
REASSESSMENT OF AGASSIZ’S WOOD TURTLE COLLECTIONS REVEALS SIGNIFICANT CHANGE IN BODY SIZE AND GROWTH RATES

MICHAEL T. JONES^{1,2,6}, LISABETH L. WILLEY^{3,4}, ALAN M. RICHMOND⁵, AND PAUL R. SIEVERT²

¹Natural Heritage and Endangered Species Program, Massachusetts Division of Fisheries and Wildlife, Westborough, Massachusetts 01581, USA

²Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts 01003, USA

³American Turtle Observatory, 90 Whitaker Road, New Salem, Massachusetts 01355, USA

⁴Environmental Studies Department, Antioch University New England, Keene, New Hampshire 03435, USA

⁵Biology Department, Morrill Science Center, University of Massachusetts, Amherst, Massachusetts 01003, USA

⁶Corresponding author; e-mail: michael.t.jones@state.ma.us

Abstract.—Mechanisms influencing body size in freshwater turtles are complex, but important because body size influences reproductive output, survivorship, and behavior. Two proximate drivers of body size in freshwater turtles are temperature-related factors and density-dependent factors. Large museum collections from the 19th Century provide a basis by which to evaluate environmental drivers of body size. One of the largest series from the 1800s is a collection of Wood Turtles (*Glyptemys insculpta*) from Lancaster, Massachusetts, USA, studied by Louis Agassiz. We compared shell dimensions, growth rates, and sexual dimorphism in the Agassiz sample to a sample of living turtles from Lancaster. Adult turtles living today are 20% larger in dimensions than 1850s turtles, and 1850s males are below the modern range of variation. The sexes are more dimorphic today, and modern juveniles grow significantly faster than 1850s counterparts. We used a recent, statewide sample to evaluate whether adult body size has changed significantly as a partial response to a warmer climate, or as a density-dependent response to population decline. Modern Wood Turtle body size across Massachusetts is positively associated with growing degree-days, and adult male body size is negatively correlated with population density. Our results suggest that the 1850s growth rate may have been reduced due to a cooler growing season, and that 1850s adult body size may have been constrained by density-dependent factors. Evidence for Wood Turtle population decline at Lancaster is anecdotal, but noteworthy: Agassiz reported collecting “over one hundred in an afternoon”; we estimated approximately 2.2 turtles per survey in 2009.

Key Words.—body size; climate change; density dependence; Emydinae, *Glyptemys insculpta*; intraspecific competition; Louis Agassiz; Massachusetts; New England; paleoecology

INTRODUCTION

The full suite of mechanisms influencing adult body size in freshwater turtles is complex (Congdon et al. 2013) but understanding the environmental drivers and plasticity of adult body size in freshwater turtles is important because adult body size influences survivorship and total reproductive output. Body dimensions of adult turtles have been shown to be positively associated with reproductive output as a result of larger clutch size (Congdon and Gibbons 1983) and larger egg dimensions (Congdon and Gibbons 1985; Congdon and Gibbons 1987; Ryan and Lindeman 2007; Walde et al. 2007). In some species of turtle, such as Blanding’s Turtle (*Emydoidea blandingii*), there is no clear link between age and body size in adults, but there is strong individual variation in adult body size (Congdon et al. 2001). Adult turtles of different sizes within one population may reflect long-term patterns in the environmental conditions that drive growth rates and/or adult body size and influence reproductive output.

Warmer environments have been shown experimentally to increase growth rates in turtles (Gibbons 1967; Thornhill 1982; Avery et al. 1993; Brown et al. 1994; Rhen and Lang 1999; Gotthard 2001), and studies have also shown that egg incubation temperatures may partly explain variation in post-hatchling growth rates (Roosenburg and Kelley 1996; Roosenburg 1996; O’Steen 1998; Rhen and Lang 1999; Janzen and Morjan 2002), though this effect sometimes varies by sex (Roosenburg and Kelley 1996; Janzen 2002). Through these and other mechanisms, increased temperature can result in changes to reproductive output, so understanding the influence of regional warming on body size and growth of freshwater turtles has implications for long-term conservation science and conservation planning. Climate models project the continuation of a pronounced warming trend for the northeastern U.S. (Hayhoe et al. 2007; Karmalkar and Bradley 2017), which is expected to have complex effects on ecosystems and species, including freshwater turtles (Ilhow et al. 2012). For example, a warming

climate is likely to reduce habitat availability for species with limited ranges (Barrows 2011; Ilhow et al. 2012; Lovich et al. 2014), may upset reproductive patterns and temperature-dependent sex ratios of even widespread and locally common species (Janzen 1994; Hulin et al. 2009; Ilhow et al. 2012; Telemeco et al. 2013), and may also influence growth rates, adult body size, and size-related reproductive parameters (Walde et al. 2007).

Adult body size and growth in freshwater turtles can also be influenced by density-dependent mechanisms. While most studies of density dependence in turtles have focused on nest depredation rates (e.g., Bustard and Tognetti 1969; Girondot et al. 2002; Caut et al. 2006) or estimates of cohort survivorship (Fordham et al. 2008), some authors have examined population-level compensation to experimental population declines (Fordham et al. 2009; Spencer and Janzen 2010). Across vertebrate groups, individuals in higher-density populations and resource-limited environments tend to grow more slowly, and there is often an inverse relationship between population density and growth rates (Beverton and Holt 1957, Leberg and Smith 1993; Rochet 1998; Bjorndal et al. 2000, Lorenzen and Enberg 2002). Some species of sea turtles have been observed to grow more slowly in high-density environments (Bjorndal et al. 2000), but growth rates have also been shown to increase in high-density environments under certain situations (Spencer et al. 2006). High relative population densities appear to influence adult body size in freshwater turtles indirectly by increasing competition (e.g., for food resources or basking sites), which may be relaxed at lower densities: inter- and intraspecific competition were hypothesized by Dunham and Gibbons (1990) to possibly reduce the growth rates of individual Pond Sliders (*Trachemys scripta*) exposed to greater competition. The influence of density-dependent factors on the growth and body size of most freshwater turtle species has not been studied.

