

Linking climate and physiology at the population level for a key life-history stage of turtles

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Abstract: Forthcoming climate change is expected to impact the global biota, particularly by altering range limits. However, the roles of early life stages in affecting biogeography and the impact of climate change on reptiles are both poorly understood. Fitness of neonatal reptiles depends greatly on energy reserves and body size, which themselves are affected by abiotic conditions in laboratory experiments performed during embryonic development and posthatching dormancy. To test whether these relationships between environment and physiology hold in nature, we conducted a 6-year field study on a natural northern population of red-eared slider turtles, *Trachemys scripta elegans* (Wied-Neuwied, 1839). Climatic conditions varied substantially and impacted offspring phenotypes. Consistent with bioenergetic predictions, cohorts that experienced warmer periods of posthatching dormancy had less dry residual yolk mass than similar-sized hatchlings that experienced cooler overwintering periods. Thus, global warming may exert adverse effects on turtle energy reserves important to fitness during crucial early life stages; this negative physiological impact may extend to other ectotherms with obligate, nonfeeding stages.

Résumé : Les changements climatiques futurs devraient affecter les organismes vivants à l'échelle globale, particulièrement par une modification des limites des répartitions géographiques. Le rôle joué par les jeunes stades de vie dans ces conséquences biogéographiques prévues et dans les impacts du changement climatique sur les reptiles n'est pas bien compris. La fitness des reptiles nouveau-nés dépend beaucoup des réserves énergétiques et de la taille corporelle, deux facteurs qui varient avec les conditions abiotiques dans des expériences menées en laboratoire durant le développement embryonnaire et la dormance qui suit l'éclosion. Nous avons entrepris une étude de terrain d'une durée de six ans sur une population boréale naturelle de la tortue à tempes rouges, *Trachemys scripta elegans* (Wied-Neuwied, 1839), afin de vérifier si ces relations entre le milieu et la physiologie s'appliquent aussi en nature. Les conditions climatiques ont varié considérablement et ont affecté les phénotypes des rejetons. En accord avec les prédictions bioénergétiques, les cohortes qui subissent des périodes de dormance plus chaudes après l'éclosion ont une masse résiduelle de vitellus moins importante que les nouveau-nés, de taille semblable, qui ont connu des périodes plus fraîches pendant l'hiver. Le réchauffement global pourrait ainsi affecter négativement les réserves énergétiques essentielles à la fitness durant les premiers stades de vie chez les tortues; cet impact physiologique négatif peut aussi sans doute s'appliquer à d'autres ectothermes qui ont des stades obligatoires sans alimentation.

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Introduction

Global climate change has stimulated intense interest in impacts on developmental, behavioural, and reproductive processes (Kareiva et al. 1993). Predictions of skew in sex ratios (Janzen 1994), alterations in habitat range (Humphries et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Huntley et al. 2004), loss of sustainable habitat (Hughes et al. 2003; Lal 2003), and extinction (Shinn et al. 2000; Thomas et al. 2004) all point to a dramatic shift in the orga-

nization of natural biotic systems locally, as well as globally. Changing climate also might affect organisms differently (or only) at certain life stages. Thus, evaluating ontogenetic sensitivity to climatic variation is important, especially in organisms with complex life cycles consisting of one or more stages that are plausibly linked to abiotic conditions.

Turtles are a prime example of an organism whose life stages are greatly and directly affected by abiotic factors related to climate. Numerous important aspects of embryonic development, in particular, are exquisitely sensitive to thermal and hydric conditions experienced in nests (reviewed in Deeming and Ferguson 1991; Packard 1991). The majority of turtles have flexible-shelled eggs that readily exchange water with the surrounding soil. Eggs exhibiting a positive water balance during embryonic development tend to yield larger hatchlings with correspondingly smaller residual yolks, whereas the opposite occurs in eggs that lose water during incubation (Packard 1991). Both patterns have been documented in natural nests of turtles (e.g., Packard et al. 1999). Similarly, turtles hatching from flexible-shelled eggs incubated at warmer temperatures are typically smaller and contain more residual yolk than offspring from eggs incubated in cooler environments (reviewed in Deeming and

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Ferguson 1991). Moreover, most species of turtles exhibit temperature-dependent sex determination, whereby offspring sex is largely governed by nest temperatures (Janzen and Paukstis 1991; Ewert et al. 1994). Indeed, offspring sex ratios in these species have been linked to annual variation in climatic temperature (Mrosovsky and Provancha 1992; Janzen 1994).

