Eastern Box Turtle (*Terrapene carolina carolina*) Growth and the Impacts of Invasive Vegetation Removal

Devin Edmonds[1], Andrew R. Kuhns, and Michael J. Dreslik

Illinois Natural History Survey, Prairie Research Institute, 1816 South Oak Street, Champaign, Illinois 61820, USA
[1]*Corresponding author, e-mail: dae2@illinois.edu*

Abstract.—Reptile growth is influenced by environmental, dietary, and genetic factors. Invasive vegetation alters both the thermal qualities of a habitat and food availability; therefore, removal of established invasive vegetation may impact turtle growth. We studied a population of Eastern Box Turtles (*Terrapene carolina carolina*) in Illinois, USA, to determine whether removal of invasive Autumn Olive (*Elaeagnus umbellate*) and Russian Olive (*E. angustifolia*) impacted instantaneous growth rates. Using 16-y of capture-mark-recapture data, we found no difference in instantaneous growth rate pre- and post-invasive vegetation removal. Most of the variation in growth was attributed to the individual. Comparing commonly used growth functions, sex-specific models were better than those not accounting for sex. Male carapace and plastron lengths grew faster than females. Extrapolating from growth curves and sizes at maturity, we estimate males mature at 8.2 y (95% CI = 5.0–13.3) and females mature at 7.8 y (95% CI = 4.7–21.9). Results from our study provide new insights about Eastern Box Turtle growth at the western edge of their distribution and show removing invasive woody vegetation may not negatively impact their growth.

Key Words.—allometry; conservation; *Elaeagnus*; growth function; invasive species; reptile growth; sexual dimorphism

Introduction

Studying growth and how size varies between individuals and through time can explain aspects of demography important for conservation. For example, larger female turtles produce more eggs than smaller female turtles, thus body size relates to reproductive output (Gibbons et al. 1982; Congdon and Gibbons 1985). There is also a correlation between size and survivorship for many turtle species corresponding to a decrease in predation rates as individuals grow in size (Haskell et al. 1996; Janzen et al. 2000). Accordingly, the impacts of growth on survival and lifetime reproductive output in turtles have consequences for predicting population dynamics (Armstrong et al. 2018). Therefore, understanding what drives turtle growth can help identify demographic patterns and project population persistence.

Dramatic alterations in habitat have been shown to affect turtle growth rates, both positively and negatively, with food resource availability suggested as a cause (Dodd and Dreslik 2008; Munscher et al. 2015). Autumn Olive (*Elaeagnus umbellate*) and Russian Olive (*E. angustifolia*) are aggressive invasive shrubs in the U.S., often turning grasslands into shrublands and dominating the understory of woodlands (Catling et al. 1997; Dornbos et al. 2016). The invasive olives impact food resources across all trophic levels, from nutrient availability (Mineau et al. 2011) to arthropod communities (Burghardt and Tallamy 2013) to avifaunal species composition (Fischer et al. 2012). Consequently, Russian and Autumn olives are often a target of invasive

species control programs (Moore et al. 2013), though their removal could impact turtle growth rates.

Eastern Box Turtles (*Terrapene c. carolina*) are omnivores with a diverse diet of fruits, berries, annelids, and arthropods (Ernst and Lovich 2009). Russian and Autumn olives provide a high annual crop of berries, which persist in fall when other food sources are less abundant (Moore et al. 2013); therefore, their removal might slow turtle growth rates. Alternatively, the restoration to native habitat could stimulate understory growth and increase food resource diversity, increasing growth rate. Although no study has examined how Eastern Box Turtle growth is impacted by vegetation removal, Currylow et al. (2012) found timber harvest increased the frequency of short-distance movements in the species and proposed that the behavioral change was caused by new foraging opportunities following tree removal. To make informed management decisions, it is necessary to discern whether invasive vegetation removal impacts Eastern Box Turtle growth and, if so, in what direction growth is affected.

Several notable studies have focused on Eastern Box Turtle growth. The earliest growth analysis found growth rates to slow as Eastern Box Turtles grew older and identified a difference in shell shape between the sexes (Nichols 1939). Further work has shown males grow faster than females, with males larger in all dimensions except shell height (Stickel and Bunck 1989; Dodd 1997). More recently, Dodd and Dreslik (2008) studied how habitat disturbance impacted the growth of conspecific Florida Box Turtles (*T. c. bauri*). Following a hurricane,

male growth rates increased, whereas female growth rates decreased. The decrease in female growth rates suggests they allocated resources to reproduction rather than growth when resources became scarce. Eastern Box Turtle growth has also been studied in relation to urbanization, with an increased juvenile growth rate in urban habitat where there is decreased forest cover (Budischak et al. 2006). Such results indicate dense vegetation from invasive species might slow growth. On the other hand, considering Eastern Box Turtles occupy a range of habitat types and are adapted to mixed forests with areas of closed-canopy (Kiester and Willey 2015), increased woody vegetation from invasive species might have little impact on somatic growth.

Here, we use 16 y of capture-mark-recapture data and morphometric measurements to study somatic growth in an Illinois, USA, population of Eastern Box Turtles. Our objectives were to (1) determine whether woody vegetation removal impacted instantaneous growth rates; (2) find the best growth functions to model carapace and plastron length through time; and (3) explore how shell size and shape of males, females, and juveniles differ between sexes and life stages. Our study provides the first growth analysis of Eastern Box Turtles at the western edge of their distribution and helps determine the impacts of a common habitat management practice on a once common but now declining turtle species.