We studied the relationships between growth and body size and regional warming and population density in wild populations of a long-lived vertebrate with widely overlapping generations, the Wood Turtle (*Glyptemys insculpta*). Wood Turtles are a fluvial specialist that occurs from Nova Scotia, Canada, to Minnesota, USA, and south as far as northern West Virginia and Virginia, USA (Harding and Bloomer 1979; Niederberger and Seidel 1999; Walde et al. 2003; Saumure et al. 2007; Ernst and Lovich 2009). Wood Turtles have apparently declined across their range and are a species of regional conservation concern (Jones, M.T., L.L. Willey, T.S.B. Akre, and P. Sievert. 2015. Status and Conservation of the Wood Turtle in the Northeastern United States. Technical report prepared for the Association of Fish and Wildlife Agencies (AFWA). Available from [\[rcngrants.org/sites/default/files/datasets/RCN2011-02v2.pdf\]\(http://rcngrants.org/sites/default/files/datasets/RCN2011-02v2.pdf\) \[Accessed 16 January 2017\]\).](http://</p></div><div data-bbox=)

We compared the body size of adult and juvenile Wood Turtles collected in Lancaster, Massachusetts, USA, in the 1850s, to a living population in the same town in 2009. We also explored the relationship of adult body size and growth rates in a recent (2004 to 2009) sample of living Wood Turtles from across Massachusetts to growing degree-days (an index of heat accumulation) and a relative estimate of Wood Turtle population density. Although body size and growth rate are functions of both genetic and environmental factors, we chose to focus on measurable environmental factors that have been shown to influence body size in turtles. Our study provides valuable insight into the population-level response of a high-concern freshwater turtle species to sustained, regional, environmental change.

MATERIALS AND METHODS

Museum collections from Lancaster.—The Museum of Comparative Zoology (MCZ) at Harvard University, Cambridge, Massachusetts, USA, and the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS) respectively house series of 35 and two Wood Turtles collected at Lancaster, Massachusetts in the mid-1800s. Together, the Lancaster collections form one of the largest surviving collections of Wood Turtles from the 19th Century (HerpNet. 2009. Data portal for searching online museum collections. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS). Available from <http://herpnet.org>. [Accessed 31 March 2009]; GBIF Occurrence Download; GBIF.org. Available from <https://doi.org/10.15468/dl.ywhpmz>. [Accessed 31 October 2017]). The MCZ specimens were assigned the original accession number R-1820, which is associated with the collector name Sanborn Tenney; the location Lancaster, Massachusetts; and the date 1854. Subsequently, nine specimens were assigned to the proceeding sequence R-1821–1829 and 12 were assigned to the sequence R-182718–182729, which bear the location Lancaster, Massachusetts, and the collector S. Tenney. Also, 13 specimens originally assigned the number R-1820 have been reassigned new accession numbers (MCZ# R-145853–145865) with the only location “Mass: Lancaster” but no collector or date. Two juvenile Wood Turtles attributed to Agassiz are included in SMNS 3794, with a location of Lancaster, Massachusetts, and a date of 1864; one of these was originally catalogued as “1820” and is likely from the same series as the MCZ specimens (i.e., 1854). The Tenney-Agassiz collections at MCZ and SMNS appear to represent a subset of a larger series referred to by



FIGURE 1. Plastrons of four adult female Wood Turtles (*Glyptemys insculpta*) collected by Tenney and Agassiz at Lancaster, Massachusetts, USA, about 1854, and subsequently studied by Louis Agassiz. A = MCZ 182720; B = MCZ 1823; C = MCZ 1828; D = MCZ 1821. (Museum of Comparative Zoology, Harvard University).

Agassiz (1857), who stated that he, along with Professor Sanborn Tenney and others, had “at times collected over one hundred [*G. insculpta*] in an afternoon, aided by a few friends...”

In 2009, we measured and photographed 20 Wood Turtles from the Agassiz-Tenney series at the MCZ (eight females, five males, seven juveniles; Fig. 1) and two juveniles at SMNS. We did not measure the remaining 15 specimens in the MCZ catalogue either because they were disintegrated, disintegrating, or could not be located. We digitally photographed and measured all of the intact, complete *G. insculpta* specimens at MCZ that could be confidently attributed to the 1850s Lancaster collections, and we requested photographs and measurements of the two specimens at SMNS. We recorded the straight-carapace length (hereafter, SCL) of each turtle, from the cranial end of the nuchal scute to the medial seam between the two most posterior marginal scutes, to the nearest 0.1 mm using dial calipers. We categorized a specimen as a juvenile when, if the plastral annuli showed no sign of crowding toward the medial line of the plastron, there were 14 or fewer annuli. We estimated the age of juvenile turtles by counting the inter-annular growth intervals of the left abdominal scute of the plastron (Richard et al. 2014). If the left abdominal scute was absent, we counted the growth intervals on the right abdominal scute. Counting



FIGURE 2. Plastrons of four adult male Wood Turtles (*Glyptemys insculpta*) collected by Tenney and Agassiz at Lancaster, Massachusetts, USA, about 1854, and subsequently discussed by Louis Agassiz (1857). A = MCZ 1822; B = MCZ 1824; C = MCZ 1826; D = MCZ 1827. (Museum of Comparative Zoology, Harvard University).

annuli has been found to be reliable estimates of age in juvenile *G. insculpta* (Harding and Bloomer 1979; Lovich et al. 1990; Wilson et al. 2003; Jones 2009).

