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ARTICLE

Body size of ectotherms constrains thermal requirements for reproductive activity in seasonal environments

Jared W.H. Connoy, Jessica A. Leivesley, Ronald J. Brooks, Jacqueline D. Litzgus, and Njal Rollinson

Abstract: Body size may influence ectotherm behaviour by influencing heating and cooling rates, thereby constraining the time of day that some individuals can be active. The time of day at which turtles nest, for instance, is hypothesized to vary with body size at both inter- and intra-specific levels because large individuals have greater thermal inertia, retaining preferred body temperatures for a longer period of time. We use decades of data on thousands of individual nests from Algonquin Park, Ontario, Canada, to explore how body size is associated with nesting behaviour in Painted Turtles (*Chrysemys picta* (Schneider, 1783); small bodied) and Snapping Turtles (*Chelydra serpentina* (Linnaeus, 1758); large bodied). We found that (*i*) between species, Painted Turtles nest earlier in the evening and at higher mean temperatures than Snapping Turtles, and (*ii*) within species, relatively large individuals of both species nest at cooler temperatures and that relatively larger Painted Turtles nest later in the evening compared with smaller Painted Turtles. Our data support the thermal inertia hypothesis and may help explain why turtles in general exhibit geographic clines in body size: northern environments experience more daily variation in temperature, and larger size may evolve, in part, for retention of preferred body temperature during terrestrial forays.

Key words: Painted Turtle, *Chrysemys picta*, Snapping Turtle, *Chelydra serpentina*, thermoregulation, biogeography, ectothermy.

Résumé : La taille du corps pourrait influencer le comportement des ectothermes en influant sur les taux de réchauffement et de refroidissement, restreignant ainsi la période de la journée durant laquelle certains individus peuvent être actifs. Il est par exemple postulé que la période de la journée durant laquelle les tortues nidifient varie en fonction de la taille du corps tant au sein d'une même espèce que d'une espèce à l'autre, puisque les grands individus ont une plus grande inertie thermique, pouvant ainsi maintenir leur température de prédilection durant une plus longue période. Nous utilisons des données sur plusieurs décennies pour des milliers de nids distincts dans le Parc Algonquin (Ontario, Canada) pour examiner l'association entre la taille du corps et le comportement de nidification chez les tortues peintes (*Chrysemys picta* (Schneider, 1783); à petit corps) et les tortues serpentines (*Chelydra serpentina* (Linnaeus, 1758); à grand corps). Nous constatons que (*i*) entre ces espèces, les tortues peintes nidifient plus tôt le soir et à des températures moyennes plus élevées que les tortues serpentines, et (*ii*) au sein de l'espèce, les individus relativement grands des deux espèces nidifient à des températures plus faibles et les tortues peintes plus grandes nidifient plus tard le soir que les tortues peintes plus petites. Nos données appuient l'hypothèse de l'inertie thermique et pourraient aider à expliquer pourquoi les tortues en général sont caractérisées par des clines géographiques de la taille du corps : les milieux nordiques présentent une plus grande variation journalière des températures, et une évolution vers de plus grandes tailles pourrait, en partie, permettre le maintien de la température corporelle de prédilection durant les sorties en milieu terrestre. [Traduit par la Rédaction]

Mots-clés : tortue peinte, *Chrysemys picta*, tortue serpentine, *Chelydra serpentina*, thermorégulation, biogéographie, ectothermie.

Introduction

Reproductive timing is a life-cycle event that can affect all components of fitness (Rowe and Ludwig 1991; Rowe et al. 1994; Einum and Fleming 2000; Edge et al. 2017). Major drivers of reproductive timing include environmental factors, especially temperature (Rodel et al. 2005; Love et al. 2010; Janzen et al. 2018), as well as individual characteristics, such as age, body size, and condition (Price et al. 1988; Jonsson et al. 1990; Rowe et al. 1994). Variation in reproductive timing has received increased attention in recent years, as rapid climate warming has led to widespread phenological advance in first breeding date of many species and populations (Menzel et al. 2006; Poloczanska et al. 2013). A majority of studies have focussed on variation in reproductive timing within populations across years (Chiba et al. 2008; Staudinger et al. 2013; Yiming et al. 2013; Cohen and et al. 2018), presumably because variation at this scale is associated with relatively large fitness consequences (Miller-Rushing et al. 2010; Yang and Rudolf 2010; Edge et al. 2017). Yet, reproductive timing also varies at much finer scales. For example, in many species of ectotherms, nesting can be completed in less than an hour, and interactions between individual characteristics and environmental effects may underlie variation in nesting time at these fine scales. Although such fine-scale

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studies may reveal ecologically important drivers of behaviour, such relationships are rarely examined.

Freshwater turtles are interesting study organisms with which to explore the drivers of variation in nest timing. Freshwater turtles are typically semi-aquatic, and all turtles oviposit on land. Thus, turtles often transition from water, a relatively stable environment with high thermal inertia, to land, a more thermally dynamic environment. Once on land, a turtle's body temperature changes relatively rapidly, usually gaining heat quickly in the hot midday sun or losing it quickly in the early morning or late evening. It is therefore interesting that nest time with respect to time of day (henceforth nest hour) varies across turtle species and populations, with some nesting exclusively at night or entirely avoiding midday (Table 1). Iverson et al. (1997) were the first to propose what we term the "thermal inertia hypothesis", where geographic patterns in nest hour are caused by thermal constraints: overnight lows in cool, northern environments preclude nesting in all but the largest individuals, as large individuals have the greatest propensity to retain heat from thermally stable water bodies. Frye et al. (2017) found that Painted Turtles (*Chrysemys picta*) nest later into the night when temperatures are warmer, and based on this finding, they suggested that broader patterns in nest hour are at least partly explained by the fact that air temperatures are likely to limit nest hour of small-bodied species. Small-bodied species have less thermal inertia and hence their body temperatures conform more rapidly to cool morning temperatures or hot midday temperatures, after emergence from thermally stable water bodies.

