayhoe 2004; IPCC 2007; Takle 2011), even if females alter the nesting date to maintain oviposition temperature (fig. 4). This change in sex ratio could be observed after as little as ∼1°C uniform increase in temperature. Our conclusion that adjustments in oviposition phenology cannot fully compensate for warming is concordant with empirical evidence that nesting date plasticity has only minor effects on the sex ratios of Thomson painted turtles at the population level (Schwanz and Janzen 2008).

Mechanisms independent of phenology could buffer populations from climate change. Our model shows that temperature changes at the onset of the TSP (M′) drive variation in sex ratio. If females control M′, maintaining either current or slightly reduced values, mixed-sex ratios could be maintained. For moderate levels of regional warming, M′ must be reduced 2°–4°C. Nesting even earlier will not be a viable strategy because temperatures will be near Tp if females oviposit in the very early spring. This process lengthens the first third of development but fails to reduce M′. Alternatively, females might reduce M′ by constructing nests in wetter or more shaded areas, both of which would reduce nest temperature. Numerous reptiles, including painted turtles, have shifted nesting behavior accordingly through either local adaptation or phenotypic plasticity (e.g., Doody et al. 2006; Telemeco et al. 2009; McGaugh et al. 2010). If behavioral changes prove insufficient, interannual and internest variation in temperature might rescue the population by allowing occasional influxes of males.

During the twentieth century, nights warmed faster than days in the midwestern United States, reducing the diel thermal range, and climate change models predict that this trend will continue (IPCC 2007; Takle 2011). Such a reduction in diel thermal range, 2R, could also buffer nests from sex ratio shifts. However, to reduce the CTE ∼1°C, the diel thermal range must contract ∼4°C (fig. 5B). Climate change models do not support such a large change (IPCC 2007; Takle 2011). While contracted diel thermal ranges should reduce CTE values, these reductions will be insufficient to counter the effects of increased average temperatures.

Egg mortality might increase in addition to sex ratio shifts. Even after the nesting date is altered, regional warming of <2°C is predicted to result in nests spending much of each day above the critical thermal maximum for successful development (TMAX). Brief exposure of embryos to temperatures slightly above TMAX is not fatal, but prolonged exposure to these temperatures and brief exposure to more extreme temperatures are fatal (Du et al. 2003; Shine et al. 2003; Neuwald and Valenzuela 2011). Counterintuitively, because predicted CTE values initially fall when nest temperatures exceed TMAX, it is theoretically plausible that exposure to high temperatures could yield male offspring (e.g., Neuwald and Valenzuela 2011). Our model predicts this only under extreme conditions and never under scenarios where only M′ and w are adjusted. Thus, increased mortality should be the primary effect of nests spending increased time above TMAX (e.g., 1988 in Janzen 1994a and in response to El Niño–Southern Oscillation cycles in Tomillo et al. 2012).

**Potential Effects of Model Assumptions on Conclusions**

The CTE model successfully predicted sex ratios in 40 of 46 natural painted turtle nests (see the appendix). Model error might reflect natural among-nest variation in Tprev or the TRT, improper placement of temperature loggers within nests, or nests having TSPs outside the July data logger deployment period. Nonetheless, our results support the view that the CTE model can be a powerful tool for predicting population trends in sex ratio. Moreover, the success of our simple model with TMAX reveals a general alternative to curvilinear approaches. In fact, an inter-

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**Figure 5:** Predicted effects of slope (w) during the thermosensitive period (TSP) on the constant temperature equivalent (CTE) of nests for different values of (A) temperature at the onset of the TSP (M′), (B) the diel thermal range of temperature (2R), and (C) the critical thermal maximum for development (TMAX). For C, dotted lines represent when TMAX ≠ 34°C to clarify where predicted CTE values overlap. When not marked otherwise, parameters were set at M′ = 26.0°C, R = 5.0°C, TMAX = 34.0°C, Tp = 14.0°C, and TSP length = 30 days, which are approximately the mean values from current nests. The dotted vertical line marks the slope of temperature change over the TSP that results from 4.0°C warming given that females advance their nesting date such that they nest at the same temperatures annually. CTE values within the shaded transitional range of temperatures (TRT) may result in either single- or mixed-sex nests, with Tprev representing the CTE that is predicted to result in a 1 : 1 sex ratio. CTE values above the TRT are predicted to result in 100% female nests, whereas CTE values below the TRT are predicted to result in 100% male nests. To aid interpretation, a few scenarios are described in the text.
mediate model, simpler than proposed curvilinear models but more realistic than our model, yielded almost identical results (supplemental material).