Sampling the current population.—For comparative purposes, we obtained the same measurements from a living sample of Wood Turtles in the same town (Lancaster, Worcester County, Massachusetts, USA). Because the precise collection site by Tenney in Lancaster is not known, we searched suitable Wood Turtle habitat throughout the entire town, including the Nashua River and several of its tributaries. Lancaster is largely forested, with several suburban residential centers and a large military installation, the Devens Reserve Forces Training Area. One or two observers surveyed suitable streams during 25 half-day surveys between March and October 2009. When Wood Turtles were captured, we used the same measuring methodology as for the MCZ specimens to measure size and age. Finally, we collected the same shell dimensions of adult and juvenile Wood Turtles at 17 discrete sites across Massachusetts between 2004 and 2009 (hereafter referred to as the statewide sample; Jones 2009).

Analysis.—We compared morphometric data for adult turtles from the 1850s and 2009 Lancaster samples for each sex using Monte Carlo permutation tests



FIGURE 3. Specimen photos of two juvenile Wood Turtles (*Glyptemys insculpta*) collected by Agassiz at Lancaster, Massachusetts, about 1864, with the original specimen label. Top = SMNS 3794.1; Bottom = SMNS 3794.2. (Photographed by Günter Stephan).

(following the two-sample test of Manly 1997) with the package `asbio` (Aho 2012) in R (R Core Team 2012). We assessed sexual size dimorphism by calculating the Sexual Size Dimorphism Index (SDI) provided by Lovich and Gibbons (1992). We compared male and female body dimensions for each sample using the t-test of Welch (1947). We estimated growth rates of juvenile turtles from both samples using linear regression in R (R Core Team 2012). The slopes of the growth rates of juveniles between the 1850s and 2009 samples were evaluated by testing the age X year interaction term (ages of individuals) using ANCOVA in R (R Core Team 2012).

We explored the hypotheses that increased temperature and/or decreased population density may account for some of the observed differences in shell dimensions between the 1850s and 2009, using the unpublished statewide morphometric dataset of Jones (2009). We used the recent statewide sample to explore

whether body size might be positively correlated to temperature or population density. As a proxy for temperature, we measured growing degree-days at each capture location of a turtle and we measured Wood Turtle density at the population level. Growing degree-days are a measure of heat accumulation calculated by averaging daily temperature minimum and maximum values at a given location, subtracting a base temperature (10°C), and summing across an entire year. We used the regression model developed by Hall (2003) to estimate growing degree-days at each turtle capture location using ArcGIS (Esri, Redlands, California, USA). We then fit individual-based, simple linear regression models to predict SCL of males, females, and juveniles using growing degree-days as a predictor. We included age as a covariate in the juvenile models and used ANOVA to evaluate the independent effects of growing degree-days on body size, given age in years. To evaluate the spatial autocorrelation in the residuals of all three regression

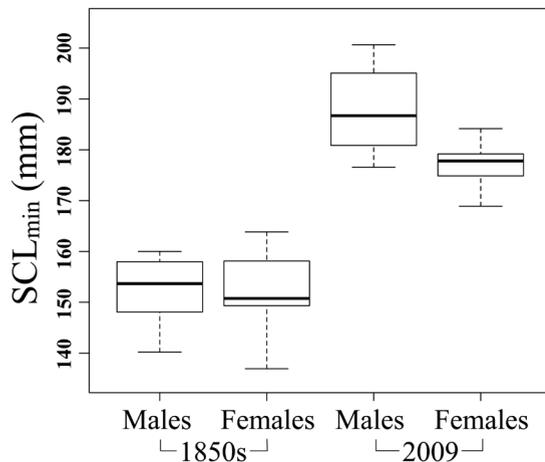


FIGURE 4. Straight-carapace length (SCL) of adult Wood Turtles (*Glyptemys insculpta*) taken at Lancaster, Massachusetts, USA, in the 1850s and 2009. The dark line in the center of the box is the median value measured in the population. The outer margins of the box represent the lower (25%) and upper (75%) quartiles. The whiskers represent the highest and lowest observations.

models, we used `lm.morantest` in the `spdep` package in R (Bivand 2010) to calculate Moran's I.

As a relative estimate of population density at each of the 17 discrete sites comprising the statewide sample, we used the package `Rcapture` (Baillargeon and Rivest 2009) in R (R Core Team 2012) to fit loglinear models (Chao's moment estimator; Chao 1987, generalized by Rivest and Baillargeon 2007) from recapture histories of animals during surveys at each site. All of our estimates were spread over a single activity season (April to October) to minimize the probability of mortality or emigration/immigration between sampling events. Closed population models are suitable for our purposes, namely, to obtain relative density estimates among populations rather than absolute population sizes. We divided the estimated population size for each site by the length of stream in the study area to obtain a relative estimate of adult turtles per kilometer of stream, which was used in the regression models to predict site-specific average body size for each sex.