Consistent with Frye et al. (2017)'s hypothesis, a synthesis of nesting patterns for North American freshwater turtles (Table 1) suggests that small turtles nest in the evening and at night in colder climates, while larger turtles have a wider range of nest hour. For example, female Painted Turtles in Wisconsin (USA) typically nest in the morning (i.e., after sunrise; Mahmoud 1968), while 30% of females nest in the morning in Pennsylvania (USA) (Ernst and Lovich 2009), 24% in Michigan (USA) (Congdon and Gatten 1989), 12% in Illinois (USA) (Frye et al. 2017), but only 2% in southwestern Quebec (Canada) (Christens and Bider 1987), and none in Minnesota (USA) (Legler 1954) or Nebraska (USA) (Frye et al. 2017). A weaker pattern can be seen for the large-bodied Snapping Turtle (*Chelydra serpentina*), with 94% of females nesting in the morning in South Dakota (USA) (Hammer 1969), 65% in Michigan (Congdon et al. 1987), 63% in New Jersey (USA) (Hotaling 1990), 44% in New York (USA) (Petokas and Alexander 1980), 36% in Nebraska (Iverson et al. 1997), and 35% in Algonquin Park, Ontario (Canada) (Steyermark et al. 2008). Although these studies differ in their methods, durations, and sample sizes, wide geographic variation in nest hour is apparent. Clearly, there is considerable descriptive work performed on nest hour in turtles, but little quantitative work has explored the factors driving such variation.

Freshwater turtles also exhibit puzzling geographic clines in body size (Ashton and Feldman 2003; Litzgus et al. 2004; Litzgus and Smith 2010; Santilli and Rollinson 2018), and classic ecological literature suggests size clines may be related to thermal inertia, at least in birds and mammals (Bergmann 1847; James 1970). Thermal inertia is a viable hypothesis for size clines in some ectotherms as well, as body size has a nontrivial influence on heating and cooling rates. For instance, a 1% increase in mass results, on average, in a 0.5% decrease in cooling rate of a turtle in water (Weathers and White 1971). Given that thermal inertia is greater in larger ectotherms (Stevenson 1984*a*), thermal inertia during terrestrial forays, including during nesting, may also help explain why body size of turtles increases along with latitude.

There is no comprehensive analysis of factors affecting nest hour in turtles, even for the well-studied Painted Turtle and Snapping Turtle. A comparative study of nest hour in Painted Turtles and Snapping Turtles from the same location may shed light on the validity of the thermal inertia hypothesis and hence may help uncover the factors affecting nest time both locally and over a latitudinal gradient. In the present study, we use long-term nesting data to fill this knowledge gap, offering an analysis of the drivers of turtle nest hour, as well as some insight into why nest hour varies within and between species across broad geographical scales. The thermal inertia hypothesis states that small body size constrains nest hour in turtles, at both interspecific and intraspecific levels, by virtue of the positive association between body size and thermal inertia. We therefore predict that (1) turtle nesting preferences with respect to temperature are non-random and thus the mean and variance of temperature at nest hour will be different from a null distribution of temperature. We also expect that small turtles will exhibit faster heating and cooling rates and are therefore more constrained by temperature than larger turtles, and thus predict that (2) between and within species, smaller turtles will nest at relatively higher temperatures than larger turtles, because larger turtles are able to conserve heat more effectively and hence nest at cooler temperatures. Because temperatures decline throughout the evening and are generally coolest in the early morning, we also predicted that (3) larger turtles, within and between species, will nest later into the night (and into the early morning for Snapping Turtles). For clarity, we refer to these predictions as predictions 1–3 in the Materials and methods and Results.

Materials and methods

Study sites and populations

Our study is part of a larger life-history study of turtles initiated in 1972 (Snapping Turtles) and 1978 (Painted Turtles). All methods were approved under the Animal Use Protocols from the University of Toronto (No. 20011948) and Laurentian University (2008-12-02, 2017-02-01), and a Scientific Collectors Permit from Ontario Parks (No. 1093596).

All study sites were along the Highway 60 corridor in the west end of Algonquin Provincial Park, Ontario, Canada. These sites included the Arowhon ponds, which includes Wolf Howl Pond and West Rose Lake (45°34′N, 78°41′W), the shoulders of Highway 60 from the Two Rivers campground to the Highland Trail entrance (45°34′N, 78°30′W and 45°34′N, 78°31′W, respectively), the Lake Sasajewun dam on the Algonquin Wildlife Research Station (AWRS) property (45°35′N, 78°30′W), and Mew Lake campground (45°34′N, 78°30′W). Some miscellaneous sites were also included in the data if turtles were seen and reported outside these zones, but still within the boundaries of the Highway 60 corridor in the west side of the park. The Arowhon ponds have a very large population of Painted Turtles (400 individuals; Samson 2003), resulting in the Painted Turtle data coming from these sites. Conversely, most Snapping Turtle data came from the shoulders of Highway 60 and the Lake Sasajewun dam, with the maximum distance between all sites being approximately 30 km. A vast majority of nesting activity for Snapping and Painted turtles occurs in June in Algonquin Provincial Park, with a few exceptions occurring at the end of May and early July.