The posthatching stage in turtles may also be greatly influenced by environmental conditions. Neonates often remain in the nests for many months after hatching, subsisting on yolk left over from embryogenesis (Gibbons and Nelson 1978; Ultsch 1989; Tucker et al. 1998a; Filoramo and Janzen 1999). Because turtles are ectotherms, the rate of expenditure of internalized energy stores by nest-bound hatchlings is presumably determined almost solely by thermal conditions. As nest thermal conditions are a function of local climate (e.g., Weisrock and Janzen 1999), variation in climatic temperatures necessarily impacts the morphology, physiology, and survival of such terrestrially overwintering turtles (e.g., Nagle et al. 2000; Costanzo et al. 2004). In turn, the nutrients and energy available to surviving animals, as well as their body size, may shape their probability of surviving the critical period of transition from terrestrial to aquatic habitats that follows emergence from nests and ends when hatchlings reach their aquatic home (e.g., Janzen et al. 2000a, 2000b; Tucker 2000).

We conducted a 6-year study of a natural northern population of red-eared slider turtles, *Trachemys scripta elegans* (Wied-Neuwied, 1839), to explore how climatic conditions might influence morphological and physiological traits of neonates prior to emergence from the nest, with ramifications for subsequent survivorship. Red-eared slider turtles are common and widely distributed in the central United States (Ernst et al. 1994), with other subspecies and related species distributed throughout the New World (Ernst and Barbour 1989). Embryos of *T. s. elegans* develop in the eggs for several months and the resulting offspring overwinter in terrestrial nests for many additional months in the highly variable northern temperate climate (Tucker 1997); similar behaviour is also exhibited by sliders and their relatives elsewhere (Gibbons and Nelson 1978; Morjan and Stuart 2001). We specifically evaluated relationships between body size and residual yolk mass for cohorts of field-collected neonates and general measures of climatic conditions during both embryonic development and posthatching dormancy. Our results provide empirical documentation of the physiological effects of climatic variation in nature on early life stages of reptiles and the possible impacts of climate change.

Materials and methods

The natural population examined here is the focus of a long-term study of the demography and life history of *T. s. elegans* near the northern edge of its range. The field site is located at Stump Lake adjacent to the Illinois River in Jersey County, Illinois. Hundreds of *T. s. elegans* nest each year at this site, primarily during June, producing thousands of offspring (e.g., Tucker et al. 1998b). Young sliders in this population, which generally hatch from eggs in August, are obligated to overwinter in their terrestrial nests prior to emergence the following spring. For this study and related

ongoing projects, neonatal turtles that recently emerged from nests were collected in late April and May (1999–2003), using drift fences constructed of 30 cm high aluminum flashing (for details, see Tucker 1997). These turtles were placed in sealed plastic bags and then frozen at -20°C for subsequent evaluation. Turtles were collected under scientific permits to J.K.T. from the Illinois Department of Natural Resources, thus the research complies with the law.

Approximately 50 frozen turtles were haphazardly chosen for examination in each year of the project. Turtles were removed from the freezer and allowed to thaw for 15 min to facilitate measuring and dissecting. Fresh mass of each turtle was measured to the nearest 0.01 g on an electronic balance and carapace length was recorded to the nearest 0.1 mm with a dial calipers. Next, each turtle was opened, the residual yolk was carefully excised and placed into a preweighed aluminum dish, and the dish plus fresh yolk was weighed. When this process was completed, all ~50 aluminum dishes with fresh residual yolk were placed into a drying oven at 40°C for 3 days (i.e., until constant mass had been achieved). After the drying period, the dishes were removed from the oven and individually reweighed to the nearest 0.01 g. Turtle carcasses from which residual yolks were extracted were labeled individually with numbered museum tags and preserved in ethanol as voucher specimens. This entire process was repeated during each year of the study. Information on neonates and their residual yolks from 1994/1995 at the same field site was obtained from Tucker et al. (1998a) to supplement the 5 years of new data collected herewithin where applicable. Climate data were acquired from the Illinois State Climatology recording station at Jerseyville, Illinois (Illinois State Water Survey 2004), about 23 km northeast of the study site.

Based on extensive prior research at the site (e.g., Tucker 1997; Tucker et al. 1998a; Janzen et al. 2000a, 2000b), the period of embryonic development was defined as 1 June – 31 August and the period of posthatching dormancy was defined as 1 September – 30 April. Climate variables of interest for embryonic development were mean ambient temperature and total precipitation for the first period, because incubation temperature and soil moisture influence yolk use and offspring size in reptiles (Deeming and Ferguson 1991; Packard 1991). Similarly, mean ambient temperature was evaluated for the period of posthatching dormancy because of its strong impact on metabolic rates of neonatal turtles (e.g., O'Steen and Janzen 1999). Variation in three phenotypic variables (body mass, carapace length, and dry residual yolk mass) was evaluated in the context of these three climate variables.

