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**Life in the slow lane? A dynamic energy budget model for the western
swamp turtle, *Pseudemydura umbrina***

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Abstract

Dynamic energy budget (DEB) theory provides a generalised way to quantify how an organism assimilates and utilizes energy throughout its life cycle. Over 800 DEB models have been created to date, typically under the assumption of constant food supply. The Critically Endangered, semi-aquatic western swamp turtle occupies an ephemeral wetland environment in which food resources fluctuate from abundant to absent with the seasonal filling and drying of swamps. Approximately six months of each year are spent in aestivation underground when the swamps are dry and conditions are warm. We estimated DEB parameters for the western swamp turtle with the explicit incorporation of these seasonal fluctuations in food and temperature. A metabolic depression factor was applied during the aestivation stage, for which a value of around 50% best matched our life-history data. The swamp turtle had a very high Arrhenius temperature, being almost 2.5-fold greater than that of the other Testudine species for which there are DEB models (typical Arrhenius temperatures are around 8000K; western swamp turtle is 19371K). It also had the second highest somatic maintenance costs of the reptiles in the DEB 'Add My Pet' collection, and the highest for Testudines. We explore these results in context of the 'waste-to-hurry' hypothesis, which we suggest may apply for this species. We also consider how a DEB model for this species might be applied in its future conservation and management.

Keywords: Dynamic Energy Budget, western swamp turtle, *Pseudemydura umbrina*, aestivation, metabolic depression, waste to hurry.

1. Introduction

A mechanistic understanding of the energetic requirements of an organism can be critical for conservation management (Tomlinson *et al.* 2014 and references therein). However, ecological energetics can be difficult to quantify, especially in systems that are highly variable across time (such as boom-bust ecosystems; e.g. Bunn *et al.* 2006; Letnic & Dickman 2006). Dynamic Energy Budget (DEB) theory (Kooijman 2010) provides a generalised means for quantifying how an organism assimilates and utilizes energy over time throughout its life cycle, from embryo to adult. It captures the dynamics of how energy is allocated to maintenance, growth, maturity, and reproduction as a function of age, sex, and size, and also as a function of nutritional state and environmental condition (Nisbet *et al.* 2000; Jusup *et al.* 2017). DEB models can be powerful tools for examining how species have responded to historic fluctuations in their environment (e.g. van der Meer *et al.* 2011). Similarly, they can be extended to forecast performance under novel environments such as climate change. Indeed, several DEB models have already been incorporated within mechanistic niche models (e.g. Kearney 2012; Kearney 2013; Schwarzkopf *et al.* 2016).

The western swamp turtle, *Pseudemydura umbrina*, is one of Australia's rarest reptiles and it inhabits an environment that is characterised by marked fluctuations in food density. Endemic to the south-west of Western Australia, the turtle occupies shallow ephemeral swamps that fill with winter rainfall and dry over summer (Burbidge 1981). Each year turtles can spend over six months without water in a state of obligatory summer aestivation within leaf-litter or shallow underground burrows (Burbidge *et al.* 2010). Consequently, turtles have a narrow window for feeding each year, constrained to the wet winter and spring months when swamps hold water. The life history of the

turtle is strongly influenced by energy acquisition during this time and, importantly, survival at particular life stages seems to be influenced by body size. For example, hatchlings must reach a critical mass of at least 18 g to survive their first summer aestivation event (Mitchell *et al.* 2013) and sexual maturity appears to be a function of body length rather than age (Kuchling & Bradshaw 1993).

Adequate growth is paramount to the persistence of *P. umbrina* in the wild, and DEB theory offers an avenue to formally quantify the environmental sensitivity of growth rate. The most commonly used DEB model is the standard DEB model, which deals exclusively with isomorphic organisms (organisms that do not change shape, from a metabolic point of view, as they mature; Kooijman 2010) and whose biomass is partitioned into three stoichiometrically fixed pools. These three abstract pools are reserve (E , J), structure (structural volume; V , cm³), and reproductive buffer (E_R , J). Together these act as state variables, i.e. they specify the state of the system at any given time (Kooijman 1993). Assimilated energy is initially stored as reserve which does not require any energy expenditure to maintain and which is continuously used and replenished (Kooijman 2010; Nisbet *et al.* 2010). A fixed fraction κ of the continually mobilised reserve is used to fuel somatic maintenance and growth (i.e. to build and maintain structure). The remaining energy ($1 - \kappa$) is initially allocated towards maturation (and maturity maintenance), with maturity (E_H , J) being the fourth state variable in the model. Maturity thresholds determine two life history events: birth, when feeding commences, and ‘puberty’, when an individual first begins to allocate energy to its reproduction buffer (Kooijman 2010). When the puberty threshold is passed, the animal is considered to be an adult and the $1 - \kappa$ allocation switches towards reproduction (and maturity maintenance). Henceforth, the majority of the $1 - \kappa$ is allocated to a biomass component within the organism called the reproductive buffer,

which has the same composition as reserve, and which empties as gametes are released to the environment (Fig. 1). Freshly-laid eggs are considered pure reserve, drawn from the reproduction buffer of the mother (Kooijman 2010).