Materials and Methods

Study site.—Between 1999 and 2015, we conducted a capture-mark-recapture study at South Shore State Park, Clinton County, Illinois, USA (Fig. 1). South Shore State Park is managed by the Illinois Department of Natural Resources and the U.S. Army Corps of Engineers. The park consists of degraded prairie, bottomland forest, upland forest, and wetland situated along the southeast side of Carlyle Lake, a 102 km² impoundment of the Kaskaskia River. Between 2004 and 2007, land managers removed woody vegetation throughout the park, first by hand, and later more intensively through aerial herbicide treatments. The removal program targeted Autumn Olive and Russian Olive. These shrubs were once promoted by the U.S. Department of Agriculture as ideal for providing wildlife food and cover (Surrency and Owsley 2001). Unfortunately, as is often the case with introduced species, the olives proved invasive and disrupted natural plant succession. Our 16-y capture-mark-recapture surveys occurred before, during, and after woody vegetation removal, with survey effort mainly taking place within a 20-ha parcel representing the core wooded section of the state park.

Data collection.—We sampled turtles during herpetological surveys of the park, which have taken place annually since 1999 (see Crawford et al. 2020).
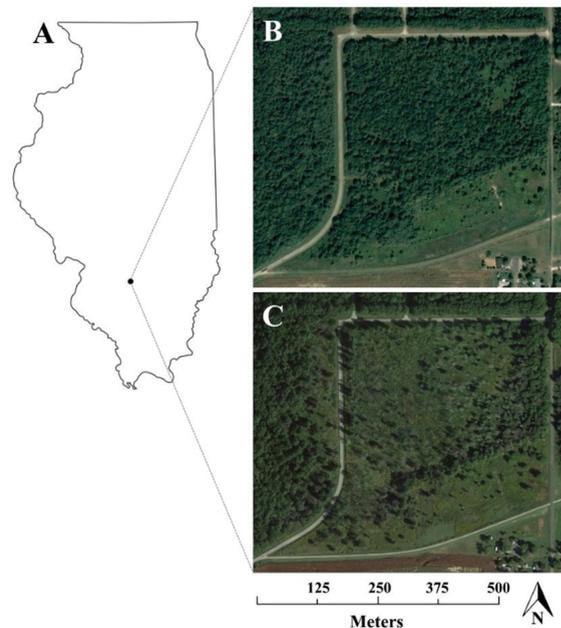
Figure 1. (A) Location of the study site in Illinois. (B) Aerial photographs of the 20-ha parcel sampled before invasive vegetation removal, September 2005 and (C) after vegetation removal, September 2015. (Taken from Google and Maxar Technologies; https://earth.google.com/web/).

We used visual encounter surveys, whereby two or three people scanned the ground for 2–6 h daily and recorded all reptiles and amphibians encountered. Surveys took place between March and July, with most captures (79%) occurring in April and May. Additionally, we used data from four incidental captures in September and October of 2002. During the 16-y study, we captured 381 individual Eastern Box Turtles and recaptured 134. There were 176 females (46%), 168 males (44%), and 37 of unknown sex (10%). Before invasive woody vegetation removal, we recorded 225 captures and 58 recaptures; following removal, we recorded 239 captures and 75 recaptures.

When a turtle was encountered, we flagged the location of capture and transported the turtle to a workstation. We used forestry calipers to measure carapace length (CL), carapace width (CW), and shell height (SH) to the nearest 1 mm. Eastern Box Turtles have a hinged plastron, so we measured and summed anterior and posterior plastral lobe lengths with digital calipers to estimate plastron length (PL). We also measured anterior plastral lobe width, posterior plastral lobe width, and left pectoral scute length to the nearest 0.1 mm with digital calipers. We recorded maximum dimensions rather than center line. We used a metric tape measure to measure curved carapace length to the nearest 1 mm and an Ohaus digital scale to measure weight to the nearest 1 g. Most turtles remained closed in their shell during measurements, and we placed them right side up on the scale. We weighed active individuals upside down and repeatedly picked up

TABLE 1. Adjusted Akaike Information Criterion (AIC$_c$) results for instantaneous growth rates of Eastern Box Turtles (*Terrapene carolina carolina*) at South Shore State Park, Illinois, USA. Pre-vegetation removal n = 37 and post-vegetation removal n = 62. Acronyms and abbreviations are K = number of parameters, w_i = Akaike weight, and Veg = vegetation removal. The global model, which includes additive effects and the interaction, is Growth ~ Sex×Veg.

	Carapace				Plastron			
Model	K	AIC$_c$	ΔAIC$_c$	w_i	Model	K	AIC$_c$	ΔAIC$_c$	w_i
Growth ~ Veg	4	267.18	0.000	0.50	Growth ~ Sex+Veg	5	261.93	0.00	0.44
Growth ~ Sex+Veg	5	268.14	0.955	0.31	Growth ~ Sex×Veg	6	262.78	0.86	0.29
Growth ~ Sex×Veg	6	270.23	3.046	0.11	Growth ~ Veg	4	263.01	1.08	0.26
Null	3	272.13	4.947	0.04	Growth ~ Sex	4	270.54	8.62	0.01
Growth ~ Sex	4	272.59	5.408	0.03	Null	3	271.92	10.00	0.00

and placed down until they stopped moving to record an accurate weight. We also measured front (down the midline), side (between the second and third vertebral scutes), and rear (down the midline) carapace angles to the nearest degree with a goniometer to better understand shell shape.

