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A Dynamic Energy Budget Model of Ornate Box Turtle Shell Growth

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Abstract

Many aspects of box turtle development may depend on size rather than age. Notable examples include sexual maturity and the development of the fully closing hinge in the shell that allows box turtles to completely hide in their shells. Thus, it is important to understand how turtles grow in order to have a complete understanding of turtle biology. Previous studies show that turtle shell growth behaves in a logistic manner. These studies use functional models that fit the data well but do little to explain mechanisms. In this work we use the ideas found in dynamic energy budget theory to build a model of box turtle shell growth. We show this model fits the data as well as previous models for ornate box turtles *Terrapene ornata ornata*, but also offers explanations for observed phenomena, such as maximum sizes and the appearance of biphasic growth.

Keywords: turtles, growth models, dynamic energy budget, dynamical systems

1 Introduction

Understanding how the individuals of an endangered or threatened species grow over time is an important part of conservation efforts. In conjunction with knowledge of population size, demographics, and habitat we can get a full picture of the species situation and make informed decisions about conservation efforts. Life history studies can help us understand individual growth rates, size and characteristics at sexual maturity and how large we can expect individuals to grow. [8]

Ornate box turtles are a terrestrial turtle that live mainly in sandy grasslands throughout the Midwest region of the United States. They are not yet endangered, but are a species of concern with decreasing numbers likely due to habitat loss from increased agricultural use as well as impacts from the illegal pet trade and use of herbicides. [4, 24] As these turtles grow their shells display a ring displaying the amount of growth that occurred over the year. Some of the earliest studies of ornate box turtle life histories come from Legler's work studying the species in Kansas. In his work he found that the size of the growth rings are positively correlated with the amount of precipitation during the growing season. [19] Other studies have reported sizes of adult turtles, but data on growth rates is hard to determine since juvenile turtles are difficult to find in the field. Because observational data is difficult to obtain, mathematical models may help understand scientists understand this species.

There are some previous studies modeling life histories of turtle species. Several studies use data to fit von Bertalanffy models, Gompertz, or other models with sigmoidal functions to describe turtle growth for a variety of turtle species. [12, 3, 20, 15, 28, 2] In particular, Bernstein et. al show that a 4 parameter Richards model fits shell length versus growth rings relatively well for ornate box turtles. Each of these studies assumes turtle growth obeys one functional form over the entire life of the turtle. Armstrong and Brooks use piece-wise linear models to examine growth of snapping turtles. In their model they assume that the turtles in their study follow one growth rate before reaching sexual maturity and a much slower growth rate after, presumably because energy is being devoted to reproduction and not growth. [1]

The models described above are entirely phenomenological. They describe the sigmoidal shapes observed in turtle growth curves, but cannot explain why the mechanisms behind the curve. We extend the knowledge of turtle growth by developing a mechanistic model that not only matches data, but provides a understanding for the shape of these growth curves. We build our model using ideas from dynamic energy budget theory which describes a balance between energies acquired and tasks that use that energy such as growth and reproduction. [18, 16] This framework is flexible and allows for modeling to connect ideas related to individuals and the choices they encounter in their life histories with ideas for how species fit into larger ecosystems. [21, 23] Dynamic energy budget models have been used to successfully describe the growth and reproduction of several organisms, including

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fish and oysters. [11, 25] Using this theoretical framework and data collected from ornate box turtles in Iowa, we build a differential equation model of turtle shell growth. We then analyze this model's equilibrium solutions and discuss how turtle environment affects various components of the model.