This ‘ κ -rule’ DEB model has been successfully applied to over 800 species across numerous phyla, including five species of Chelidae (Kooijman & Lika 2014; Jusup *et al.* 2017; AmP 2017; Marn *et al.* 2017). It has also been applied to understanding how species might exploit environments where resources are uncertain or temporally dynamic (e.g. in the ‘waste to hurry’ hypothesis; Kooijman 2013). Here we aim to produce a whole-of-life energy budget for the western swamp turtle using the κ -rule DEB model, and explore what this implies about their capacity to face periods of starvation. Additionally, we examine how the growth of wild *P. umbrina* compares to that of captive individuals and, importantly, describe the modifications that were required in order for the standard DEB model to be able to capture periods of aestivation in the juvenile and adult. These advancements will be particularly important for western swamp turtle conservation planning, which is progressing towards the establishment of new translocation populations (Mitchell *et al.* 2013; Dade *et al.* 2014; Mitchell *et al.* 2016). Because DEB modelling provides a way to mechanistically quantify the uptake and use of material by individuals, it can be used to explore the energetic constraints of survival, growth, development, and reproduction in new translocation environments. This in turn can facilitate conservation decision making, and inform ecosystem-level management (e.g. through the calculation of environmental carrying capacities to prevent translocation locations from becoming over-stocked and compromising ecosystem health; Filgueira *et al.* 2014).

2. Materials and methods

We adopted the simplest implementation of DEB theory: the ‘standard DEB model’ (Kooijman 2010). Dynamic energy budget model parameters cannot be measured directly because the state variables E , V , E_R , and E_H are abstract quantities (Kooijman 2010). However, life history observations of the energy budget (such as wet mass, physical length and growth rate) can be estimated inversely from a wide range of empirical observations using the ‘covariation method’, provided that temperatures for the observations are known and corrected for (Lika *et al.* 2011a; Lika *et al.* 2011b; Kearney 2013). Due to the one-to-many relationship between DEB parameters and life history observations, only a small number of types of observations can be used to estimate the parameters, and those minimally required are age, mass and size at birth (a_b ; W_b ; L_b respectively), age, mass and size at puberty (a_p ; W_p ; L_p respectively), lifespan (a_m), maximal mass (W_i), maximal size (L_i), and reproductive rate (R_i ; Kooijman 2004). We obtained these observations from individuals maintained in captivity since 1963 (Kuchling *et al.* 1992; Section 2.1). We then generated temperature corrections for these data (Section 2.2) and parametrised a standard DEB model in three ways, testing how best to capture the dynamics of growth during periods of aestivation and feeding (Sections 2.3 and 2.4). All modelling was completed in MATLAB[®] (The MathWorks[™] Inc. USA) and we refer the reader to Kooijman (2010) for detailed particulars of the underlying DEB theory.

2.1 Data observations

We sourced all *P. umbrina* life history observations from individuals maintained in a captive breeding population at Perth Zoo (South Perth, Western Australia). Turtles bred in captivity are hatched after being artificially incubated at two nominal temperatures: 29→24°C and 24°C constant, where individuals in the former are incubated at 29°C for

10 weeks (median time period) before temperatures are reduced to 24°C for the remainder of incubation, which promotes hatching. Any unhatched eggs are removed from incubators at the beginning of April (29→24°C treatment) or May (24°C treatment) and manually hatched if they fail to emerge within 14 days. Thus L_b (mm, carapace length), W_b (g, wet weight) and a_b (d) were best derived from data for individuals that hatched from 24°C incubators prior to 1st of May each year as they experienced a constant 24°C across the entire incubation period. While turtles have been held in captivity since 1963, allocation of eggs to specific incubators (with precise incubation temperatures) commenced in 2006 and so L_b , W_b , and a_b were derived from the average of eight individuals that met the following criteria: a) born after 2006, b) incubated at nominal constant 24°C, and c) hatched prior to May 1st. Temperature loggers (Thermocron iButtons model DS1921G; Maxim Integrated) set to log at hourly time steps were placed adjacent to embryos developing in these incubators to record the actual incubation temperatures (T_{ab}) experienced by the embryos which can sometimes deviate from the programmed incubation temperatures.