Data were analyzed using JMP version 4.0.4 (SAS Institute Inc. 2001). One-way analyses of variance were performed to evaluate among-year variation in phenotypes of the cohorts of turtles. Simple and multiple linear regression analyses were used to explore potential relationships between (i) the three original phenotypic variables at the cohort level, (ii) average capture dates and all six phenotypic and climate variables, (iii) climate variables, and (iv) all three phenotypic variables and all three climate variables. For most analyses, two-tailed tests were employed to evaluate statistical significance. Beyond those general assessments, analyses that focused on testing laboratory- and

Table 1. Descriptive statistics for climate variables and for capture date and phenotypes of neonatal red-eared slider turtles, *Trachemys scripta elegans*, collected in drift fences in a natural population near the northern edge of the geographic range.

Year (number of turtles)	June–August precipitation (cm)	June–August temperature (°C)	September–April temperature (°C)	Capture date (Julian days)	Body mass (g)	Carapace length (mm)	Dry residual yolk mass (g)
1994/1995 (<i>n</i> = 147) ^a	20.50	23.37	7.19	na	6.79±0.85 (4.93–8.59)	30.8±1.3 (27.5–34.1)	0.02±0.02 (0–0.17)
1998/1999 (<i>n</i> = 50) ^b	26.06	23.91	8.02	130±9 (119–146)	6.10±1.14 (4.02–8.62)	31.4±1.9 (27.3–34.8)	0.01±0.03 (0–0.15)
1999/2000 (<i>n</i> = 49) ^c	20.57	23.68	8.07	127±1 (125–128)	6.79±1.29 (4.28–9.42)	31.8±2.3 (26.1–36.4)	0.01±0.01 (0–0.07)
2000/2001 (<i>n</i> = 48) ^d	46.79	23.26	5.81	122±4 (114–129)	6.04±1.20 (3.93–9.43)	30.8±2.1 (26.6–35.5)	0.02±0.03 (0–0.13)
2001/2002 (<i>n</i> = 50)	31.80	23.43	7.94	113±2 (110–115)	5.90±1.07 (3.86–7.88)	30.7±2.2 (25.4–34.5)	0.02±0.02 (0–0.10)
2002/2003 (<i>n</i> = 50)	30.00	24.98	6.08	118±5 (106–125)	6.56±1.11 (3.82–8.11)	31.3±2.1 (26.1–34.4)	0.03±0.03 (0–0.17)

Note: Values for precipitation are sums, for temperature are means, and for the remaining variables are means ± 1 SD (range). na, not available.

^aResults for body mass, carapace length, and dry residual yolk mass were obtained from Tucker et al. (1998a).
^b*n* = 28 for capture date.

^c*n* = 50 for capture date.

^d*n* = 50 for carapace length and for capture date.

bioenergetically based predictions concerning the relationships between phenotype and climate (i.e., those described in *iv* above) used one-tailed tests to evaluate statistical significance. Specifically, warmer, drier conditions during embryonic development were expected to yield smaller offspring with relatively larger residual yolks; warmer weather encountered by neonates after hatching was expected to induce greater consumption of residual yolk by the turtles. While none of the statistical analyses in this study accounted for possible clutch effects, the haphazard sampling scheme leaves no reason to expect that the turtles from one year were more or less related to each other than the turtles from any other year. Thus, clutch effects should not impact the results of this study.