We determined sex using secondary sexual characteristics, including tail size (whether cloaca extended past plastron), eye coloration, curvature of the hind claws, and plastron concavity (Leuck and Carpenter 1981; Dodd 2002; Ernst and Lovich 2009). We classified individuals as juvenile if they were smaller than the smallest male exhibiting secondary sexual characteristics (CL < 102 mm). Following the method outlined by Cagle (1939), we assigned each turtle a unique combination of notches to marginal scutes. We released all turtles at their point of capture after collecting morphological data. Most individuals were not retained for more than a couple of hours. In rare instances, when weather was inclement, we held turtles overnight in individual ventilated plastic totes and released them the following day.

Statistical analysis.—First, to examine how woody vegetation removal may have affected turtle growth, we compared instantaneous growth rates before and after habitat restoration using mixed-effects models in package lme4 in program R version 3.4.1 (R Core Team 2018; Bates et al. 2019). We labeled individuals with a capture-recapture event before 2006 as pre vegetation removal (n = 37) and individuals with a capture-recapture starting in or after 2006 as post vegetation removal (n = 62). We included a random effect of individual to account for non-independence associated with 18 individuals with both pre and post vegetation removal capture-recapture occasions. We then calculated instantaneous growth rates for each individual, as in Dodd and Dreslik (2008), who used a modified version of Brody (1945):

$$\Delta GR = (log_e X_2 - log_e X_1)/((t_2 - t_1)/365)$$

where ΔGR is the change in instantaneous growth rate, X_i is CL at the ith capture occasion, and t is the time interval between capture occasions in days. We only used turtles with complete data and at least 6 mo between capture and recapture in the analysis. We compared mixed-effects models with pre/post vegetation and/or the effect of sex as a predictor of instantaneous growth rates (Table 1). We used Akaike's information criteria (AIC) adjusted for small sample sizes (AIC$_c$) to evaluate models and a threshold of ΔAIC$_c$ < 2 to determine the most parsimonious model(s) in the set.

Second, to identify the best growth function for modeling PL and CL, we followed methods outlined by Fabens (1965) and used AIC$_c$ to compare commonly used growth curves. Only turtles with a capture-recapture event could be used in the analysis (60 females, 56 males, 18 juveniles). We considered the mark-recapture analogs of the von Bertalanffy (von Bertalanffy 1957; Fabens 1965), Gompertz (Gompertz 1825; Dodd and Dreslik 2008), logistic (Verhulst 1838; Schoener and Schoener 1978), Richards (Richards 1959; Dodd and Dreslik 2008), and Schnute-Baker (Schnute 1981; Baker et al. 1991) growth functions in our analysis. The von Bertalanffy is a widely used decaying exponential growth function where the rate slows towards the asymptote. Compared to the von Bertalanffy, the logistic and Gompertz growth functions both have an inflection point, thus producing a sigmoidal curve. The Gompertz model accelerates early growth but produces a slower approach towards the asymptote compared to the logistic. The Richards and Schnute-Baker are the broadest of the five growth functions and incorporate von Bertalanffy, Gompertz, and Logistic equations as special cases, with the Schnute-Baker including the Richards function as a special case.

For refinement iterations minimizing sums of squares, we started with an initial asymptotic size of 159 mm for CL and 151 mm for PL, corresponding to the largest turtles in our dataset. We set the characteristic growth rate $k = 0.1$ because our time interval was in years. For Richards and Schnute-Baker models, we also included starting estimates for the shape parameter values of 0.5 (*m*) and 10 (*b*). Once parameter estimates were derived, we rooted growth curves with an initial hatchling size of 30.3 mm for CL and 29.9 mm for PL, as reported in Ernst and Lovich (2009).

In addition to the five growth functions, we also included sex-specific versions of each growth model because males and females may exhibit differential growth rates and patterns. Following the approach of Dreslik et al. (2017), we incorporated sex into models by creating two new variables (Female, Male) and coding those as binary integers 0 or 1 for the respective sex of the turtle (e.g. a female codes as 1,0 respectively). Then we created sex-specific parametrizations as follows using asymptotic size as an example: $(S_F \times A_F + S_M \times A_M)$ where S_F and S_M are the binary sex-specific coding parameters, and A_F and A_M are the female- and male-specific asymptotic sizes. We compared all five growth functions and their sex-specific variants using AIC_c, with a $\Delta AIC_c < 2$ to determine the most parsimonious models using package AICcmodavg (Mazerolle and Linden 2019). We then used growth curves to extrapolate the age of maturity with a minimum CL for each sex from Minton (2001).

Lastly, to characterize shell morphology associated with male, female, and juvenile turtles, we performed a discriminant function analysis (DFA) using the lda function in package MASS (Ripley et al. 2019) and all 11 measured morphometric traits. We included measurements from 93 males, 78 females, and 25 juveniles in the analysis. We set prior probabilities of 0.4 for males, 0.4 for females, and 0.2 for juveniles, which is comparable to the stage and sex distribution in wild Eastern Box Turtle populations (Kiester and Willey 2015).