2 Methodology

2.1 Dataset

We have data from 510 ornate box turtles collected from Hawkeye Wildlife Area in eastern Iowa in 1993 and between 2013–2015. We measure carapace length, width, height, and turtle mass. In addition, we count the number of growth rings on each turtle. These data include 226 female, 231 male, and 53 juvenile turtles. We assume turtles produce one growth ring each year. Juvenile turtles (≤ 4 growth rings) could not be sexed and their data are included in both male and female data sets. Data collection is done under State of Iowa Scientific Collector Permit SC95, and we follow the American Society of Ichthyologists and Herpetologists (2004) guidelines when collecting the data. Further details about this dataset can be found in. [2]

2.2 Model development

To develop our model we assume turtles perform four tasks: eat, maintenance, grow, reproduce. Using the language of [18] we build a *net production* dynamic energy budget model. The main concept of the model is that after eating to collect energy resources, turtles use some of this energy to maintain themselves. A fraction of the excess is used for growth while the rest is used for reproduction. We let $L(t)$ be the length of the carapace of the turtle shell at time t and use L as the fundamental measure of turtle size.

Ornate box turtles collect energy by eating. They are omnivorous with a varied diet including plant matter, insects, and even carrion. [24] It has been observed that larger turtles tend to outcompete smaller ones. [19] Thus our expression for the rate of energy resource collection, R , should be an increasing function of size or length. In the absence of more detailed data we assume a linear relationship,

$$R(L) = R_s L + R_b,$$

where $R_s > 0$ and R_b are parameters to be determined.

In addition to eating, turtles must maintain their bodies. We model this maintenance through a metabolic rate term that is proportional to mass. Data collected show that turtle mass goes as length cubed. See Figure 1. Combining these ideas yields a maintenance term in the form

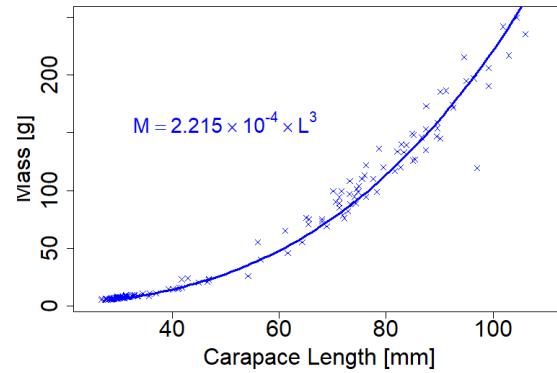


Figure 1: Cubic relationship between length and mass of ornate box turtles.

of mL^3 , where m is a constant of proportionality to be determined through parameter fitting.

Growth and reproduction

We assume a fraction $0 \leq \alpha \leq 1$ of resources not consumed for maintenance are used for growth. The rest, $1 - \alpha$, are used towards reproduction. We assume α is a function of length, and there is some evidence sexual maturity depends on size (L_m). [19] All excess resources are used for growth until turtle reaches sexual maturity, $\alpha = 1$, then α decays to zero as turtle ages. This decay should be monotonic and have a form representative of a phase transition between two states as turtle's behavior changes from focused on growth to more focused on reproduction.

$$\alpha(L) = \begin{cases} 1, & L < L_m \\ \frac{(L_{1/2} - L_m)^n}{(L_{1/2} - L_m)^n + (L - L_m)^n}, & L \geq L_m \end{cases} \quad (1)$$

In this model, when the turtle just reaches sexual maturity all energy is used for growth, $\alpha(L_m) = 1$, and then decays to 0. In this equation, $L_{1/2}$ represents the length at which the turtle is equally devoting excess energy resources to growth and reproduction. The parameter $n > 0$ describes the abruptness of the switch in behavior from using excess energy toward growth to using excess energy for reproduction. When n is large the behavior transitions quickly and occurs near $L = L_{1/2}$. When n is small, the change in behavior is more gradual. See Figure 2. Parameters L_m , $L_{1/2}$, and n are determined through parameter fitting.