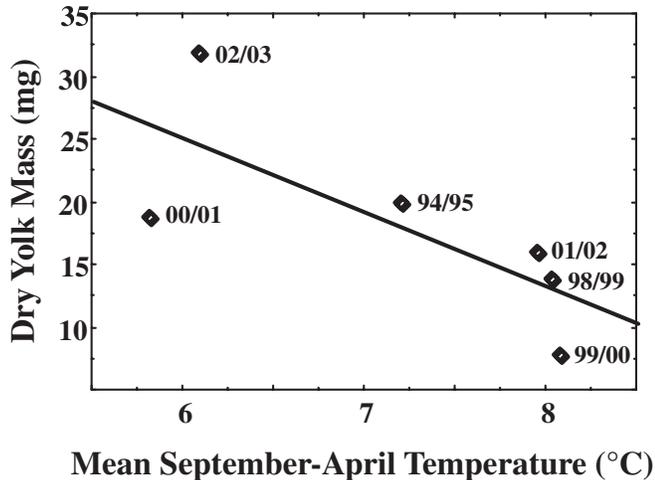
Results

Turtles used in this study were captured at the drift fence as early as 16 April (three individuals; Julian day 106) and as late as 26 May (one individual; Julian day 146), with the vast majority (213 out of 228) being captured after 23 April (Julian day 113). Evaluating the most recent 5 years of the study, phenotypes of the captured turtles varied both within and among years (body mass: $F_{[4,242]} = 5.24$, $P = 0.0005$; carapace length: $F_{[4,244]} = 2.21$, $P = 0.0687$; dry residual yolk mass: $F_{[4,242]} = 5.87$, $P = 0.0002$), with most of the variation being among individuals within years (Table 1). At the cohort level ($n = 6$ years), the three phenotypic variables were independent of each other (dry residual yolk mass vs. body mass: $r = 0.06$, $P = 0.9149$; dry residual yolk mass vs. carapace length: $r = -0.33$, $P = 0.5253$; body mass vs. carapace length: $r = 0.47$, $P = 0.3466$). Average capture dates (for the 5 years for which such data were available) were unrelated to any of the phenotypic or climate variables ($P > 0.05$ for all six comparisons).

Climatic conditions also varied substantially across the 6 years of the study (Table 1). The summer of 2000 (i.e., June–August) was one of the coldest and wettest documented in the area since recording began in 1950. Similarly, the summer of 2002 was one of the warmest and the summer of 1994 was one of the driest. As for the overwintering period (i.e., September–April), 2000/2001 was the 11th coolest and 1998/1999, 1999/2000, and 2001/2002 were among the 12 warmest. Wetter summers tended to be cooler and to be followed by cooler overwintering periods, but neither relationship was statistically significant during this study ($r = -0.38$, $P = 0.4578$ and multiple regression $r^2 = 0.60$, $P = 0.2540$, respectively). Analyses of available data for the area since 1950, though, suggest that both climate relationships are real phenomena ($r = -0.30$, $P = 0.0298$ and multiple regression $r^2 = 0.11$, $P = 0.0660$, respectively).

Not one of the three phenotypic variables was significantly correlated with either measure of climate during embryonic development (one-tailed $P > 0.05$ for all six comparisons, $n = 6$ years). Multiple regression analyses revealed that combinations of the two climate variables also did not significantly impact any of the offspring cohort measures (one-tailed $P > 0.05$ for all three comparisons, $n = 6$ years). Thus, neither total precipitation nor mean ambient temperature from June–August each year alone or in combination predicted the phenotypes of the offspring cohort the follow-

Fig. 1. Six-year relationship between mean ambient temperature from 1 September to 30 April and dry residual yolk mass of cohorts of neonatal red-eared slider turtles, *Trachemys scripta elegans*, captured in a natural population near the northern edge of the geographic range.



ing spring (i.e., in April–May of the subsequent calendar year).

Across the 6 years of this study, neither body mass nor carapace length was correlated with September–April temperature ($r = 0.02$, one-tailed $P = 0.4867$ and $r = 0.38$, one-tailed $P = 0.2290$, respectively). However, dry residual yolk mass was affected by thermal conditions during that time. As expected, turtle cohorts contained less residual yolk upon emerging from the nests after warmer dormancy periods ($r = -0.75$, one-tailed $P = 0.0435$). Consequently, as predicted under bioenergetic principles, cohorts of hatchlings that experienced warmer conditions prior to emerging from the nests consumed more yolk reserves than cohorts that encountered cooler nest environments after hatching (Fig. 1). If this yolk is composed of 40.5% lipid (Marlen and Fischer 1999), then the difference in dry residual yolk mass between hatchling cohorts from 1999/2000 and 2002/2003 comprises 10 mg lipid. This energy source alone would provide about 2 extra days of survival at standard metabolic rate at 28 °C (Marlen and Fischer 1999), similar to the length of time hatchlings take to migrate from nest to water at our site.

Discussion

The swift pace of climate change has raised substantial concern over its biotic impacts (Kareiva et al. 1993). A major focus of research in this area has emphasized the relationship between climatic temperature and geographic range (Parmesan and Yohe 2003; Root et al. 2003), with particular emphasis on energetic constraints in endotherms (Root 1988; Loison et al. 1999; Canterbury 2002; Humphries et al. 2002; Hallett et al. 2004). In contrast, relatively little is known about how the energetics of vulnerable early life stages may affect persistence and geographic range for reptilian taxa in general with respect to climate change.