RESULTS

Impacts of invasive vegetation removal on growth.— We did not detect a difference in the instantaneous growth
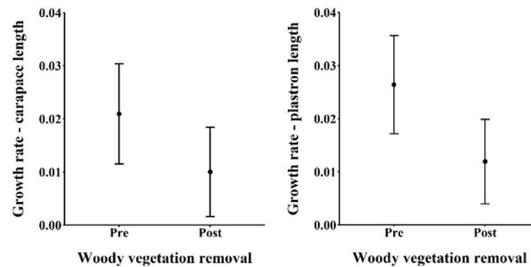
FIGURE 2. Estimated instantaneous growth rates of carapace (left) and plastron (right) length for Eastern Box Turtles (*Terrapene carolina carolina*) at South Shore State Park, Illinois, USA, pre- and post-invasive woody vegetation removal, estimated from the model Growth ~ Veg. Error bars are 95% confidence intervals.

rate following invasive vegetation removal (Fig. 2). For both carapace and plastron length, the most parsimonious models included vegetation removal as a parameter, either alone or with additive or interactive effects with sex (Table 1). Despite this, most of the variance accounted for in the models was ascribed to the random effect of turtle ID. No model had a marginal r^2 value greater than 0.08. $\beta_{veg\ removal}$ in the most parsimonious carapace model was 0.323 (95% confidence interval [CI] = 0.091–0.566). In the most parsimonious plastron model, $\beta_{veg\ removal}$ was 0.431 (95% CI = 0.183–0.705) and β_{sex} was 0.384 (95% CI = -0.030–0.796). The most parsimonious model describing growth of carapace length estimated a pre-vegetation removal growth rate of 0.021 (95% CI = 0.012–0.030) mm per day and a post-vegetation removal growth rate of 0.010 (95% CI = 0.002–0.018). The most parsimonious model describing growth of plastron length estimated a pre-vegetation removal growth rate of 0.026 (95% CI = 0.017–0.036) mm per day and a post-vegetation removal growth rate of 0.012 (95% CI = 0.004–0.020).

TABLE 2. Adjusted Akaike Information Criterion (AIC_c) results of nonlinear growth functions and their sex-specific counterparts for Eastern Box Turtles (*Terrapene carolina carolina*) at South Shore State Park, Illinois, USA. The sex-specific von Bertalanffy Growth Function (VBGF) is well-suited for both carapace and plastron length. Results are sorted by ΔAIC_c. Acronyms are K = number of parameters and w_i = Akaike weight.

		Carapace Length					Plastron Length		
Model	K	AIC_c	ΔAIC_c	w_i	Model	K	AIC_c	ΔAIC_c	w_i
VBGF-Sex	5	792.87	0.00	0.35	Gompertz-Sex	5	679.03	0.00	0.28
Schnute-Baker-Sex	6	793.94	1.07	0.21	Logistic-Sex	5	679.26	0.23	0.25
Richards-Sex	6	793.94	1.07	0.21	VBGF-Sex	5	679.43	0.40	0.23
Gompertz-Sex	5	794.67	1.80	0.14	Schnute-Baker-Sex	6	681.29	2.26	0.09
Logistic-Sex	5	796.77	3.91	0.05	Richards-Sex	6	681.29	2.26	0.09
Schnute-Baker	4	799.05	6.19	0.02	VBGF	3	684.40	5.37	0.02
Richards	4	799.05	6.19	0.02	Gompertz	3	684.51	5.47	0.02
VBGF	3	800.92	8.06	0.01	Logistic	3	685.59	6.56	0.01
Gompertz	3	803.89	11.02	0.00	Richards	4	686.46	7.43	0.01
Logistic	3	806.91	14.04	0.00	Schute-Baker	4	686.46	7.43	0.01
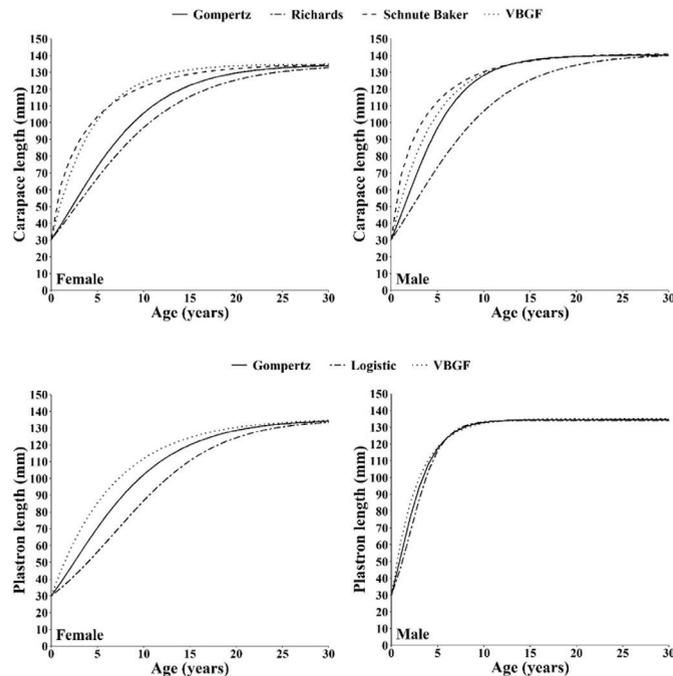
FIGURE 3. Top growth functions for carapace length (top) and plastron length (bottom) of male and female Eastern Box Turtles (*Terrapene carolina carolina*) at South Shore State Park, Illinois, USA. The abbreviation VBGF = von Bertalanffy growth function.