Data collection

We brought all captured turtles to the AWRS for measurements. Carapace length of Snapping Turtles was measured to the nearest 0.1 cm using Haglof tree calipers. Plastron length of Painted Turtles was measured to the nearest 0.01 cm using Vernier calipers. Painted Turtles in our study sites had a mean plastron length of 14.85 cm, whereas Snapping Turtles had a mean carapace length of 28.6 cm. Painted Turtles had minimum and maximum plastron lengths of 11.64 and 17.95 cm, respectively. Snapping Turtles had minimum and maximum carapace lengths of 22.3 and 35.8 cm, respectively. Plastron length is a better measure of Painted Turtle body size than carapace length, as the latter varies due to spiked features in the cervical scute (Hawkshaw et al. 2019). Snapping Turtles, however, have very small plastrons and a

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Table 1. Nest-time patterns for North American freshwater turtles.

Species	Common name	Relative size	Maximum female length (cm)	Nesting time	Nesting climate	Notes
Chelydra serpentina (Linnaeus, 1758)	Snapping Turtle	Large	36.66	Dawn, dusk	Cold–warm	
Macrochelys temminckii (Troost in Harlan, 1835)	Alligator Snapping Turtle	Large	46	Dawn	Warm	Females prefer warm moist mornings and nest into the day
Actinemys marmorata (Baird and Girard, 1852)	Pacific Pond Turtle	Small–medium	20	Dawn, dusk	Medium–warm	
Chrysemys picta (Schneider, 1783)	Painted Turtle	Small	25.4	Dawn, dusk	Cold–warm	Nesting at dawn occurs more in southern and eastern populations
Clemmys guttata (Schneider, 1792)	Spotted Turtle	Small	14.25	Dawn, dusk, nighttime	Cold–warm	Nesting happens earlier in the night in northern populations
Emydoidea blandingii (Holbrook, 1838)	Blanding's Turtle	Small–medium	21.8	Dusk	Cold–medium	
Glyptemys insculpta (Le Conte, 1830)	Wood Turtle	Small	20.4	Dawn, dusk	Cold–medium	Nesting is more frequent at dusk for northern populations
Glyptemys muhlenbergii (Schoepff, 1801)	Bog Turtle	Small	9.63	Dusk–nighttime	Medium	
Graptemys barbouri Carr and Marchand, 1942	Barbour's Map Turtle	Large	33	Dawn	Warm	
Graptemys ernsti Lovich and McCoy, 1992	Escambia Map Turtle	Medium	28.5	All times	Warm	
Graptemys geographica (Le Sueur, 1817)	Northern Map Turtle	Large	27.3	Dawn	Cold–medium	
Graptemys nigrinoda Cagle, 1954	Black-knobbed Map Turtle	Small	22.1	Nighttime	Warm	
Graptemys ouachitensis Cagle, 1953	Ouachita Map Turtle	Medium	24	Dawn	Medium–warm	
Graptemys pseudogeographica (Gray, 1831)	False Map Turtle	Medium–large	27	Dawn	Medium–warm	
Malaclemys terrapin (Schoepff, 1793)	Diamond-backed Terrapin	Small–medium	28.8	Daytime	Medium–warm	Lives in coastal or brackish areas. Nesting time also dependent on tides
Pseudemys alabamensis Baur, 1893	Alabama Red-bellied Cooter	Large	33.5	Nighttime	Warm	
Pseudemys peninsularis Carr, 1938	Peninsula Cooter	Large	40.3	Dusk	Warm	
Terrapene carolina (Linnaeus, 1758)	Eastern Box Turtle	Small	19.8	Dusk	Cold–warm	Some individuals have been seen nesting in morning
Trachemys gaigeae (Hartweg, 1939)	Big Bend Slider	Medium	25.9	Dusk	Warm	
Kinosternon subrubrum (Bonnaterre, 1789)	Eastern Mud Turtle	Small	12.1	Dawn, dusk	Medium–warm	
Sternotherus odoratus (Latreille in Sonnini and Latreille, 1801)	Stinkpot	Small	15	Dawn–nighttime	Cold–warm	Nesting in northern range occurs mostly in evening
Apalone ferox (Schneider, 1783)	Florida Softshell	Large	67.3	Daytime	Warm	
Apalone mutica (Le Sueur, 1827)	Smooth Softshell	Medium–large	35.6	Dawn	Medium–warm	
Apalone spinifera (Le Sueur, 1827)	Spiny Softshell	Large	54	Dusk	Cold–warm	

Note: Patterns of nest time and body size in freshwater turtles across North America. All the information used to create this table comes from Ernst and Lovich (2009). Nesting climate and nest time is generalized and only for the purpose of illustrating patterns on a very broad geographical scale. Nesting climate is considered warm for tropical and subtropical climates, medium for temperate oceanic climates, and cold for temperate continental climates.

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significant amount of exposed flesh, making carapace length a better measure of body size for this species. Mass is highly variable throughout the nesting season and is therefore not a good measure of body size for female turtles during this period. Following measurement, females were marked with their ID (assigned to them through unique notches in the carapace when they are first caught in the long-term study) by painting their carapace so that they could be identified without being disturbed while nesting. If an unmarked female was seen while laying eggs, she was captured after she had completed nesting and was then brought back to the laboratory and measured as above.