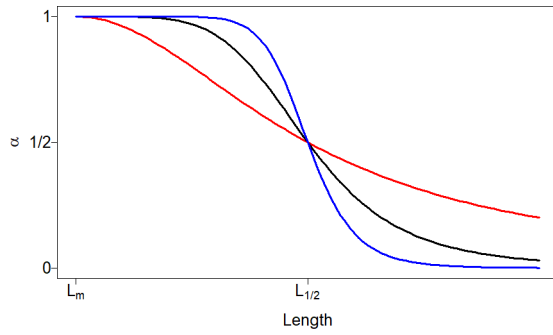


Figure 2: Behavior of $\alpha(L)$ for $n = \{2, 5, 10\}$ in red, black, and blue, respectively.

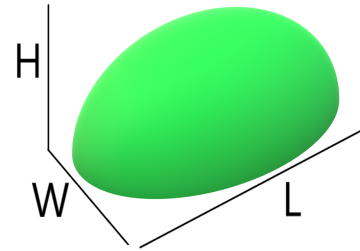


Figure 3: Hemiellipsoid model of turtle carapace.

Shell growth and allometry

We model the carapace of the turtle shell as a hemiellipsoid. See Figure 3. The energy a turtle uses for growth increases the time rate of change in the surface area of the carapace, $\frac{dSA}{dt}$. Formulas describing the surface area of ellipsoids require elliptic integrals that cannot be computed analytically. [29] In order to avoid these issues we approximate the surface area of the shell using the approximation

$$SA \approx \frac{2\pi}{\sqrt[3]{3}} \sqrt[3]{\left(\frac{LW}{4}\right)^p + \left(\frac{LH}{2}\right)^p + \left(\frac{WH}{2}\right)^p},$$

with $p = 1.6$. [30]

We simplify this expression by exploiting allometric relationships in the turtle carapace. Figure 4 shows scatter plots of the carapace widths W and heights H against lengths for the turtles in our dataset. These plots show two strong linear relationships, $W = 0.89736L$ and $H = 0.51349L$. Substituting these relationships into our surface area expression above we see

$$SA \approx \frac{\pi L^2 \sqrt[3]{0.89736^p + 0.51349^p + 0.89736^p 0.51349^p}}{2 \sqrt[3]{3}}.$$

Differentiating with respect to time and simplifying yields

$$\frac{dSA}{dt} = 2.9833L \frac{dL}{dt}.$$

Combining the ideas above and including an initial condition we have our model for turtle shell growth.

$$\begin{aligned} 2.9833L \frac{dL}{dt} &= \alpha(L) (R_s L + R_b - mL^3), \\ L(0) &= L_0 \end{aligned} \tag{2}$$

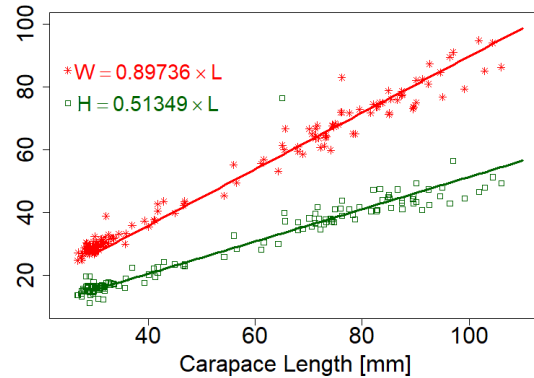


Figure 4: Allometric relationships in the dimensions of ornate box turtle shells. We see that as ornate box turtle shells grow, there is a constant ratio between the length and width of the shells and the length and height of the shells.

2.3 Parameter fitting and model comparisons

This model contains six parameters in the differential equation and an additional initial condition parameter for a total of seven parameters. Our fitting scheme consisted of looping over the parameter space for L_m and $L_{1/2}$ and then using built in R routines for nonlinear fitting of other parameters. For each $(L_m, L_{1/2})$ pair we use the `nls` routine in R to fit the other five parameters (for several starting values) and calculate the residual sum of squares (RSS) for this parameter set. We then find the best fit to the model by selecting the parameter values with the lowest RSS among these values. We calculate the RSS for each fit

$$RSS = \sum_{i=1}^n p(L_i - \hat{L}(t_i))^2,$$

where (t_i, L_i) are the values of the i^{th} data point, \hat{L} is the model prediction, and np is the number of points in our dataset. This procedure minimizes the RSS between the data and numerical solutions of Equation 2 with different parameter sets. Numerical solutions are computed using the ‘Isodes’ numerical differential equation solver based on Backward Differentiation Formula (BDF) methods for stiff problems. [5]