We estimated site-specific body sizes for both males and females by averaging the SCL for each sex across the entire site. We then fit simple linear regression models to predict average body sizes for both males and females at each site using the relative density estimates as the explanatory variable. We also fit a juvenile model by first developing an individual based linear model of body size against age and pooling the juveniles captured at the 17 sites with population estimates. For each site, we averaged the residuals from the regression, and the average residual value was predicted via linear regression using relative site density as a predictor variable. We assessed the residuals of all

parametric tests to ensure they met the assumptions of normality and homoscedasticity (Quinn and Keough 2002). We used $\alpha = 0.05$ for all statistical analyses. To evaluate the temperature change from the mid-1800s to 2009, we obtained historical weather station data from Framingham, Massachusetts, USA, which at 29 km from the study location is the closest station with a long-term record.

RESULTS

In the 1850s sample, adult female SCL averaged 152.2 mm (± 8.24 [SD], range 136.9–163.8 mm, $n = 8$) and SCL of males averaged 152.0 mm (± 8.02 , range 140.2–160.0 mm, $n = 5$). The adult series from the 1850s does not exhibit any significant sexual size dimorphism (SDI = 0.00; $t = 0.03$, $df = 8.82$, $P = 0.975$). We captured 29 living Wood Turtles 54 times at three discrete sites in Lancaster over 25 visits between 25 April and 11 October 2009 (seven females, eight males, 14 juveniles), an average of 2.2 turtles per survey (including recaptures). In the sample of living turtles from Lancaster, female SCL averaged 177.0 mm (± 4.78 , range 168.9–184.2 mm, $n = 7$), and male SCL averaged 187.8 mm (± 8.90 , range 176.5–200.7 mm, $n = 8$).

There was a significant difference in SCL between Lancaster Wood Turtles of both sexes in the 1850s and 2009 (females: $t = -7.00$, $df = 13$, $P < 0.001$; males: $t = -7.31$, $df = 11$, $P < 0.001$; Fig. 4). In fact, there is no overlap in the male samples. The largest turtle in the 1850s sample (SCL = 163.8 mm) is 5 mm smaller than the smallest (SCL = 168.9 mm) in the recent sample. Overall, the difference in SCL is equivalent to a 16% increase in females and a 24% increase in males (SCL), or 20% overall, between the 1850s and 2009. Modern-day male and female Wood Turtles are significantly dimorphic with regard to SCL (SDI = -0.06; $t = -2.98$, $df = 10.98$, $P = 0.013$).

Juvenile Wood Turtles in the 2009 sample achieve larger sizes at earlier ages and grow faster than their 1850s counterparts. Growth rates of turtles were significantly higher in the 2009 Lancaster sample than the sample from the 1850s ($F_{1,19} = 7.95$, $P = 0.011$). By the time Wood Turtles reached maturity in 2009 (about 14 y) they were as much as 40–50% larger than their 1850s counterparts (Fig. 5).

In the statewide sample, juveniles captured in areas with a higher number of growing degree-days were significantly larger for their age than those in areas with fewer growing degree-days ($F_{1,148} = 6.70$, $P = 0.010$), but growing degree-days had no relationship with body size of adult male ($F_{1,148} = 0.149$, $P = 0.700$) or female ($F_{1,175} = 0.064$, $P = 0.800$) Wood Turtles. Moran's I values for all three models were within the range of those expected by chance ($P > 0.50$ for all models),

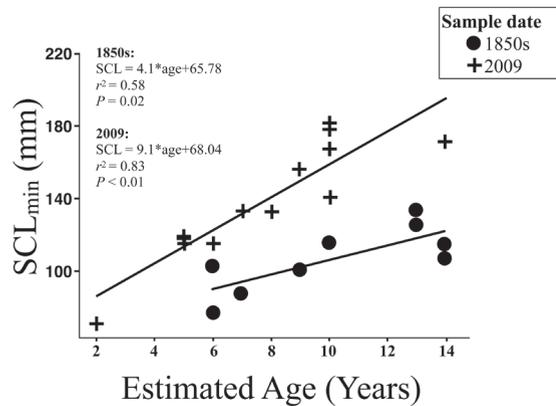


FIGURE 5. Relationship of carapace length (SCL) to age of juvenile Wood Turtles (*Glyptemys insculpta*; ≤ 14 y) taken at Lancaster, Massachusetts, USA, in the 1850s (triangles) and observed in 2009 (circles).

suggesting residuals were not spatially autocorrelated. At the site level, turtles in denser populations tended to be smaller than those in less dense populations, though the relationships were not significant (males: $F_{1,15} = 4.20$, $P = 0.058$, females: $F_{1,13} < 0.001$, $P = 0.990$, juveniles: $F_{1,15} = 0.690$, $P = 0.420$).

DISCUSSION

Our results demonstrate that adult Wood Turtles in the recent Lancaster population are on average larger in body dimensions, and juvenile Wood Turtles grow faster, than their 1850s counterparts. The observed body-size increase would correspond to an even larger increase in body mass. The difference occurred in 155 y, which may be equivalent to fewer than four wood turtle generations (van Dijk and Harding 2011). It is possible that Tenney and Agassiz actively selected smaller adult turtles (biasing their sample), because they fit better in museum jars or because smaller specimens were easier to transport. Preservation bias is documented in vertebrate fossil assemblages (Cooper et al. 2006; Brown et al. 2013) but is believed to minimally influence archeological collections of mussels (Peacock 2013). We point out that the males from the 1850s sample are entirely outside the range of variation observed in Lancaster and across Massachusetts (1850s maximum = 160.0 mm; 2009 minimum = 164.0 mm), suggesting that the underlying body-size distributions were different, even if collection practices were biased. In fact, some studies suggest that recent harvests of freshwater turtles for food have disproportionately affected larger animals (e.g., Shipman and Riedle 2008), which does not seem likely to be true in Massachusetts.