Growth curves.—Sex-specific growth curves performed better than those not considering sex (Table 2). For CL, there was strong support for the sex-specific von Bertalanffy, Schnute-Baker, Richards, and Gompertz models, whereas for PL the most parsimonious models were sex-specific Gompertz, Logistic, and von Bertalanffy. At age 30, the most parsimonious models predicted a CL of 140.0–141.0 mm for males and 132.8–134.9 mm for females, and a PL of 134.2–135.2 mm for males and 133.5–134.7 mm for females. Growth curves suggest male CL and PL increased faster than females (Fig. 3). Extrapolating from the minimum CL at

maturity reported by Minton (2001), the sex-specific von Bertalanffy growth curve indicates males mature at 8.2 y (95% CI = 5.0–13.3) and females mature at 7.8 y (95% CI = 4.7–21.9; Fig. 4).

Shell size and shape.—Although DFA is not a test for significant differences, males had longer and flatter shells than females (Fig. 5). Specifically, mean CL, CW, and left pectoral scute length were all greater for males, whereas mean SH was greater for females. Females also had greater mean front, back, and side shell angles, corresponding to their higher domed shell. Size
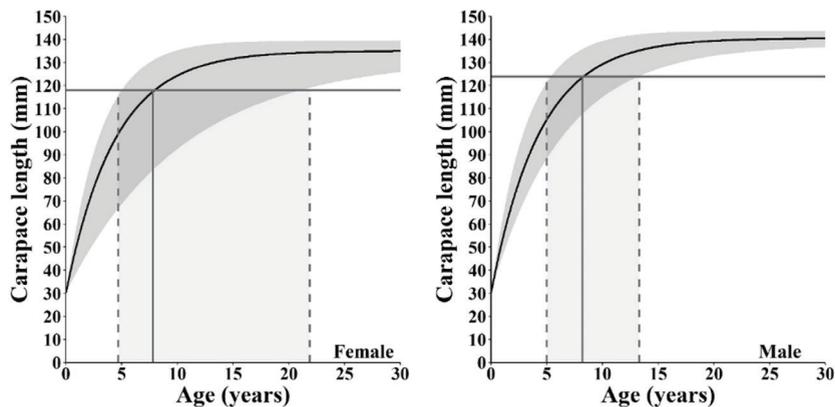
FIGURE 4. Sexual maturity age range for female (left) and male (right) Eastern Box Turtles (*Terrapene carolina carolina*). The growth function is sex-specific von Bertalanffy. The solid gray horizontal line is minimum carapace length at maturity from Minton (2001). The solid gray vertical line is the corresponding age at maturity. The dotted lines are 95% confidence intervals of sexual maturity age range extrapolated from the growth function.
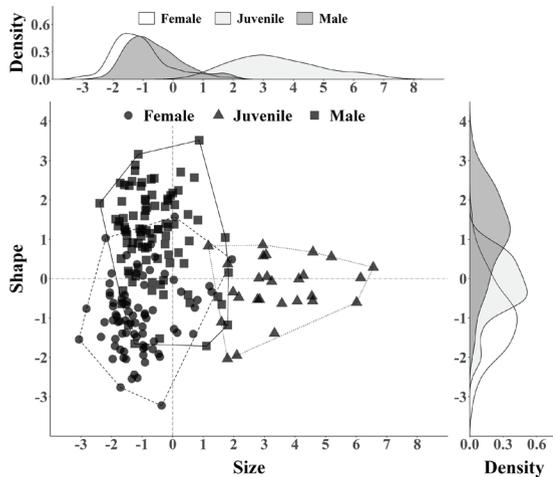
FIGURE 5. Results from discriminant function analysis of shell size and shape of male, female, and juvenile Eastern Box Turtles (*Terrapene carolina carolina*) at South Shore State Park, Illinois, USA.

explained life stage better than shell shape, whereas shell shape was better for characterizing sex (Fig. 5).

DISCUSSION

Numerous studies have demonstrated habitat quality affecting turtle growth (e.g., Brown et al. 1994; Koper and Brooks 2000; Dodd and Dreslik 2008; Daly et al. 2018; Howell et al. 2020), so it was surprising invasive vegetation removal was not a factor driving growth in our study. Rather, most of the variation in growth explained by our models was attributed to the random effect of individual. Reptile growth is determined not only by environmental conditions and food resources, but also by genetic factors (Avery 1994). Therefore, within a population experiencing roughly the same environmental conditions, growth can vary individually. Understanding the impacts of habitat management practices on turtle growth rates also could require finer-scale data on the specific habitat variables affecting growth, such as temperature or precipitation. Currylow et al. (2012) found too much open space from timber harvest can expose Eastern Box Turtles to unfavorable extreme temperatures, affecting movement and behavior. While the thermal qualities of our site were likely altered from vegetation removal, turtles may have responded behaviorally, thus growth rates were similar throughout the study. Conversely or additionally, although Autumn Olive fruits are eaten by Wood Turtles (*Glyptemys insculpta*) and likely Eastern Box Turtles as well (Weiss 2009; McCoard et al. 2018), their removal may not have impacted food availability enough to effect growth rates. Our results indicate conservation managers can remove invasive Autumn and Russian olives without detrimental effects on Eastern Box Turtle growth rate.