We began nesting patrols when turtles displayed signs of bearing eggs, which we assessed by inguinal palpation (that we performed from sampled turtles daily in the month leading up to the nesting season). At the Arowhon sites, nesting surveys typically began in the late afternoon and ended when nesting behaviour ceased, typically between 2230 and 0100. Surveys ended only when turtles were not seen for extended periods of time (typically 2 h or more) and (or) if temperatures seemed low enough to discourage both turtle species from nesting (typically <10 °C). At all other sites, the methods described above were conducted in addition to morning surveys, which began daily at 0500. Thus, there is a high probability that morning nests of both species were missed at the Arowhon sites (except in a small subsample of years when morning surveys occurred), but it is unlikely that bias exists at any other sites.

We recorded nest hour as the time of day at which a female left a completed nest and was measured to the nearest minute. Air temperature was recorded at that time at the nest to the nearest 0.1 °C using a digital probe thermometer. If females were missed leaving the nest by a narrow window of time (usually estimated at less than 10–15 min), then temperature was taken and nest hour was recorded as the estimated time.

Data vetting

Our nesting data spanned 1972–2018 for Snapping Turtles and 1996–2018 for Painted Turtles. The data were screened for data-entry or data-recording errors by creating histograms for each factor of interest (plastron length, carapace length, air temperature, nest hour) and removing impossible and highly implausible values. Sample sizes differ at the intraspecific level for the analyses below, even when analyses are based on the same study area. Unless otherwise described, the difference arises because some nesting records had complete nesting information (nest hour and temperature), whereas only nest hour was recorded for some nests.

Exploring nest-hour bias in the Painted Turtle data

We did not typically perform morning surveys at the Arowhon sites, but these sites represent the overwhelming majority of nest-hour data for Painted Turtles. If morning nesting is common in our Painted Turtles, then our nest-hour data and temperature data from Arowhon are biased. Therefore, before testing the thermal inertia hypothesis, we explored the possibility of bias in the Arowhon Painted Turtle data. Between 2000 and 2018, regular morning (approximately 0500 to 1000) and evening (approximately 1600 until between 2230 and 0100) patrols were performed at several sites with low densities of Painted Turtles and Snapping Turtles (namely, Lake of Two Rivers, Mew Lake, the Highway 60 Corridor, Pog Lake, and Whitefish Lake). We used these data to explore the proportion of Painted Turtles that nest in the morning, relative to evening. If the proportion of Painted Turtles that nest in the morning is very low, then our Arowhon data (where morning surveys are not typically performed) comprise a representative sample of Painted Turtle nests with which to explore the thermal inertia hypothesis.

Are nesting patterns non-random with respect to temperature?

We tested whether the mean and variance of temperature at nest hour is different from a null distribution (i.e., prediction 1). We compared the distribution of air temperatures at nest hour for all nests in the month of June (which encompasses the overwhelming majority of turtle nesting observations) to the entire distribution of June air temperatures for the years 2005 to 2018. This period was analyzed because climate data were not available for years prior to 2005. For this analysis only, the climate data used were not directly measured at the study sites themselves, but instead came from a nearby weather station, 21 km from the nearest study site, and 34 km from the farthest site. The use of weather station data was necessary because we endeavoured to directly compare the air temperatures selected by turtles to a null distribution of air temperatures (i.e., all available temperatures), and a null distribution was available only from the weather station. To perform this comparison, turtle nest times were rounded to the nearest hour and the air temperature at nest hour measured at the study site was replaced by the air temperature measured at the weather station at that time. Using these data, the distributions of (*i*) air temperature at nest hour for both species and (*ii*) all air temperatures were created in R version 3.6.2 (R Core Team 2019). These data were then used to test for differences in median temperatures among test groups, as well as differences in temperature variance among groups, to thereby address the question of whether temperature at nest hour for Painted and Snapping turtles is different from a null distribution.

We used a Levene's test to explore whether variances differed among the three groups (all hourly June air temperatures, air temperature at nest hour for Painted Turtles, and air temperature at nest hour for Snapping Turtles). Given that the Levene's test suggested that the assumption of homogeneity of variances was not satisfied across the three groups, we used a Kruskal–Wallis test to determine if median temperature differed among the test groups.

Do large-bodied turtles nest at cooler temperatures?

We tested whether larger turtles, between and within species, nest at relatively lower temperatures than smaller turtles (i.e., prediction 2). The test of this prediction uses a different data set than prediction 1 (immediately above), as we leverage direct temperature measurements taken at nest hour at our study sites. To test this prediction at the interspecific level, we compared mean temperature at nest hour between Painted Turtles and Snapping Turtles. We fit a linear mixed model using the lmer function in the lme4 package (Bates et al. 2015) in R, with air temperature at nest hour as the dependent variable and species as a fixed effect, with random intercepts for year, individual days within a given year, turtle ID, and nest site (Arowhon Ponds vs. Sasajewun dam, etc.). To test this prediction at the intraspecific level, we fit a linear mixed model, separately for each species, with air temperature at nest hour as the dependent variable and body size as a fixed effect (carapace length for Snapping Turtles, plastron length for Painted Turtles), with random intercepts for year, individual days within a given year, turtle ID, and nest site.

Do large-bodied turtles nest later in the evening?