The disparity in size and growth rates of juvenile turtles is intriguing but should be interpreted cautiously for two reasons. First, estimating the age of young

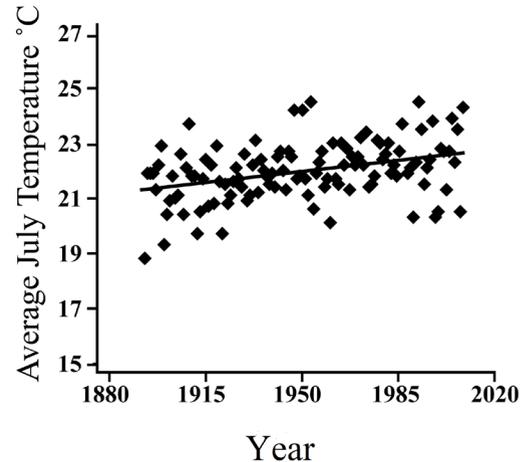


FIGURE 6. Weather station data from Framingham, Massachusetts, USA.

turtles can be relatively imprecise (Wilson et al. 2003), and it has been shown that juvenile emydine turtles may develop multiple small rings that are difficult to accurately classify as annual in origin (Belzer and Siebert 2007). However, scute rings have been found to be accurate in juveniles of many species of turtles (Lovich et al. 1990; Germano and Bury 1998) and juvenile Wood Turtles appear to add clear annual rings (Lovich et al. 1990; Harding and Bloomer 1979). Future comparative studies of the Tenney-Agassiz samples, or other historical collections, should consider the approach of Ernst et al. (1973), using the interabdominal lengths of the annuli to estimate earlier PL.

While we cannot be certain that the factors driving growth rate and body size in the 1850s are the same as those in 2009, current environmental and growth data may inform the potential mechanisms behind the observed differences and guide future research. Results from our regressions using current statewide data suggest that juveniles grow faster in areas with higher values for growing degree-days. Similar results have been observed for a number of turtle species (Brown et al. 1994; Rhen and Lang 1999), including Painted Turtles (Frazer et al. 1993), which suggests that an increase in temperatures over the past 150 y could have contributed to an increase in juvenile size and growth rates. Turtles incubated at higher temperatures have been shown to grow at faster rates after several years (Rhen and Lang 1999; Roosenburg and Kelley 1996; O'Steen 1998), suggesting that incubation temperatures may also have been an important factor in determining juvenile growth rates. Weather station data from Framingham, Massachusetts, USA (about 28 km southeast of Lancaster, the closest station with a long-term record), suggests that average summer temperature has significantly increased over the past 100 y ($F_{1,113} = 54.8$, $P < 0.010$) at a rate of 0.016°C per year (Fig. 6).

Our analyses of current statewide data also suggest that while an increase in growing degree-days may have resulted in increased juvenile growth rates, adult body size has no relationship to present-day growing degree-days in the recent sample, suggesting that while climate may influence growth in juveniles, the factors affecting adult body size in turtles may be more complex. Indeed, many species of turtles exhibit larger body sizes in high latitudes and colder climates (Ashton and Feldman 2003), suggesting that increased growing degrees days could even be associated with smaller adult body sizes. The larger-bodied adults in the modern sample may have, instead, resulted from a relaxation of density-dependent competition, as turtles at less dense sites in the recent sample tend to be larger, though not significantly. There is some support for this hypothesis in statements by Agassiz indicating that Wood Turtles were extremely abundant in the 1850s, as well as our observation that Wood Turtle abundance in Lancaster appears to be lower than indicated by Agassiz. It also cautions that while climate change is often cited as a cause of various ecological differences (e.g., McCarty 2001; Parmesan and Yohe 2003; Parmesan 2006), and similar increases in turtle growth rate and younger age at maturity has been attributed to climate change (Frazer et al. 1993), factors including (but not limited to) density dependent relationships may also play an important role.

Our evaluation of the relationship between current body size and temperature and population density indicates that multiple variables are important in predicting body size change in Wood Turtles, and there are several additional factors we were unable to measure. For instance, we were unable to test whether body size was influenced by increased availability of invertebrate prey, such as European earthworms (e.g., Lumbricidae; Kaufmann 1986), or increased nutrient deposition in the watershed as a result of changing land-use practices, or a dramatic increase in forest cover (Hall et al. 2002). Although we cannot conclusively attribute the measured increase in body size and growth rates to decreased population density and warmer summers, respectively, it is clear that additional comparisons of historic and current populations are warranted.

Acknowledgments.—We are indebted to Jose Rosado and Joe Martinez of the Museum of Comparative Zoology, Harvard University (MCZ), Cambridge, Massachusetts, USA, for providing access to the herpetological collections, and to Alexander Kupfer, curator of the State Museum of Natural History Stuttgart (SMNS), Germany. Tom Poole, Natural Resource Specialist for the U.S. Army, and Brian Butler of Oxbow Associates coordinated access to the Devens Reserve Forces Training Area. Support was provided by the Massachusetts Natural Heritage and Endangered Species Program, the

Massachusetts Cooperative Fish and Wildlife Research Unit, and the Klingener Natural History Collections Scholarship at the University of Massachusetts, Amherst. For assistance in the field, we thank Lori Johnson and Derek Yorks. Duncan Irschick provided helpful comments on earlier versions of this manuscript. Our studies were conducted under a protocol approved by the Institutional Animal Care and Use Committee of the University of Massachusetts (protocol 24-02-01 and 27-02-02) and research permits issued by the Massachusetts Division of Fisheries and Wildlife between 2004 and 2009 (138.08SCRA). All original photography of MCZ specimens is © President and Fellows of Harvard College.