A nutrient reserve, particularly residual yolk, is essential for survival of neonates of oviparous reptiles (Kraemer and Bennett 1981; Troyer 1983; Vleck and Hoyt 1991). This is-

sue is not trivial, especially for species in which the young remain in the nest for many months before undertaking the crucial journey to their future aquatic home to forage for their first meal (Gibbons and Nelson 1978; Ultsch 1989; Tucker 2000; Costanzo et al. 2004). During this enforced period of terrestrial dormancy, these ectothermic neonates are subject to the vagaries of a variable abiotic environment. Thermal extremes in ambient meteorological conditions can translate into thermal extremes in nests (e.g., Weisrock and Janzen 1999), and thus impact survival of offspring via freezing (e.g., Packard et al. 1997) or energy use of offspring due to elevated metabolism caused by increased temperature (e.g., Costanzo et al. 2004). Of particular note, the relationship between metabolic rate and ambient temperature in most ectotherms is exponential (e.g., Scholander et al. 1953), thus even small increases in temperature translate into considerable increases in energy use. Consequently, the level and frequency of extreme thermal conditions in nature govern key features of the dormancy biology of many ectotherms and, in turn, potentially play an important role in the range limits of these species.

With only 6 years of available data, we detected the signature of a major climatic factor (i.e., ambient temperature) on an important morphological and physiological trait during a critical life-history stage of neonatal turtles. This phenotypic effect was in the direction predicted based on bioenergetic principles. Specifically, climatic temperatures during post-hatching dormancy were inversely related to residual yolk mass of young turtles emerging from nests in the spring — warmer periods resulted in smaller yolk masses, whereas cooler periods yielded larger yolk masses. These effects appear to be unrelated to body size, as neither body mass nor carapace length was correlated with dry residual yolk mass (see Results). This pattern has significant implications for the fitness of these animals before and after emergence from the nests. For example, the probability of survival of neonates during the migration to their future aquatic homes is linked to locomotor performance (F.J. Janzen, J.K. Tucker, and G.L. Paukstis, unpublished data), which likely depends on available energy stores.

If climatic conditions play such a critical role in the post-hatching dormancy period of northern populations of turtles, then what can be said for populations that exist in climatically milder environments? Although the phenomenon of terrestrial overwintering by neonatal aquatic turtles has often been considered a characteristic of cooler climate populations, extended periods of terrestrial quiescence without feeding by these young turtles are also common in the southern United States (e.g., Morjan and Stuart 2001; but see Aresco 2004) and elsewhere worldwide, having been reported in South Africa, Panama, Australia, and Japan, among other locations (reviewed in Gibbons and Nelson 1978; Ultsch 1989). How turtles in these regions have adapted behaviourally, physiologically, and (or) evolutionarily to the warmer thermal conditions in nests during posthatching dormancy is unknown. Perhaps populations inhabiting warmer regions provision eggs with relatively more yolk to sustain neonates after hatching (sensu Finkler et al. 2004). More research, especially an experimental approach like a reciprocal transplant of neonates in the field (e.g., Crozier 2004), is required to clarify the mechanism(s) involved.

The observed variation in both offspring phenotypes and climatic conditions during this study improved our ability to detect biologically meaningful correlations between the two categories (Table 1). This analysis also allowed us to rule out other potential causes of the significant patterns that we observed. Capture dates of offspring were not correlated with any phenotypic or climate variables nor were any phenotypic variables correlated with climate variables recorded during embryonic development. Thus, at the cohort level, residual yolk mass of neonates captured in the spring appears to be unrelated to other measured aspects of body size or to climatic conditions noted prior to hatching. Therefore, in addition to studies that suggest climate change may unfavourably affect sex ratio in the many reptiles like *T. s. elegans* that have temperature-dependent sex determination (Mrosovsky and Provancha 1992; Janzen 1994), changes in climatic temperature during posthatching dormancy may directly and adversely affect the physiology, morphology, and survivorship of these turtles during early life stages.

Winter temperatures during the 21st century and beyond are expected to rise disproportionately relative to summer temperatures (IPCC 2001). Furthermore, the location of the study population places it on the edge of the Great Plains region of North America, precisely where a climatic warming effect on the continent is predicted to be most severe in the future (Johns et al. 1997; IPCC 2001). Already hardiness zones across the continental United States have shifted dramatically northward (National Arbor Day Foundation 2004). Notably, the 1990 delineation between the “−10 to −20°F” and the “−20 to −30°F” hardiness zones closely matches the northern range limit for *T. s. elegans*; the 2004 data place this transition line hundreds of kilometers farther north in some areas. This rapid, substantial winter climate shift could have considerable influence on the early life-history stage addressed in our study. Consequently, the most plausible scenario of global warming bodies ill for the physiology, and perhaps fitness, of *T. s. elegans* and similar species, as well as of other ectotherms with obligate, nonfeeding winter stages.

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