Once we have computed the parameters for our model we compare the fit to other commonly used models in practice. Three such models are the von Bertalanffy, logistic, and Richards models, which are all members of a class generalized Richards models. [32, 26, 31] These models have three, three, and four parameters, respectively, and each can be written as a differential equation. See Table 1. We fit the parameters in these model equations similarly to above using the `nls` routine in R.

The RSS is a good way to measure how close a model fits the data, but models with more parameters can generally fit datasets more closely than those with fewer at cost of increased complexity. A way to evaluate the balance of accuracy and complexity between models within a single dataset is with the Akaike Information Criteria (AIC). Using the RSS we calculate the AIC as

$$AIC = n \ln \left(\frac{RSS}{n} \right) + 2(k + 1),$$

where k is number of parameters. [17] This form of the AIC is appropriate when the residuals are normally distributed. QQ-plots (not shown) and a Shapiro-Wilk tests for normality show this to be the case for all proposed models. With this formulation of the AIC function we are not interested in the raw value of the AIC, but rather the how these values compare to AIC calculations of other

models. Models with lower AIC values have more statistical support and a higher likelihood of representing the true nature of the dynamics. [27]

3 Results

Qualitative analysis

Since $\alpha(L) > 0$ for all L in our model, we know equilibrium solutions will occur when the resource collection terms balance the maintenance term, i.e., when $R_s L + R_b = mL^3$. We can rewrite this as

$$R_s L + R_b - mL^3 = 0. \quad (3)$$

This is a depressed cubic equation. The behavior of roots of such equations has been studied as far back as the 1500s and we know there will be either one or three real roots. [7] From biological arguments we have $R_s, m > 0$ and $R_b < 0$. Using this we see that one real root is negative and thus not biological. Using Cardano’s formulas [6] we know that there are positive real roots only when

$$\frac{R_b^2}{4m^2} - \frac{R_s^3}{27m^3} \leq 0,$$

or

$$m \leq \frac{4R_s^3}{27R_b^2}.$$

This shows the relationship that must exist between resource collection, which may be more dependent on external factors such as climate, habitat, etc., and maintenance (metabolism) for there to be a positive equilibrium solutions.

We know a bifurcation from zero to two biologically relevant solutions occurs when the positive equilibrium solution of Equation 3 is a repeated root, i.e., when $m = 4R_s^3/27R_b^2$. In this case there is one non-biological negative equilibrium solution and one semistable positive equilibrium solution. If m exceeds this fraction it is impossible for a turtle to eat enough to survive. If m is strictly less than this fraction there are two equilibrium solutions. The smaller of the two is unstable and behaves like a viability length. Turtles that hatch smaller than this length cannot grow and thus die, while turtles that hatch above this length grow toward the larger, stable equilibrium solution. This larger equilibrium is the theoretical maximum length.

Results from our parameter fits show we are in the situation where there are two positive equilibrium solutions. See Figure 5. For females the viability threshold is 22.85 mm and the theoretical maximum length is 115.9 mm. For males these values are 16.3 mm and 128.7 mm, respectively.

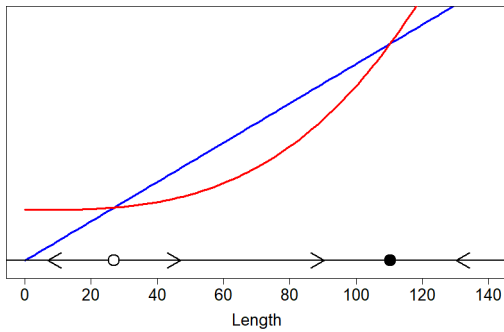


Figure 5: Resource collection $R_s L + R_b$ (blue) and maintenance mL^3 (red). Equilibrium solutions occur where the curves intersect ($R_s L + R_b - mL^3 = 0$). A phase diagram showing stability shows two equilibria. The smaller of the two is unstable and behaves as a viability threshold. The larger is stable and can be interpreted as a maximum length.