There are several explanations why male and female Eastern Box Turtles exhibit sexual dimorphism in growth curves, and thus, why sex-specific growth functions are better than growth functions not incorporating sex. Males may grow faster than females because of the trade-off between reproduction and survival, which is fundamental to life-history theory (Stearns 1989). Female chelonians must allocate resources to both eggs and growth, and as a result, female growth should be slower than males. Male-to-male combat has also been proposed as a selection pressure driving larger male body size in terrestrial chelonians (Berry and Shine 1980) and could also contribute to faster growth. In Eastern Box Turtles, male-to-male aggression occurs (Grace 2000), but because females also engage in combat, the advantages offered to larger males in combat may not be as likely an explanation for the size difference between sexes. Instead, Dodd (1997) has proposed the mechanical advantage offered by being a larger male when mounting females would account for the greater length of male box turtles. Our results show not only are male Eastern Box Turtles longer but that they grow faster than females in length.

We also found males and females differed in shell size and shape. Males were longer and flatter, whereas females were shorter and domed. Other studies have observed similar sexually dimorphic shell shape characteristics in Eastern Box Turtles (Stickel and Bunck 1989; Budischak et al. 2006), although the difference in SH between males and females varies between populations (Boucher 1999). At South Shore State Park, the traits with the greatest degree of sexual dimorphism were shell angles, followed by SH and CL. Sexual shape dimorphism relates to reproduction because selection favors female turtles with a greater capacity to carry eggs and, accordingly, a higher domed shell (Leuck and Carpenter 1981; Bonnet et al. 2010). Temperature, precipitation, and habitat type all affect the degree of sexual size dimorphism exhibited within a turtle species (Agha et al. 2018), so comparing the magnitude of morphological differences between males and females at South Shore State Park with sites differing in habitat type could reveal sex-specific factors driving sexual dimorphism.

A final takeaway relates to the relationship between the age of maturity and growth. Faster growing juvenile turtles typically mature younger and larger than slower growing juveniles (Congdon and van Loben Sels 1993; Congdon et al. 2018). Extrapolating from the top sex-based growth curves and using minimum sizes from Minton (2001), we estimated Eastern Box Turtles mature at around 8 y. Other authors have noted Eastern Box Turtles maturing as early as 5 y or as late as 14 y (Nichols 1939; Ernst et al. 1998; Dodd 2002). Such variation in age at maturity helps explain the size range of adult turtles in a population, with important life-history

implications. For example, turtles maturing late may be at a disadvantage in terms of lifetime reproductive output given the fecundity advantage offered to larger early maturing females (Armstrong et al. 2018; Congdon et al. 2018). Further research is needed not only on the environmental, dietary, and genetic components of somatic growth but also on the size of primiparous individuals to better understand age at maturity and its relationship to adult body size.

Literature Cited

Agha, M., J.R. Enne, A.J. Nowakowski, J.E. Lovich, S.C. Sweat, and B.D. Todd. 2018. Macroecological patterns of sexual size dimorphism in turtles of the world. Journal of Evolutionary Biology 31:336–345.

Armstrong, D.P., M.G. Keevil, N. Rollinson, and R.J. Brooks. 2018. Subtle individual variation in indeterminate growth leads to major variation in survival and lifetime reproductive output in a long-lived reptile. Functional Ecology 32:752–761.

Avery, R.A. 1994. Growth in reptiles. Gerontology 40:193–199.

Baker, T.T., R. Lafferty, and T.J. Quinn. 1991. A general growth model for mark-recapture data. Fisheries Research 11:257–281.

Bates, D., M. Maechler, B. Bolker, S. Walker, R.H.B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, and J. Fox. 2019. Lme4. R package version 1.1-21. https://cran.r-project.org/package=lme4.

Berry, J.F., and R. Shine. 1980. Sexual size dimorphism and sexual selection in turtles (Order Testudines).

Oecologia 44:185–191.

Bonnet, X., V. Delmas, H. El-Mouden, T. Slimani, B. Sterijovski, and G. Kuchling. 2010. Is sexual body shape dimorphism consistent in aquatic and terrestrial chelonians? Zoology 113:213–220.

Boucher, T.P. 1999. Population, growth and thermal ecology of the Eastern Box Turtle, *Terrapene carolina carolina* (L.), in Fairfax County, Virginia. Ph.D. Dissertation, George Mason University, Fairfax, Virginia, USA. 227 p.

Brody, S. 1945. Bioenergetics and Growth with Special Reference to the Energetic Efficiency Complex in Domestic Animals. Reinhold Publishers, New York, New York, USA.

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.

Budischak, S.A., J.M. Hester, S.J. Price, and M.E. Dorcas. 2006. Natural history of *Terrapene carolina* (box turtles) in an urbanized landscape. Southeastern Naturalist 5:191–204.

Burghardt, K.T., and D.W. Tallamy. 2013. Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods. Diversity and Distributions 19:1553–1565.

Cagle, F.R. 1939. A system of marking turtles for future identification. Copeia 1939:170–173.