We tested whether larger turtles, within and between species, nest later into the night, and into the early morning for Snapping Turtles (i.e., prediction 3). Analysis of hourly data typically requires a circular data transformation to account for the fact that 2359 is followed by 0000. Given that our exploration of bias in the Painted Turtle data revealed that morning nesting is rare in Painted Turtles (see Results), and in fact comprise ~2% of Arowhon nesting data ($n = 49$), we removed morning nests from the data set. The benefit of this approach was that minimal data were removed and statistical clarity was achieved, as a circular analysis

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became unnecessary for Painted Turtles, given that all nests in the analysis occurred in the evening before midnight.

First, to visualize the data, we created daily nest-hour profiles using the "circular" package in R (Agostinelli and Lund 2017). Next, we constructed linear mixed models using the lmer function in the lme4 package in R with nest hour as the dependent variable and body size as the independent variable for Painted Turtles and Snapping Turtles separately. For Painted Turtles, we generated one mixed model with plastron length as a fixed effect and random intercepts for year, individual days within a given year, turtle ID, and nest site.

A circular analysis was not possible for Snapping Turtles, as nest hour exhibited a bimodal distribution and bimodality violates the assumption of a projected normal distribution in circular analysis (Cremers et al. 2018). To overcome this issue, we divided the data into "morning" and "evening" nesting periods, creating two data sets with unimodal distributions that could be analyzed using linear models. The periods were defined as 0300–1200 (a 9 h period; morning) and 1200–300 (a 15 h period; evening, including into the morning of the following day). To facilitate linear analysis and interpretation, the data in these periods were transformed so that the first hour was hour 0. We analyzed these two data sets in two separate mixed models, fit as above for Painted Turtles, with carapace length as a fixed effect.

Lastly, we tested the prediction that larger bodied turtles nested later in the evening at the interspecific level, by examining differences between Snapping Turtle and Painted Turtle nest hour during this period. This analysis was restricted to the evening data (1200–0300), comparing mean nest hour between Painted Turtles and Snapping Turtles. We fit a linear mixed model using the lmer function in the lme4 package in R, with species as a fixed effect and random intercepts for year, individual days within a given year, turtle ID, and nest site. Finally, we tested whether body size of Snapping Turtles differed between morning and evening nests, using mixed model analysis, with time of day (i.e., evening vs. morning) as a fixed effect and with random effects fitted as above.

Results

Exploring nest-hour bias in the Painted Turtle data

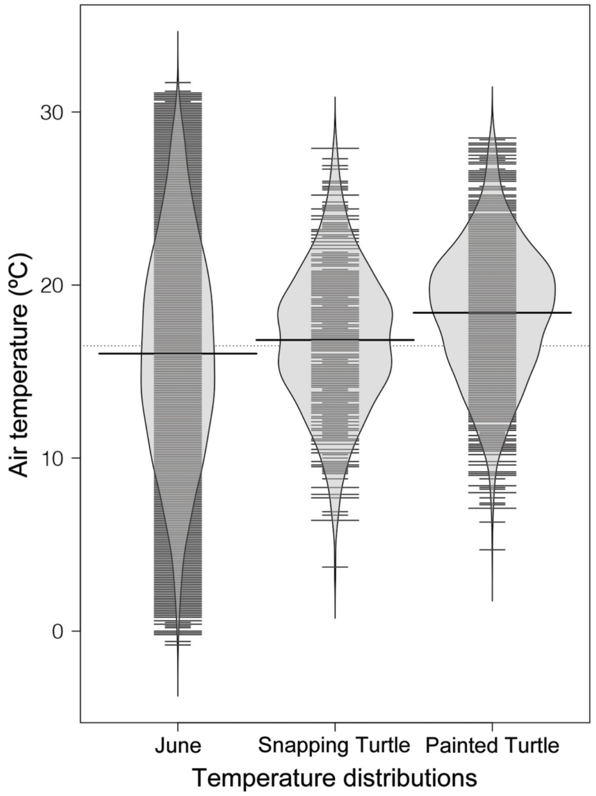
We recorded 201 Painted Turtle nests during our regular morning and evening surveys (occurring at all sites other than the Arowhon ponds). The number of nests recorded between 0500 and 1200 was 5, representing 2.5% of nests. Interestingly, of the 277 Snapping Turtle nests encountered during the same surveys, 152 were in the morning, representing 55% of the data. Because only a small proportion of Painted Turtle nests occur in the morning in our study populations, we conclude that our Arowhon Painted Turtle data are not strongly biased, even though morning nest surveys were not typically performed. We therefore used Arowhon Painted Turtle data to test predictions of the thermal inertia hypothesis in the following analyses.

Are nesting patterns non-random with respect to temperature?

We acquired 10 013 measurements of June air temperature from a weather station near our study sites. During the turtle nesting season, mean air temperature peaks around 1300 (at ~22 °C), on average, and steadily decreases to a minimum at around 0500 (at ~10 °C), on average, at which point it begins to increase.

We recorded 514 Snapping Turtle nests and 2290 Painted Turtle nests in June, for which air temperature at nest hour could be estimated from a nearby weather station. Levene's test showed that the variances of the three groups were not equal ($F_{[2,\ 12\,814]} = 343$, $P < 0.001$; Fig. 1). Variance was lower for both species compared with the distribution of June temperatures (Painted Turtles: $F_{[1,\ 12\,301]} = 591$, $P < 0.001$; Snapping Turtles: $F_{[1,\ 10\,525]} = 119$, $P < 0.001$; Fig. 1). Median temperatures also differed among the three groups (Kruskal–Wallis test, $\chi^2_{[2]} = 377$, $P < 0.001$; Fig. 1). Median temperature at nest hour for Painted Turtles was warmer than the median June temperature (Kruskal–Wallis test, $\chi^2_{[1]} = 369$, $P < 0.001$; Fig. 1), and median temperature at nest hour for Snapping Turtles was also greater than the June median temperature (Kruskal–Wallis test, $\chi^2_{[1]} = 11.3$, $P < 0.001$; Fig. 1).