Parameter fitting and numerical solutions

Figure 6 shows the solutions to Equation 2 with fit parameters for males and females on the top left and top right, respectively. We see curves that rise rapidly and level off in a sigmoidal shape, characteristic of many other growth models.

Table 1 and Table 2 show the RSS and AIC values for males and females, respectively. For males and females the RSS of the DEB models are lower than the RSS values of other models, indicating these models have the best fit of the ones compared. However the Richards model has a lower AIC value than the DEB model for both males and females. The DEB model performs better than logistic for both males and females. The von Bertalanffy model is consistently the worst model in this comparison in both RSS and AIC values.

Results show both males and females have similar reproductive maturity lengths 105.6 and 105.7 mm, respectively. Once these lengths are reached, the transition from growth to reproductive behavior is abrupt. For males this is due to a large exponent value in the $\alpha(L)$ function coupled with a half-response length near the maturity length ($n = 3.087, L_{1/2} = 107.0\text{mm}, L_m = 105.6\text{mm}$). For the female data the fit value for the exponent in $\alpha(L)$ is low at $n = 1.51$, but the half response length is only 0.2 mm beyond the maturity length. Such sharp transitions indicate biphasic behavior, and that it may be possible to simplify our model with a step function for $\alpha(L)$.

Step function $\alpha(L)$ results

Because of the abrupt transition from growth to reproductive behavior found above, we consider a simplified model where we replace $\alpha(L)$ in Equation 1 with α_{step} .

$$\alpha_{step}(L) = \begin{cases} 1, & L < L_m \\ 0, & L \geq L_m \end{cases} \quad (4)$$

Here turtles are either devoting all excess energy to growth if not reproductively mature and then to reproduction upon achieving maturity. While this model is discontinuous, there are two fewer parameters to fit. Results are shown in bottom left and bottom right of Figure 6 for males and females, respectively. We do not see substantial changes in parameter values beyond noting that the maturity length has increased about 3 mm for males and females. RSS and AIC values for male and female models are shown in Tables 1 and 2 under the DEB α -step label. Each show modestly larger RSS and AIC values. This indicates that this simplified step function model has a similar, but slightly worse, complexity to the full model with a continuous transition from growth to reproductive behavior.

4 Discussion

In this study we develop a model that uses ideas from dynamic energy budget theory to describe turtle shell growth. This model differs from previous models in that it begins by describing turtle behaviors such as eating and metabolism in a differential equation whose solution has asymptotic behavior rather than choosing from a set of functions that display roughly the same shape as the data, e.g., von Bertalanffy, logistic, etc. In the language of Ledder we are creating a mechanistic model versus an empirical model, and there is a preference for choosing mechanistic models over empirical models, especially when the AIC values are similar. [17] This is due in part to the fact that empirical models depend on the data used to create them. It is possible another dataset could show that a different empirical model works better. For example, the Richards model fit is the best empirical model for these data. All these data come from a relatively small part of the natural range of Ornate box turtles in Iowa. It is possible that a logistic model with different parameters describes the data better for a data set collected from another part of the Ornate box turtle range, say Kansas. It is possible that sometimes empirical models that fit particularly well drive research into finding mechanistic models that recreate the empirical results. [33] While the empirical models and mechanistic models here both fit the data similarly, the biological principles used to create the dynamic energy budget model here are more universal.