LITERATURE CITED

- Agassiz, L. 1857. Contributions to the Natural History of the United States of America. 1st Edition. Little, Brown, and Company, Boston, Massachusetts, USA.
- Aho, K. 2012. Asbio: a collection of statistical tools for biologists. Version 0.4. <http://CRAN.R-project.org/package=asbio>.
- Ashton, K.G., and C.R. Feldman. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57:1151–1163.
- Avery, H.W., J.R. Spotila, J.D. Congdon, R.A. Fischer Jr., E.A. Standora, and S.B. Avery. 1993. Roles of diet protein and temperature in the growth and nutritional energetics of juvenile Slider Turtles, *Trachemys scripta*. *Physiological Zoology* 66:902–925.
- Baillargeon, S., and L.P. Rivest. 2009. Rcapture: Loglinear models for capture-recapture experiments. R package version 1.2-0. <http://CRAN.R-project.org/package=Rcapture>.
- Barrows, C.W. 2011. Sensitivity to climate change for two reptiles at the Mojave–Sonoran Desert interface. *Journal of Arid Environments* 75:629–635.
- Belzer, W.R., and S. Seibert. 2007. Variable production of annual growth rings by juvenile chelonians. *Turtle and Tortoise Newsletter* 11:10–13.
- Beverton, R.J.H., and S.J. Holt. 1957. On the Dynamics of Exploited Fish Populations. Fishery Investigations. Series 2, Volume 19. Her Majesty's Stationery Office (HMSO), London, UK.
- Bivand, R. 2010. Spdep: Spatial dependence: weighting schemes, statistics and models. R package version 0.5-26. <http://CRAN.R-project.org/package=spdep>.
- Bjorndal, K.A., A.B. Bolten, and M.Y. Chaloupka. 2000. Green Turtle somatic growth model: evidence for density dependence. *Ecological Applications* 10:269–282.
- Brown, G.P., C.A. Bishop, and R.J. Brooks. 1994. Growth rate, reproductive output, and temperature

- selection of Snapping Turtles in habitats of different productivities. *Journal of Herpetology* 28:405–410.
- Brown, C.M., D.C. Evans, N.E. Campione, L.J. O'Brien, D.A. Eberth. 2013. Evidence for taxonomic size bias in the Dinosaur Park Formation (Campanian, Alberta), a model Mesozoic terrestrial alluvial-paralic system. *Palaeogeography, Palaeoclimatology, Palaeoecology* 372:108–122.
- Bustard, H.R., and K.P. Tognetti. 1969. Green Sea Turtles: a discrete simulation of density-dependent population regulation. *Science* 163:939–941.
- Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43:783–791.
- Caut, S., V. Hulin and M. Girondot. 2006. Impact of density-dependent nest destruction on emergence success of Guianan Leatherback Turtles (*Dermochelys coriacea*). *Animal Conservation* 9:189–197.
- Congdon, J.D., and J.W. Gibbons. 1983. Relationships of reproductive characteristics to body size in *Pseudemys scripta*. *Herpetologica* 39:147–151.
- Congdon, J.D., and J.W. Gibbons. 1985. Egg components and reproductive characteristics of turtles: relationships to body size. *Herpetologica* 41:194–205.
- Congdon, J.D., and J.W. Gibbons. 1987. Morphological constraint on egg size: a challenge to optimal egg size theory? *Proceedings of the National Academy of Sciences of the United States* 84:4143–4147.
- Congdon, J.D., J.W. Gibbons, R.J. Brooks, N. Rollinson, and R.N. Tsaliagos. 2013. Indeterminate growth in long-lived freshwater turtles as a component of individual fitness. *Evolutionary Ecology* 27:445–459.
- Congdon, J.D., R.D. Nagle, O.M. Kinney, and R.C. van Lobel Sels. 2001. Hypotheses of aging in a long-lived vertebrate, Blanding's Turtle (*Emydoidea blandingii*). *Experimental Gerontology* 36:813–827.
- Cooper, R.A., P.A. Maxwell, J.S. Crampton, A.G. Beu, C.M. Jones, and B.A. Marshall. 2006. Completeness of the fossil record: estimating losses due to small body size. *Geology* 34:241–244.
- Dunham, A.E., and J.W. Gibbons. 1990. Growth of the Slider Turtle. Pp. 135–145 *In* Life History and Ecology of the Slider Turtle. Gibbons, J.W. (Ed.). Smithsonian Institution Press, Washington, D.C., USA.
- Ernst, C.H., and J.E. Lovich. 2009. Turtles of the United States and Canada. Johns Hopkins Press, Baltimore, Maryland, USA.
- Ernst, C.H., R.W. Barbour, E.M. Ernst, and J.R. Butler. 1973. Growth of the mud turtle, *Kinosternon subrubrum*, in Florida. *Herpetologica* 29:247–250.
- Fordham, D.A., A. Georges, and B.W. Brook. 2008. Indigenous harvest, exotic pig predation and local persistence of a long-lived vertebrate: managing a tropical freshwater turtle for sustainability and conservation. *Journal of Applied Ecology* 45:52–62.
- Fordham, D.A., A. Georges, and B.W. Brook. 2009. Experimental evidence for density-dependent responses to mortality of snake-necked turtles. *Oecologia* 159:271–281.
- Frazer, N.B., J.L. Greene, and J.W. Gibbons. 1993. Temporal variation in growth rate and age at maturity of male Painted Turtles, *Chrysemys picta*. *American Midland Naturalist* 130:314–324.
- Germano, D.J., and R.B. Bury. 1998. Age determination in turtles: evidence of annual deposition of scute rings. *Chelonian Conservation and Biology* 3:123–132.
- Gibbons, J.W. 1967. Variation in growth rates in three populations of the Painted Turtle, *Chrysemys picta*. *Herpetologica* 23:296–303.
- Girondot, M., A.D. Tucker, M.H. Godfrey and J. Chevalier. 2002. Density-dependent nest destruction and population fluctuations in Guianan Leatherback Turtles. *Animal Conservation* 5:75–84.
- Gotthard, K. 2001. Growth strategies of ectothermic animals in temperate environments. Pp. 1–17 *In* Animal Developmental Ecology. Atkinson, D. and M. Thorndyke (Eds.). BIOS Scientific Publishers Ltd., Oxford, UK.
- Hall, B. 2003. Massachusetts Growing Degree Day and Precipitation Maps. Harvard Forest Data Archive, Petersham, Massachusetts, USA.
- Hall, B., G. Motzkin, D.R. Foster, M. Syfert and J. Burk. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. *Journal of Biogeography* 29:1319–1335.
- Harding, J.H., and T.J. Bloomer. 1979. The Wood Turtle, *Clemmys insculpta* ... a natural history. *Bulletin of the New York Herpetological Society* 15:9–26.
- Hayhoe, K., C. Wake, B. Anderson, X. Liang, E. Maurer, J. Zhu, J. Bradbury, A. DeGaetano, A. Hertel, and D. Wuebbles. 2007. Regional climate change projections for the Northeast USA. *Mitigation and Adaptation Strategies for Global Change* 13:425–436.
- Hulin, V., V. Delmas, M. Girondot, M.H. Godfrey, J.-M. Guillon. 2009. Temperature-dependent sex determination and global change: are some species at greater risk? *Oecologia* 160:493–506.
- Janzen, F.J. 1994. Climate change and temperature-dependent sex determination in reptiles. *Proceedings of the National Academy of Science* 91:7487–7490.
- Janzen, F.J., and C.L. Morjan. 2002. Egg size, incubation temperature, and posthatching growth in Painted Turtles (*Chrysemys picta*). *Journal of Herpetology* 36:308–311.