Values for L_p (mm, carapace length), W_p (g, wet weight), and a_p (d) were sourced from captive husbandry records for 12 females that had hatched at Perth Zoo and had laid at least one clutch of eggs during the study period (1963-2013). Each year, the reproductive state of females was assessed approximately weekly across the breeding period (from mating in July-August to oviposition in November-December) using an ultrasound (JustVision SSA-320A and UI IM-320A, Toshiba, Japan). The time a female was first identified as being gravid (see Kuchling & Bradshaw 1993) was used to define a_p and the corresponding W_p was also taken at this time. In contrast, L_p was taken as the carapace length measured during the year in which the female was first scanned as gravid (lengths are generally only measured once per year and do not necessarily

correspond directly to instances of ultrasound scanning). The effects of this potential error in L_p are likely to be minimal because growth post-puberty is relatively slow ($0.2 \text{ cm} \pm 0.1 \text{ s.e. per year}$, compared to $1.2 \text{ cm} \pm 0.4 \text{ s.e. per year pre-puberty}$; S. Arnall, unpublished data). Reproduction rate was taken from Burbidge (1981) who found females laid a maximum of five eggs per year, which was further supported by captive husbandry data.

Values for a_m (d), L_i (mm, carapace length) and W_i (g, wet weight) could not be directly measured because no individual *P. umbrina* whose birthdate is known has died at an advanced age. Instead, we based these values on the eldest female *P. umbrina*, who was collected as an adult in 1959, was still reproducing in 2013, and had grown less than 3 mm in the preceding 10 years. Age-length, and age-mass data were also compiled for 12 female individuals, commencing with hatching and thereafter spanning 10 to 20 years. Males were not included in this study as information on puberty was less resolved than that for females.

To understand the effects of aestivation on turtle body condition and size, we analysed the carapace length (mm) and mass (g) of 162 *P. umbrina* held in the Perth Zoo captive breeding facility measured immediately pre- (December) and post- (May) aestivation over the Austral summer of 2012-2013. Carapace lengths were measured to the nearest mm using Vernier callipers, and weights were obtained using a digital scale ($\pm 0.01\text{g}$).

Metabolic data was sourced from Arnall *et al.* (2015), who reported the standard metabolic rates of western swamp turtles, measured during the active (non-aestivation) period at Perth Zoo.

Despite data being sourced from captive conditions, food availability was not controlled as individuals were group housed in outdoor ponds with opportunistic and frequent access to natural prey items (such as mosquito larvae and tadpoles) in addition to food given through normal husbandry (refer Arnall *et al.* 2015 for housing details). Therefore, we assumed food conditions were saturated during the non-aestivation periods.

2.2 Temperature correction

After hatching at the zoo, juveniles and adults inhabit outdoor ponds and leaf-filled aestivation pens that provide a range of diurnally fluctuating microclimates. To derive a single temperature to be associated with age at puberty (T_{ap}), ultimate age (T_{am}), reproductive rate (T_{Ri}), and age-length-weight series, we used the Arrhenius relationship to convert all temperatures to temperature correction factors (using 20 °C as the reference temperature, i.e. a rate correction of 1; see Section 2.3). To obtain a constant temperature equivalent (CTE; Orchard 1975) we then estimated the mean Arrhenius temperature correction factor for the wet and dry periods experienced by turtles in this study, as informed by three years of daily maximum and minimum temperatures (2011-2013), recorded from maximum/minimum thermometers placed in turtle enclosures and checked at approximately the same time each day (Fig. 2). We then converted the mean Arrhenius temperature correction factor to the respective temperature, and used this latter value as the CTE.

2.3 DEB parameter estimation

The free software package DEBtool (<http://www.bio.vu.nl/thb/deb/deblab/debtool>) was used to estimate the parameters of a DEB model for *P. umbrina*, using the covariation method described in Lika *et al.* (2011a, b). DEBtool estimates all parameters

simultaneously, minimising the weighted sum of squared differences between the real observed values and the estimates through regression (Lika *et al.* 2011a, b). Mean relative error (MRE) was scored after Lika *et al.* (2011a), and we used the Nelder Mead simplex method (implemented in the ‘nmregr’ DEBtool routine) to search the parameter space. We followed the estimation procedures as outlined in Kooijman (2004) and Kooijman (2014), and refer the reader to the latter for background on the parameterisation steps.