Catling, P.M., M.J. Oldham, D.A. Sutherland, V.R. Brownell, and B.M.H. Larson. 1997. The recent spread of Autumn-olive, *Elaeagnus umbellata*, into southern Ontario and its current status. Canadian Field-Naturalist 111:376–380.

Congdon, J.D., and W.J. Gibbons. 1985. Egg components and reproductive characteristics of turtles: relationships to body size. Herpetologica 41:194–205.

Congdon, J.D., and R.C. van Loben Sels. 1993. Relationships of reproductive traits and body size with attainment of sexual maturity and age in Blanding's Turtles (*Emydoidea blandingi*). Journal of Evolutionary Biology 6:547–557.

Congdon, J.D., Nagle, R.D., and O.M. Kinney. 2018. Front-loading life histories: the enduring influence of juvenile growth on age, size, and reproduction of primiparous female freshwater turtles. Evolutionary Ecology Research 19:353–364.

Crawford, J.A., Dreslik, M.J., Baker, S.J., Phillips, C.A., and W.E. Peterman. 2020. Factors affecting the detection of an imperiled and cryptic species. Diversity 12:177.

Currylow, A.F., MacGowan, B.J., and R.N. Williams. 2012. Short-term forest management effects on a long-lived ectotherm. PLoS ONE 7:e40473. https://

doi.org/10.1371/journal.pone.0040473.

Daly, J.A., K.A. Buhlmann, B.D. Todd, C.T. Moore, J. Mark Peaden, and T.D. Tuberville. 2018. Comparing growth and body condition of indoor-reared, outdoor-reared, and direct-released juvenile Mojave Desert Tortoises. Herpetological Conservation and Biology 13:622–633.

Dodd, C.K., Jr. 1997. Population structure and the evolution of sexual size dimorphism and sex ratios in an insular population of Florida Box Turtles (*Terrapene carolina bauri*). Canadian Journal of Zoology 75:1495–1507.

Dodd, C.K., Jr. 2002. North American Box Turtles: A Natural History. University of Oklahoma Press, Norman, Oklahoma.

Dodd, C.K., Jr., and M.J. Dreslik. 2008. Habitat disturbances differentially affect individual growth rates in a long-lived turtle. Journal of Zoology 275:18–25.

Dornbos, D.L., Jr., M.R. Martzke, K. Gries, and R. Hesselink. 2016. Physiological competitiveness of Autumn Olive compared with native woody competitors in open field and forest understory. Forest Ecology and Management 372:101–108.

Dreslik, M.J., D.B. Shepard, S.J. Baker, B.C. Jellen, and C.A. Phillips. 2017. Body size, growth, and sexual size dimorphism in the Eastern Massasauga (*Sistrurus catenatus*). Pp. 66–78 *In* The Biology of Rattlesnakes II. Dreslik, M.J., W.K. Hayes, S.J. Beaupre, and S.P. Mackessy (Eds.). ECO Herpetological Publishing and Distribution, Rodeo, New Mexico, USA.

Ernst, C.H., and J.E. Lovich. 2009. Turtles of the United States and Canada. 2nd Edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Ernst, C.H., Wilgenbusch, J.C., Boucher, T.P., and S.W. Sekscienski. 1998. Growth, allometry, and sexual dimorphism in the Florida Box Turtle, *Terrapene carolina bauri*. Herpetological Journal 8:72–78.

Fabens, A.J. 1965. Properties and fitting of Von Bertalanffy growth curve. Growth 29:265–289.

Fischer, R.A., J.J. Valente, M.P. Guilfoyle, M.D. Kaller, S.S. Jackson, and J.T. Ratti. 2012. Bird community response to vegetation cover and composition in riparian habitats dominated by Russian Olive (*Elaeagnus angustifolia*). Northwest Science 86:39–52.

Gibbons, J.W., J.L. Greene, and K.K. Patterson. 1982. Variation in reproductive characteristics of aquatic turtles. Copeia 1982:776–784.

Gompertz, B. 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. Philosophical Transactions of The Royal Society of London 115:513–583.

Grace, M.S. 2000. *Terrapene carolina carolina* intraspecific combat. Herpetological Review 31:43–44.

Haskell, A., T.E. Graham, C.R. Griffin, and J.B. Hestbeck. 1996. Size related survival of headstarted Redbelly Turtles (*Pseudemys rubriventris*) in Massachusetts. Journal of Herpetology 30:524–527.

Howell, H.J., B.B. Rothermel, K.N. White, and C.A. Searcy. 2020. Gopher Tortoise demographic responses to a novel disturbance regime. Journal of Wildlife Management 84:56–65.

Janzen, F.J., J.K. Tucker, and G.L. Paukstis. 2000. Experimental analysis of an early life-history stage: direct or indirect selection on body size of hatchling turtles? Journal of Evolutionary Biology 13:947–954.

Kiester, R., and L. Willey. 2015. *Terrapene carolina* (Linnaeus 1758) – Eastern Box Turtle, Common Box Turtle. Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the International Union for Conservation of Nature/Species Survival Commission Tortoise and Freshwater Turtle Specialist Group. Rhodin, A.G.J., P.C.H. Pritchard, P.P. van Dijk, R.A. Saumure, K.A. Buhlmann, J.B. Iverson, and R.A. Mittermeier (Eds.). Chelonian Research Monographs 5:085.1–25. https://doi.org/10.3854/crm.5.085.carolina.v1.2015

Koper, N., and R.J. Brooks. 2000. Environmental constraints on growth of Painted Turtles (*Chrysemys picta*) in northern climates. Herpetologica 56:421–432.