- Jones, M.T. 2009 Spatial Ecology, Population Structure, and Conservation of the Wood Turtle (*Glyptemys insculpta*) in Central New England. Ph.D. Dissertation. University of Massachusetts, Amherst, Massachusetts, USA. 243 p.
- Karmalkar, A.V., and R.S. Bradley. 2017. Consequences of global warming of 1.5°C and 2°C for regional temperature and precipitation changes in the contiguous United States. PLoS ONE12(1): e0168697. <https://doi.org/10.1371/journal.pone.0168697>.
- Kaufmann, J.H. 1986. Stomping for earthworms by Wood Turtles, *Clemmys insculpta*: a newly discovered foraging technique. Copeia 1986:1001–1004.
- Leberg, P.L., and M.H. Smith. 1993. Influence of density on growth of White-Tailed Deer. Journal of Mammalogy 74:723–731.
- Lorenzen, K., and K. Enberg. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the Royal Society of London Biology 269:49–54.
- Lovich, J.E., and J.W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. Growth, Development, and Aging 56:269–281.
- Lovich, J.E., C.H. Ernst, and J. McBreen. 1990. Growth, maturity, and sexual dimorphism in the wood turtle, *Clemmys insculpta*. Canadian Journal of Zoology 68:672–677.
- Lovich, J.E., C.B. Yackulic, J. Freilich, M. Agha, M. Austin, M.P. Meyer, T.R. Arundel, J. Hansen, M.S. Vamstad, and S.A. Root. 2014. Climatic variation and tortoise survival: has a desert species met its match? Biological Conservation 169:214–224.
- Manly, B.F.J. 1997. Randomization and Monte Carlo Methods in Biology. 2nd Edition. Chapman and Hall, London, UK.
- McCarty, J.P. 2001. Ecological consequences of recent climate change. Conservation Biology 15:320–331.
- Niederberger, A.J., and M.E. Seidel. 1999. Ecology and status of a Wood Turtle (*Clemmys insculpta*) population in West Virginia. Chelonian Conservation and Biology 3:414–418.
- O'Steen, S. 1998. Embryonic temperature influences juvenile temperature choice and growth rate in Snapping Turtles *Chelydra serpentina*. Journal of Experimental Biology 201:439–449.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.
- Peacock, E. 2000. Assessing bias in archaeological shell assemblages. Journal of Field Archaeology 27:183–196.
- R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Rhen, T., and J.W. Lang. 1999. Temperature during embryonic and juvenile development influences growth in hatchling Snapping Turtles, *Chelydra serpentina*. Journal of Thermal Biology 24:33–41.
- Richard, M.G., C.P. Laroque and T.B. Herman. 2014. Relating annual increments of the endangered Blanding's Turtle plastron growth to climate. Ecology and Evolution 4:1972–1980.
- Rivest, L.P., and S. Baillargeon. 2007. Applications and extensions of Chao's moment estimator for the size of a closed population. Biometrics 63:999–1006.
- Rochet, M.J. 1998. Short-term effects of fishing on life history traits of fishes. Journal of Marine Science 55:371–391.
- Roosenburg, W.M. 1996. Maternal condition and nest site choice: an alternative for the maintenance of environmental sex determination? American Zoologist 36:157–168.
- Roosenburg, W.M., and K.C. Kelley. 1996. The effect of egg size and incubation temperature on growth in the turtle, *Malaclemys terrapin*. Journal of Herpetology 30:198–204.
- Ryan, K.M., and P.V. Lindeman. 2007. Reproductive allometry in the common map turtle, *Graptemys geographica*. American Midland Naturalist 158:49–59.
- Saumure, R.A., T.B. Herman, and R.D. Titman. 2007. Effects of haying and agricultural practices on a declining species: the North American Wood Turtle, *Glyptemys insculpta*. Biological Conservation 135:581–591.
- Shipman, P.A., and J.D. Riedle. 2008. Status and distribution of the Alligator Snapping Turtle (*Macrochelys temminckii*) in southeastern Missouri. Southeastern Naturalist 7:331–338.
- Spencer, R.-J. and F.J. Janzen. 2010. Demographic consequences of adaptive growth and the ramifications for conservation of long-lived organisms. Biological Conservation 143:1951–1959.
- Spencer, R.-J., F.J. Janzen, and M.B. Thompson. 2006. Counterintuitive density-dependent growth in a long-lived vertebrate after removal of nest predators. Ecology 87:3109–3118.
- Telemeco, R.S., K.C. Abbott, and F.J. Janzen. 2013. Modeling the effects of climate change-induced shifts in reproductive phenology on temperature-dependent traits. American Naturalist 181:637–648.