We fitted the DEB model using the observational data from Section 2.1, giving all measures of length a greater weighting than measures of mass because turtles occasionally void their bladder on handling (Table 1). We fitted the model in three ways, progressively altering the mechanisms for accommodating aestivation. In the first instance (model fit 1, hereafter termed ‘MF1’), we set the scaled functional response (f , with values of 0 and 1 representing an absence of food, and saturated feeding conditions, respectively) to 0.5 for all processes except egg development and oxygen consumption, to reflect the approximately half year where turtles are without food. Second, we implemented a customised function to explicitly simulate fluctuating food and temperature conditions such that f alternated between 0 and 1 over time, mimicking the seasonal filling and emptying of wetlands (‘MF2’). Third, we multiplied all rate parameters by a fractional value (between 0 and 1) in conjunction with the second approach to simulate metabolic depression through periods of aestivation (‘MF3’).

In each case, we characterised the thermal rate-response by implementing a five-parameter Arrhenius temperature function as described in Kooijman (2010), after Sharpe & DeMichele (1977). This was recalculated from *P. umbrina* oxygen consumption rates (in mL g⁻¹ hr⁻¹; Arnall *et al.* 2015) as follows:

$$c_T(T) = \exp\left(\frac{T_A}{T_{Ref}} - \frac{T_A}{T}\right) \left(\frac{1 + \exp\left(\frac{T_{AL}}{T_{Ref}} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_{Ref}}\right)}{1 + \exp\left(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}\right)} \right) \quad (1)$$

where T_A is the Arrhenius temperature, T_L and T_H are the critical lower and upper boundaries of the thermal tolerance range respectively, T_{AL} and T_{AH} are the Arrhenius temperatures for these boundaries, T_{Ref} is the reference temperature (20 °C) and T is the observed (zoo) temperature in Kelvin (e.g. $T_{Ref} = 20 \text{ °C} = 20 + 273.15 \text{ K}$).

We estimated the T_A from the exponential phase of measurement (i.e. only 12° to 30 °C; refer Fig. 1 of Arnall *et al.* 2015) by taking the slope of the natural log of metabolic rate against the inverse of temperature in Kelvin. The remaining four parameters, required for describing the reduction of physiological rates at low and high temperatures due to enzyme inactivation, were manually adjusted to provide the best fit.

2.4 Incorporating aestivation and metabolic depression into the parameter estimation procedure

For MF2 and MF3, we used a customised function for the parameter estimation procedure that solved the ordinary differential equations for development, growth and reproduction under fluctuating food and temperature conditions, rather than at a single level. This allowed for a metabolic depression factor to be optionally applied during periods where food was absent. The length of aestivation periods in the wild and in captivity vary from year to year, with the former being dependent on natural rainfall, and the latter conditional upon whether individuals are required for periodic public display (e.g. Fig. 3; where 10 of the 12 females used to fit the DEB model were placed on public display at least once). For simplicity, we imposed a 182-day (6 month)

dormancy period for each year simulated to represent the obligatory aestivation phase, which approximately mirrored both captive (mean 132.24 days \pm 2.74 s.e.) and wild (mean 164.65 days \pm 6.72 s.e.) aestivation periods (S. Arnall, unpublished data).

The 'spline0' function in MATLAB was used to obtain food and temperature values for the time steps required by the solver (MATLAB's standard differential equation solver; ode45). Starting as a hatchling, we simulated 50 years, extracting the age, length and weight at puberty, in addition to the reproduction rate over the last four events of the simulation (by which stage the turtle was at maximum size). For the first 182 days of each year modelled, we simulated a full pond by setting f to 1 and applied the corresponding temperature correction factor for the CTE of the water over that period. The change in scaled reserve density was described as:

$$\frac{de}{dt} = c_T v \frac{(f - e)}{L} \quad (2)$$

where c_T is the temperature correction factor (see section 2.3), v is the energy conductance, f is the scaled functional response, e is the scaled reserve density ($[E]/[E_m]$; where $[E]$ is the reserve density, and $[E_m]$ is the maximum reserve density; Eq. 2.11, Kooijman 2010), and L is the structural length.