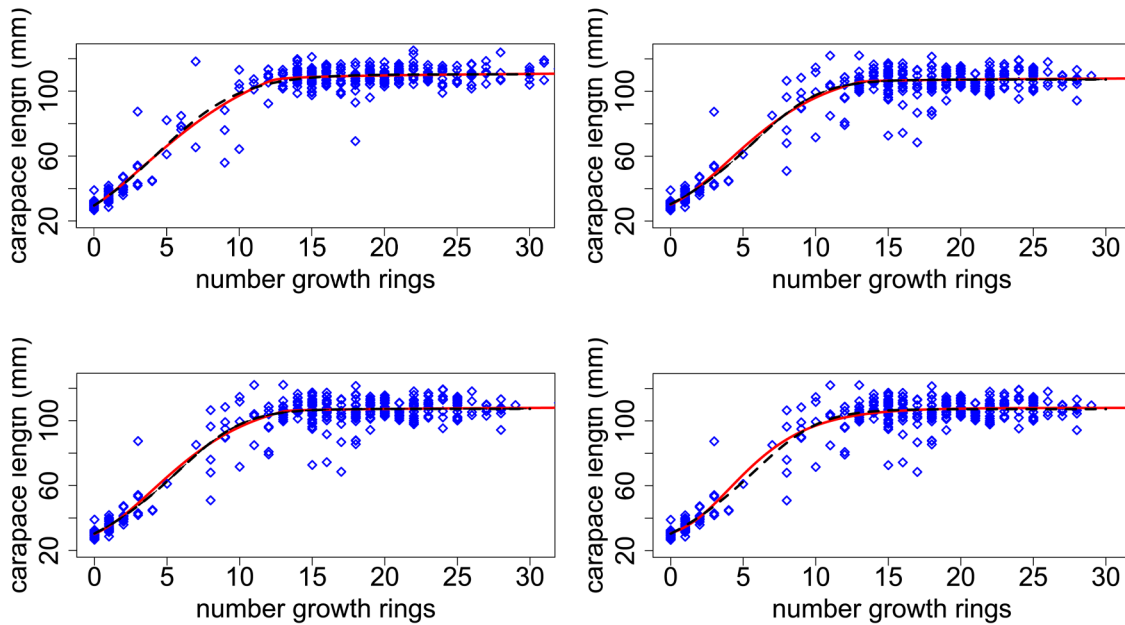


Figure 6: Data fits of DEB models (solid red) compared to Richards model (dashed black). In all four cases we see the similarity between the data fits of the two models. (top left) DEB males parameter values: $L_{1/2} = 107.0$, $L_m = 105.6$, $n = 3.08$, $R_b = -683$, $R_s = 42.42$, $m = 0.00224$, $L_0 = 29.39$; (top right) DEB females parameter values: $L_{1/2} = 105.9$, $L_m = 105.7$, $n = 3.01$, $R_b = -1292$, $R_s = 58.38$, $m = 0.00352$, $L_0 = 30.10$; (bottom left) DEB α -step males parameter values: $L_m = 109.3$, $R_b = 106.3$, $R_s = 21.03$, $m = 0.000602$, $L_0 = 28.59$; (bottom right) DEB α -step females parameter values: $L_m = 109.3$, $R_b = -2070$, $R_s = 81.06$, $m = 0.005303$, $L_0 = 30.69$

Table 1: Comparison of model fits for males. Models are ranked by lowest AIC values. Δ AIC values refer to difference between the model and top model.

Model	DE Form	Solution	RSS	AIC	Δ AIC
Richards	$\frac{dL}{dt} = aL \left(1 - \left(\frac{L}{L_\infty} \right)^{\nu-1} \right)$	$L_\infty \left(1 + \left(\left(\frac{L_\infty}{L_0} \right)^\nu - 1 \right) e^{-a\nu t} \right)^{-1/\nu}$	15765	1265.8	—
DEB	$cL \frac{dL}{dt} = \alpha(L) (R(L) - mL^3)$	numerical	15490	1266.1	0.3
Logistic	$\frac{dL}{dt} = aL(L_\infty - L)$	$\frac{L_\infty L_0}{L_0 + (L_\infty - L_0) e^{-aL_\infty t}}$	15882	1266.2	0.4
DEB α -step	$cL \frac{dL}{dt} = \alpha_{\text{step}}(L) (R(L) - mL^3)$	numerical	15693	1266.3	0.5
von Bertalanffy	$\frac{dL}{dt} = a(L_\infty - L)$	$L_\infty - (L_\infty - L_0)e^{-at}$	18748	1319.7	57.1

Table 2: Comparison of model fits for females. Models are ranked by lowest AIC values. Δ AIC values refer to difference between the model and top model.