Fig. 1. Beanplots showing distributions of temperatures from 2005 to 2018 for the month of June from Algonquin Provincial Park, Ontario, Canada, as well as air temperature at the time of nesting for all Painted Turtles (*Chrysemys picta*) and Snapping Turtles (*Chelydra serpentina*) in our study.



Do large-bodied turtles nest at cooler temperatures?

At the interspecific level, our mixed model analysis revealed that temperature at nest hour differed significantly between species, being 2.54 ± 0.0283 °C ($P < 0.001$) greater for Painted Turtles than Snapping Turtles. At the intraspecific level, we found that body size and temperature at nest hour were significantly negatively related for both species (Figs. 2*a* and 2*b*), indicating that larger individuals nest at cooler temperatures.

Do large-bodied turtles nest later in the evening?

Visualization of Painted Turtle nesting at the Arowhon ponds was concentrated between 1400 and 2400, with approximately 1% of Painted Turtles nesting outside this range ($n = 3725$; Figs. 3*a* and 3*b*). On the other hand, nest-hour data suggest Snapping Turtles nest around the clock, with few nesting between 0200 and 0500 and between 1200 and 1600 ($n = 2304$; Figs. 3*c* and 3*d*). The mean nest hour for Painted Turtles was 1945, and the mean nest hours for Snapping Turtles were 0818 and 1926 for the morning and evening periods, respectively (Figs. 3*a*–3*d*). We found that Painted Turtles nested 1.44 ± 0.210 h earlier in the evening, on average, than Snapping Turtles ($P < 0.001$), supporting the thermal inertia hypothesis at the interspecific level.

At the intraspecific level, we found that relatively large individual Painted Turtles nested significantly later in the evening: for

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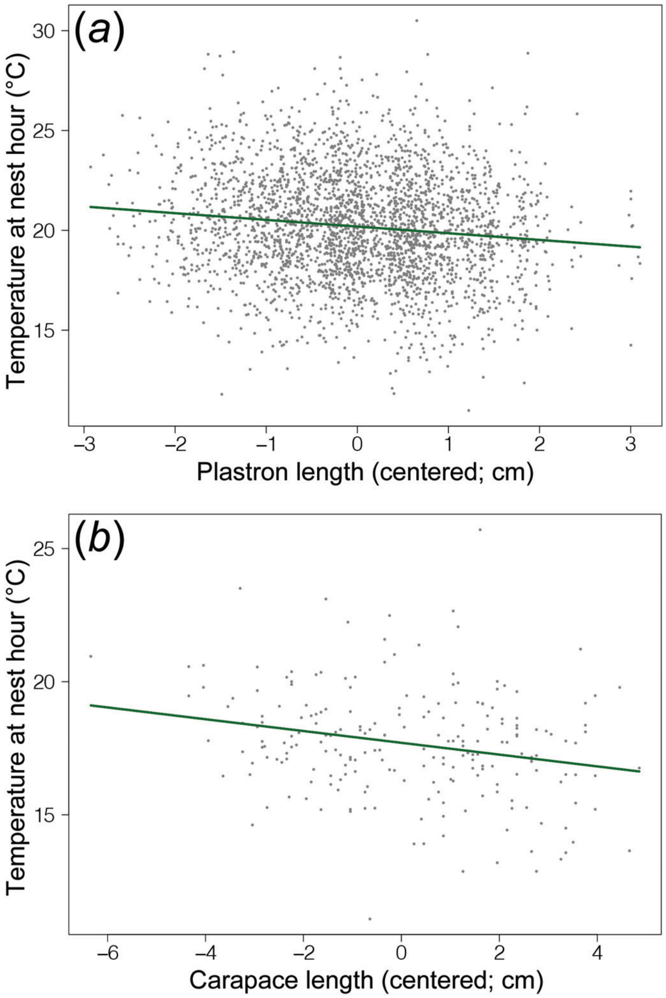
Fig. 2. The relationship between air temperature at nest hour and (*a*) Painted Turtle (*Chrysemys picta*) plastron length (−0.335 ± 0.0806 (slope ± SE), $P < 0.001$) and (*b*) Snapping Turtle (*Chelydra serpentina*) carapace length (−0.211 ± 0.919 (slope ± SE), $P = 0.0170$). Colour version online.



every 1 cm increase in plastron length, nest hour increased by 0.140 ± 0.0374 h ($P < 0.001$, $n = 3299$). However, we did not find an association between body size and nest hour in Snapping Turtles in the morning (0.0477 ± 0.0472 h (slope ± SE), $P = 0.32$, $n = 194$) or in the evening (0.140 ± 0.0764 h (slope ± SE), $P = 0.07$, $n = 224$). Body size of Snapping Turtles nesting in the evening was not significantly larger (difference of 0.053 ± 0.064 cm (mean ± SE), $P = 0.41$) than those nesting in the morning, despite the mean temperature at nest hour being significantly cooler (difference of −0.930 ± 0.454 °C (mean ± SE), $P = 0.04$) in the morning.