Jones et al.—Wood Turtle body size and growth rates.

- Thornhill, G.M. 1982. Comparative reproduction of the turtle, *Chrysemys scripta elegans*, in heated and natural lakes. *Journal of Herpetology* 16:347–353.
- van Dijk, P.P., and J.H. Harding. 2011. *Glyptemys insculpta*. International Union for Conservation of Nature Red List of Threatened Species. Version 2012.2. www.iucnredlist.org.
- Walde, A.D., J.R. Bider, C. Daigle, D. Masse, J.-C. Bourgeois, J. Jutras, and R.D. Titman. 2003. Ecological aspects of a Wood Turtle, *Glyptemys insculpta*, population at the northern limit of its range in Québec. *Canadian Field-Naturalist* 117:377–388.
- Walde, A.D., J.R. Bider, D. Masse, R.A. Saumure, and R.D. Titman. 2007. Nesting ecology and hatching success of the Wood Turtle, *Glyptemys insculpta*, in Québec. *Herpetological Conservation and Biology* 2:49–60.
- Welch, B.L. 1947. The generalization of "Student's" problem when several different population variances are involved. *Biometrika* 34:28–35.
- Wilson, D.W., C.R. Tracy, and C.R. Tracy. 2003. Estimating age of turtles from growth rings: A critical evaluation of the technique. *Herpetologica* 59:178–194.



MICHAEL T. JONES is the Massachusetts State Herpetologist for the Natural Heritage and Endangered Species Program of the Massachusetts Division of Fisheries and Wildlife, Westborough, USA. Mike is co-chair of the Northeast Wood Turtle Working Group and co-founder of American Turtle Observatory (ATO), for which he coordinates field studies of freshwater turtles in Mexico and Florida. Mike is the co-editor of *Eastern Alpine Guide: Natural History and Conservation of Mountain Tundra East of the Rockies* (University Press of New England, 2018). Mike lives in New Salem, Massachusetts, USA, with his wife, Liz; son, Everett, and 14 y-old Labrador Retriever. (Photograph by Bradley W. Compton).



LISABETH L. WILLEY is a core faculty member in the Environmental Studies Department at Antioch University in Keene, New Hampshire, USA. She has coordinated regional conservation planning efforts for Blanding's Turtle (*Emydoidea blandingii*) in the northeastern U.S. and works with turtle species from Maine to the Yucatán peninsula. Aside from northeastern wetlands and woodlands, Liz' favorite place to be is on one of the alpine summits of eastern North America. She is pictured holding a Florida Box Turtle (*Terrapene carolina bauri*) in Collier County, Florida, USA. (Photograph by Michael T. Jones).



ALAN M. RICHMOND is a Senior Lecturer and the Curator of Herpetology at the University of Massachusetts, Amherst, USA, where he teaches Herpetology, Evolution, Comparative Anatomy, and Biology of Marine Vertebrates. When not teaching or studying amphibians and reptiles in Massachusetts, Al can be found on his motorcycle somewhere between the southern Sierra Nevada and the Olympic Peninsula. He is pictured holding MCZ R-1827, an adult Wood Turtle collected in 1854. (Photograph by Michael T. Jones)



PAUL R. SIEVERT received a B.S. in Fisheries and Wildlife Biology from Iowa State University, Ames, USA (1981), M.S. in Wildlife Ecology from the University of Wisconsin, Madison, USA (1984), and Ph.D. in Biology from the University of Pennsylvania, Philadelphia, USA (1996). Since 2000, he has been the Assistant Unit Leader for Wildlife in the U.S. Geological Service, Massachusetts Cooperative Fish and Wildlife Research Unit at the University of Massachusetts, Amherst, USA. Paul's research interests are in Conservation Biology, Physiological Ecology, and Biostatistics. His research group studies populations of threatened and endangered species (freshwater turtles, salamanders, butterflies and moths) to better understand, and hopefully reverse, their declines. (Photograph by Sean Werle).