Although we explored the behavior of our model for different values of the diel thermal range parameter ($R$), we assumed that $R$ is constant throughout the growing season. Seasonal variation in $R$ could affect the pre-TSP period and link $R$ to nesting phenology, ultimately affecting offspring sex ratio. Although data collected by a Geostationary Operational Environmental Satellite (GOES-8) show that $R$ constricts substantially from spring to summer, this trend appears to be an artifact of not accounting for increased cloud cover in spring (Sun et al. 2006). The trend is not observed in data from weather stations that record under all sky conditions, where instead the diel thermal range from May to August is relatively constant (Sun et al. 2006). Our assumption of a constant $R$ therefore appears appropriate.

It is difficult to know how climate change will affect seasonal/annual temperature trends. Winter temperatures are increasing faster than summer temperatures globally (Balling et al. 1998; Stine et al. 2009). This disparity will dampen the slope of temperature change across spring and could increase the correlation between temperatures at nesting and at the onset of the TSP, thereby increasing the power of females to buffer offspring sex ratios by adjusting the nesting date. However, this global trend is highly variable, and current models have a difficult time capturing it (Balling et al. 1998). Because of this difficulty, we assumed that spring and summer temperatures would increase uniformly. While it is evident that relative differences in summer and winter warming could change our specific results, we expect our qualitative conclusions to hold for a broad range of scenarios (fig. 5).

Our model also assumes that female phenology will shift such that oviposition occurs at the same soil temperature each year. Given a 4°C increase in temperature, the nesting date would need to advance ~3 weeks. Such shifts are plausible for reptiles (Doody et al. 2006; Tucker et al. 2008; Telemeco et al. 2009); however, thermal reaction norms for female painted turtles encompass shifts in nesting phenology of only ~10 days (Schwanz and Janzen 2008). Females therefore may not be able to nest early enough to track climate change. However, nesting date plasticity appears to have little effect on TSP temperatures—and thus on sex ratios (fig. 4)—because slight increases in temperature should induce 100% female sex ratios regardless of nesting date.

Conclusions

Our model suggests that painted turtles will not be able to buffer their progeny from climate change by adjusting phenology alone. We considered a broad range of parameter values; thus, this result should be general across species and thermally dependent biological processes. Nesting earlier fails to buffer nest temperatures from climate change because temperatures at oviposition and during the period when embryonic sex is labile become increasingly mismatched as the nesting date advances. Similar disparities have been observed in other species and are likely common among temperate species with thermally plastic phenologies (e.g., Visser and Both 2005; Parmesan 2006; Telemeco et al. 2009). The consequences of these discordances vary. For example, mismatches in phenology can separate development from suitable temperatures, as demonstrated here, but they also can disconnect important ecological interactions, such as those between predators and prey and between pollinators and flowers (reviewed in Visser and Both 2005; Parmesan 2006).

It is plausible that high egg mortality will have earlier and greater effects on population persistence than skewed sex ratio in species with TSD. This may be especially true in long-lived species such as painted turtles, where occasional influxes of the rare sex could maintain viable population sex ratios. In such cases, egg mortality might be a more pressing climate change concern. Indeed, all species that deposit eggs terrestrially could be susceptible to these predicted increases in egg mortality. Still, temperature-sensitive species might respond such that they can persist in the face of impending climate change by controlling the temperature at the onset of the thermosensitive period, $M^*$, but multiple biological responses might be necessary. Future studies of taxa observed to plastically respond to climatic variation should focus on jointly examining the effects of all responses.

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Nesting painted turtle (*Chrysemys picta*). Photograph by F. J. Janzen.