Leuck, B.E., and C.C. Carpenter. 1981. Shell variation in a population of Three-toed Box Turtles (*Terrapene carolina triunguis*). Journal of Herpetology 15:53–58.

Mazerolle, M.J., and D. Linden. 2019. AICcmodavg. R package version 2.2-2. http://cran.r-project.org/package=AICcmodavg.

McCoard, K.R.P., N.S. McCoard, and J.T. Anderson. 2018. Observations of Wood Turtle activity, diet, movements, and morphometrics in the Central Appalachians. Northeastern Naturalist 25:513-531.

Mineau, M.M., C.V. Baxter, and A.M. Marcarelli. 2011. A non-native riparian tree (*Eleagnus angustifolia*) changes nutrient dynamics in streams. Ecosystems 14:353–365.

Minton, S.A. 2001. Amphibians and Reptiles of Indiana. 2nd Edition. Indiana Academy of Science, Indianapolis, Indiana, USA.

Moore, M.R., D.S. Buckley, W.E. Klingemann, III, and A.M. Saxton. 2013. Distribution and growth of Autumn Olive in a managed forest landscape. Forest Ecology and Management 310:589–599.

Munscher, E.C., A.D. Walde, T. Stratmann, and B.P. Butterfield. 2015. Exceptional growth rates observed in immature *Pseudemys* from a protected spring system in Florida. Herpetology Notes 8:133–140.

Nichols, J.T. 1939. Data on size, growth, and age in the

box turtle, *Terrapene carolina*. Copeia 1939:14–20.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Richards, F.J. 1959. A flexible growth model for empirical use. Journal of Experimental Botany 10:290–300.

Ripley, B., B. Venables, D. Bates, K. Hornik, A. Gebhardt, and D. Firth. 2019. MASS. R package version 7.3-51.4. https://cran.r-project.org/package=MASS.

Schnute, J. 1981. A versatile growth model with statistically stable parameters. Canadian Journal of Fisheries and Aquatic Sciences 38:1128–1140.

Schoener, T.W., and A. Schoener. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. Copeia 1978:390–405.

Stearns, S.C. 1989. Trade-offs in life-history evolution. Functional Ecology 3:259–268.

Stickel, L.F., and C.M. Bunck. 1989. Growth and morphometrics of the box turtle, *Terrapene c. carolina*. Journal of Herpetology 23:216–223.

Surrency, D., and C.M. Owsley. 2001. Plant materials for wildlife. U.S. Department of Agriculture and Natural Resources Conservation Service. All U.S. Government Documents (Utah Regional Depository) Paper 146. 33 p.

Verhulst, P.F. 1838. Notice sur la loi que la population suit dans son accroissement. Correspondance Mathématique et Physique 10:113–121.

Von Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. Quarterly Review of Biology 32:217–231.

Weiss, J.A. 2009. Demographics, activity, and habitat selection of the Eastern Box Turtle (*Terrapene c. carolina*) in West Virginia. M.Sc. Thesis. Marshall University, Huntington, West Virginia, USA. 88 p.

DEVIN EDMONDS is a graduate student at the University of Illinois at Urbana-Champaign, USA. Prior to pursuing an advanced degree, Devin worked on conservation efforts in Madagascar and launched the national amphibian breeding center for the country. He has authored peer-reviewed publications, written books on amphibian captive husbandry, and has a frog (*Stumpffia edmondsi*) named in his honor. (Photographed by Devin Edmonds).

ANDREW R. KUHNS is the Herpetologist for the Biotic Survey and Assessment Program at the Illinois Natural History Survey within the Prairie Research Institute at the University of Illinois Urbana-Champaign, USA. As such, he conducts surveys and habitat assessments for threatened and endangered amphibians and reptiles in areas scheduled for transportation improvements. Thus, he spends more time than the average person looking for and identifying roadkill. As time and funding allows, he pursues independent research pertaining to the distribution, ecology, and conservation of amphibians and reptiles. (Photographed by Bernadette Tiemann).

MICHAEL J. DRESLIK is a Herpetologist at the Illinois Natural History Survey (INHS) and the lead of the Population and Community Ecology Lab (PaCE Lab), Champaign, Illinois, USA. He earned his B.S. (1994) and M.S. at Eastern Illinois University, Charleston, USA (1996), where he studied the population ecology of the River Cooter (*Pseudemys concinna*) under Dr. E.O. Moll and received his Ph.D. (2005) at the University of Illinois at Urbana-Champaign (UIUC) for research on the conservation and ecology of the Massasauga (*Sistrurus catenatus*) under Dr. Christopher A. Phillips. Michael serves as an expert advisor on herpetofauna for the Illinois Department of Natural Resources, Illinois Endangered Species Protection Board, and Illinois Wildlife Action Plan. He also advises herpetology graduate students as an adjunct with UIUC and the University of Louisiana at Monroe, USA. He has authored 70 scientific and popular publications primarily on amphibian and reptile ecology. Michael is a member of two International Union for Conservation of Nature specialist groups (Freshwater Turtles and Tortoise and Vipers). (Photographed by Devin Edmonds).