Discussion

We used long-term nesting data from Painted and Snapping turtles to test the thermal inertia hypothesis, in which small body size constrains nest hour in turtles by virtue of the positive association between body size and thermal inertia. First, we uncovered evidence of temperature preference for nesting, a basic pre-requisite of the thermal inertia hypothesis. Specifically, both species of turtle nested at temperatures that were warmer than the median environmental temperature, and the variance in nesting temperature for both species was lower than the variance of all available temperatures. Our subsequent analyses generally support the notion that large body size is associated with relatively cool air temperatures at nesting, and that individuals with large body size nest relatively later in the evening or in the cool morning hours.

The thermal inertia hypothesis underlines how small ectotherms may be constrained to activity that occurs during a relatively narrow window of temperature during the day. We predicted that smaller species would avoid relatively cooler temperatures, and indeed, we found that air temperature at nest hour was, on average, 2.54 °C warmer for a small-bodied species (the Painted Turtle) compared with a large-bodied species (the Snapping Turtle). It has been shown experimentally that small turtles cool faster than larger turtles (Weathers and White 1971), and it is possible that Painted Turtles avoid cool nesting temperatures because small turtles cannot maintain a sufficiently high body temperature to maintain nesting activity (e.g., digging). It is also possible that lower temperatures are avoided because they slow activity, dramatically prolonging nesting (N. Rollinson, personal observation), and potentially increasing the risk of predation on adults and nests. Differences in physiological tolerance for heat may exist between Painted Turtles and Snapping Turtles; however, our data suggest that this is unlikely to be the only explanation for Painted Turtles nesting at higher temperatures. Specifically, within both species, smaller turtles nested at higher temperatures than their larger conspecifics (Figs. 2*a* and 2*b*). A decrease of 5 cm in plastron length for Painted Turtles (a variation present in sexually mature Painted Turtles) was associated with an increase in nesting air temperature of 1.67 °C, and a decrease of 10 cm in carapace length for Snapping Turtles (a variation present in sexually mature Snapping Turtles) was associated with an increase in nesting air temperature of 2.21 °C. Thus, both within and between species, large individuals nested at relatively low mean temperatures.

If the thermal inertia hypothesis is correct, then large-bodied turtles are less constrained by temperature and can sample nest times from relatively cool hours of the day. This prediction was generally supported. At the interspecific level, Painted Turtles generally did not nest in the morning (when temperatures are relatively cool), whereas about half of all Snapping Turtle observations were during this time. Furthermore, Painted Turtles nested significantly earlier in the evening (when air temperature is typically higher) than Snapping Turtles. At the intraspecific level, we found that a 5 cm increase in plastron length for Painted Turtles was associated with a nest hour that was 0.70 h (42 min) later in the evening, on average. There was no association between size and nest hour in the evening in Snapping Turtles, although the pattern was suggestive of a relationship (0.140 ± 0.0764 h (slope ± SE), $P = 0.07$, $n = 224$), and Snapping Turtles that nested in the morning were not larger than those that nested in the evening. Broadly, these results are consistent with the idea that the large size of Snapping Turtles releases them from thermal constraints, such that individuals of this species can nest in the morning or in the evening. Given that larger individual Snapping Turtles tend to nest at cooler temperatures, but that size of Snapping Turtles is only weakly associated with nest hour, it seems reasonable to conclude that temperature, not nest hour, is a more important driver of the underlying size-specific pattern.

The thermal inertia hypothesis gains further plausibility when we consider that the fitness consequences associated with nesting at specific times of day are unclear. For instance, one could argue that small turtles are relatively vulnerable to predation by visually oriented predators, such as corvids (Loehr 2017). In the small-bodied Painted Turtle, then, the negative association between air temperature and body size, as well as the positive association between body size and nest hour, may reflect a general preference to lay eggs, when possible, under cover of darkness to avoid detection and predation. However, we observed similar relationships between body size, air temperature, and nest hour in Snapping Turtles, a species whose mean size eclipses that of Painted Turtles, rendering size-based adult predation an unlikely