Model	RSS	AIC	Δ AIC
Richards	20570	1420.4	—
DEB	20511	1421.4	1
Logistic	20973	1425.1	4.7
DEB α -step	20821	1426.5	6.1
von Bertalanffy	23831	1469.1	48.7

While parameter values may change with a new dataset, the interpretation of the model is consistent.

A consistent feature of all the models shown here is the presence of a maximum length. For the Richards, logistic, von Bertalanffy models, the presence of a maximum length is an assumption of the model. Indeed the popularity of these models to describe organism growth is because of this feature. [1, 2] In the DEB model, the maximum length appears as a consequence of the model as the stable equilibrium.

We also see a positive unstable equilibrium in this model that can be interpreted as a viability length. This does not appear in other models that assume all turtles with positive length will grow. For female turtles here, the viability lengths (22.8 mm) are slightly below fit hatching size (30.1 mm). This meshes well with optimum egg size theory ideas that posit that in animals that with no post-hatching parental involvement, eggs are optimally designed to produce viable offspring. [9] For males we do not see as close a relationship, viability and hatching sizes are 16.3 mm and 29.3 mm, respectively. It is unlikely that turtles are hatching near the viability length of 16.3 mm. None of the data presented here has a hatchling under 20 mm. This discrepancy may be due to the difficulty in observing sufficient amounts of hatchlings necessary for good model parameter fits and difficulty determining sex of hatchlings when observed skewing data. More work investigating the relationship between egg/hatchling sizes and the viability thresholds from dynamic energy budget theory in other species may provide more evidence to support this idea. Additional model analysis looking at how these viability lengths depend on other fit model parameters and possible egg size data may yield interesting results and ideas on how to further refine these models.

In the model developed here, we use growth rings as proxies for age with each growth ring representing one year of growth. There is some critical discussion about the efficacy of using growth rings to represent age. [14, 10, 34] Rings can be difficult to count leading to questions about data validity. Moreover, turtles may produce multiple minor growth rings in years where there

is a substantial temporary disruption to the growing season, e.g., drought. However, we agree with Germano and Bernstein that especially for juvenile turtles, growth rings are relatively good predictors of age. [13, 2]

A next step in this area of work is to try and find relationships between the parameters in the model and environmental cues. In particular understanding how the resource collection parameters depend on climatological and habitat factors may lead to improved conservation efforts. Headstarting is a technique of raising juvenile individuals in captivity and later releasing them into the wild. With box turtle species understanding the growth rates of juveniles until they reach a size where predation is unlikely to occur, say at the size where a closeable hinged shell occurs, is highly important to this process. [24] In order to make our model predictions more accurate, especially for juvenile turtles, more and better data is needed for turtles of this age. Since these turtles are very hard to observe in nature, a possible avenue is to record longitudinal data of juvenile turtles in zoos or nature centers. Such a study also could provide records of feeding and environment data further allowing researchers to connect environmental parameters to growth model parameters. This knowledge allows conservationists to accurately projecting the time in captivity, and thus costs, of a project. [22] Once we have a better understanding of the resource collection parameters, our mechanistic model offers researchers a framework for predicting how long a box turtle will need to be in captivity before being released.

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Author Contributions

TS had performed model development, statistical computations, analyzed results and wrote the manuscript. BA performed computations and statistical analysis, analyzed results, and created figures for the manuscript.

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