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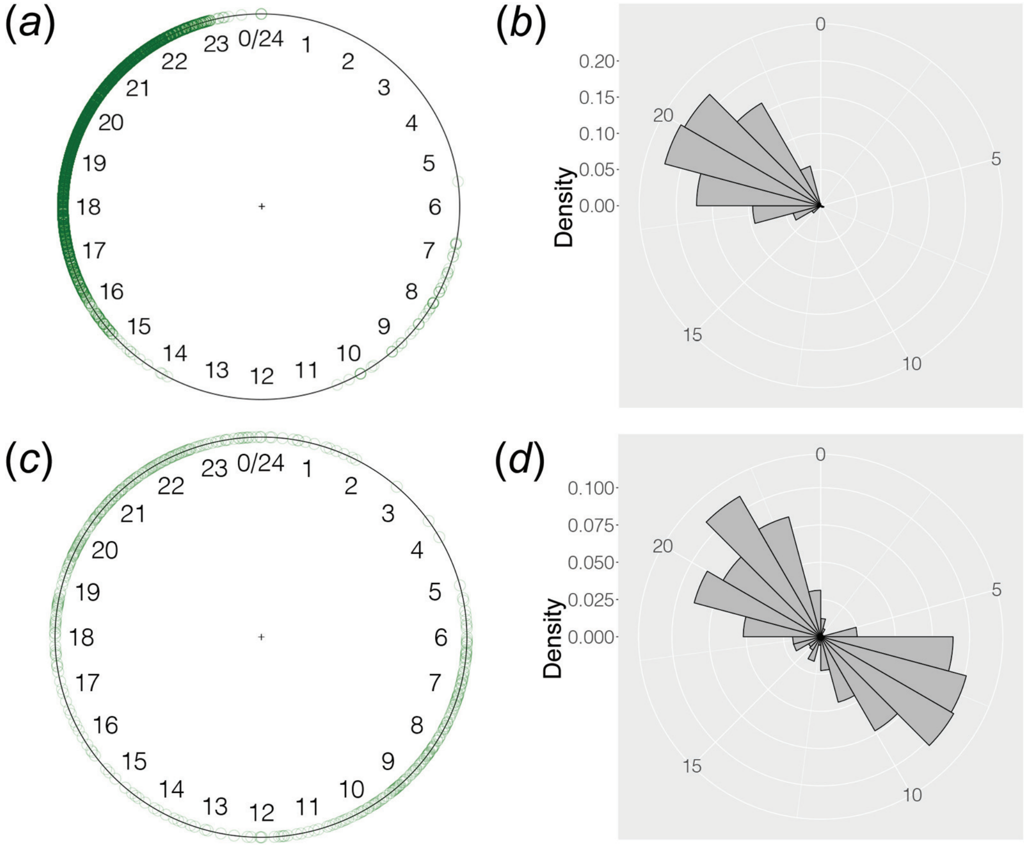
Fig. 3. Nest-hour profiles and circular histograms for (*a*, *b*) Painted Turtles (*Chrysemys picta*) and (*c*, *d*) Snapping Turtles (*Chelydra serpentina*) on a 24 h clock. The mean nest hour for Painted Turtles is 1945. The mean nest hours for Snapping Turtles are 0818 and 1926 for the morning and evening periods, respectively. Snapping Turtles have a smaller mean resultant length ($\rho = 0.0553$) than Painted Turtles ($\rho = 0.890$), indicating that the nest-hour data for Snapping Turtles has greater variation. Colour version online.



explanation for nesting patterns. On the other hand, nest predation affects recruitment in many turtle species (Congdon et al. 1983, 1987; Marchand et al. 2002; Schwanz et al. 2010), and nest predators that are strongly visually oriented are perhaps less likely to be active at night (Congdon et al. 1987; Rollinson and Brooks 2007; Riley and Litzgus 2014). Under this explanation, larger turtles gain an advantage by selecting nest hours that are associated with few nest predators, and temperature at nest hour is selected indirectly. This seems unlikely given that a majority of nest predation is probably based on olfactory cues (Congdon et al. 1983; Spencer 2002; Burke et al. 2005), or visual cues that are independent of the physical presence of the nesting female, such as markings in the sand (Congdon et al. 1983; Spencer 2002; Strickland et al. 2010). In the absence of further evidence, we suggest our data are sufficiently explained by an ability of relatively large individuals to retain heat for longer periods.

Turtles are among the only ectothermic vertebrates to broadly follow James' rule, which is the propensity for population-mean body size to become larger at cooler temperatures and (or) higher latitudes (Blackburn et al. 1999; Ashton and Feldman 2003). Currently, there is no general explanation for these clines in turtles (Santilli and Rollinson 2018). The classical explanation for James' rule (and Bergmann's rule; Bergmann 1847) is that larger body sizes have a smaller surface area to volume ratio, which would help conserve energy (heat) in relatively cool environments. Although this explanation may be adequate for endotherms, it is typically dismissed for ectotherms as a reason for geographic or elevation size clines, primarily because of a lack of clear benefit to heating or cooling rates in different environments (Stevenson 1985*b*; Watt et al. 2010; Santilli and Rollinson 2018). Recent work, however, suggests that the validity of the heat conservation hypothesis among ectotherms depends on whether the rate of heating with respect to size is greater than the rate of cooling, and as such heat conservation may be a reasonable explanation for body size clines in ectotherms (Zamora-Camacho et al. 2014). We suggest that heat conservation may explain, at least in part, why freshwater turtles consistently exhibit size clines. Specifically, air temperature is generally more variable than water temperature, and during the active season (especially in summer and early fall), water temperature may be likely to stay within the preferred range of turtles. A larger body may be more advantageous in northern environments for retention of preferred temperature during forays out of water, given that in the northern hemisphere, relatively northern (seasonal) environments experience much more diurnal variation in air temperature than southern (aseasonal) environments (Angilletta 2009). This explanation may be complementary to other existing hypotheses for body size clines in turtles, such as the oxygen limitation hypothesis (Santilli and Rollinson 2018) or the hypothesis that mortality increases with temperature (Kozłowski et al. 2004). Our explanation also draws on the idea that size clines in turtles are likely related to the semi-aquatic nature of this group, given that ectothermic vertebrates that are primarily terrestrial generally do not show geographic size clines (Ashton and Feldman 2003; Adams and Church 2008; Horne et al. 2015).

A highlight of our study is that it demonstrates how body size, both within and across species, can drive variation in behaviour in ectothermic vertebrates. Ours is the first comprehensive study, to our knowledge, to analyze the individual effects driving nest hour within and across turtle species, and is part of a larger body of

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research which has shown that other nesting behaviours are influenced by temperature (Bowen et al. 2005; Frye et al. 2017). Nesting behaviour is also related to rainfall in several species of turtle (Bowen et al. 2005), and future work should address relationships among rainfall, temperature, body size, and nest hour. Further studies on this topic could also expand to include a larger array of turtle species across geographic scales to improve our understanding of the relationships described in this paper on a scale where climate is also a variable. This work also invites new ideas on how the relationship between body size and thermal inertia may influence behaviour in turtles and other ectotherms.

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