Specific growth rate (r) became:

$$r = c_T v \frac{\left(\frac{e}{L} - 1\right)}{\left(\frac{L_m}{e} + g\right)} \quad (3)$$

where L_m is the maximum structural length, and g is the energy investment ratio ($[E_G]/\kappa[E_m]$; with $[E_G]$ being the volume specific cost of structure and κ being the allocation fraction to soma; Eq. 2.20, Kooijman 2010).

As a juvenile (i.e. when $e_H < e_H^p$), the change in scaled maturity was given by:

$$\frac{de_H}{dt} = c_T(1 - \kappa)e\left(\frac{v}{L - r}\right) - e_H(k_J + r) \quad (4)$$

where e_H is the scaled maturity density, and k_J is the maturity maintenance rate coefficient.

As an adult (i.e. when $e_H > e_H^p$), the change in the scaled reproduction buffer was:

$$\frac{de_R}{dt} = c_T \frac{(1 - \kappa)e\left(\frac{v}{L - r}\right) - e_H^p k_J L_p^3}{L^3 - re_R} \quad (5)$$

where e_H^p is the maturation threshold for reproduction (puberty), and e_R is the scaled energy allocated to reproduction (E_R/E_m ; with E_R being the energy in reserve allocated to reproduction; Section 2.7.1 Kooijman 2010).

Aestivation was then simulated for the remaining 182 days of each year. For the MF2 model fitting strategy, we simulated the dry aestivation season by setting f to 0, and used the temperature correction factor for the aestivation environment as above. For the MF3 model fitting strategy, we additionally applied a metabolic depression factor (s_M ; 0 to 1) to depress all rate parameters continuously during the 182-day aestivation period.

This was applied to conductance and the maturity maintenance rate coefficient such that:

$$v = v s_M \quad (6)$$

and

$$k_J = k_J s_M \quad (7)$$

It was not necessary to apply the depression factor to the maximum surface-area-specific assimilation rate (\dot{p}_{Am}) and the volume-specific somatic maintenance rate (\dot{p}_M) because these were present in the form of maximum size (i.e. they remained in a constant ratio within the parameter L_m).

A second simulation was also run for 20 years using only the observed pond durations at Perth Zoo during that time, to obtain the predicted lengths and weights for the same times as was observed for the female turtles in the model.

The MATLAB scripts used to estimate the parameters are available at http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/.

2.5 Comparisons with wild *P. umbrina* and other species

We constrained analyses of data from wild individuals to females from the core breeding population of *P. umbrina* at the Ellen Brook Nature Reserve (Swan Coastal Plain, Western Australia). Individuals at this reserve have been monitored since the mid-1960s and are frequently recaptured through ground searches and/or radio tracking, at which time carapace length and wet mass are recorded. To generate an ‘exclusively wild’ dataset, we compiled historical records for all adult turtles that had been located at least five times since the commencement of record collection, and eliminated any that

had spent time in captivity (turtles are occasionally returned to captivity for breeding, or can be released as head-started hatchlings having been born and reared in captivity). To ensure the curves captured the first year of growth, we excluded any individuals whose first capture record exceeded a carapace length of 60mm, as 61mm is the minimum length recorded for (sexed) turtles at one year of age when reared in captive conditions (S. Arnall, unpublished data). This resulted in a sample of six individuals. Since precise birth details for wild individuals are unknown, we assumed a birthdate of the 15th of May in the relevant year because hatchlings typically emerge in May (Burbidge 1981). Length and mass data for these individuals were then compared against the age-length-mass curves for captive *P. umbrina* produced in the DEB model.

Carapace lengths were in all instances measured to the nearest mm using Vernier callipers, while weights were obtained using a Pesola spring balance for field measurements (± 1.0 g for 100 g balances, ± 5.0 g for 500 g balances), and a digital scale for captive measurements (± 0.01 g). Primary DEB parameters were compared to other species using the Add My Pet online collection (hereafter 'AmP'; AmP 2017).

3. Results

Zero-variate data and the primary DEB parameters for *P. umbrina* as derived from the estimation procedures are given in Tables 1 and 2, respectively. The MF1 and MF2 model fitting strategies failed to capture the dynamics of *P. umbrina* growth (overestimating length and mass in both cases) while the MF3 strategy produced the best fit of observed and expected data (Figure 4a-d). The adult life stage was particularly well captured by this model (e.g. ages, lengths, and masses at puberty were best matched), but reproductive rate and age at birth were both underestimated (Table 1). The MF3 strategy was also able to replicate mass loss over aestivation well, with an

average loss of $7.73 \text{ g} \pm 0.89 \text{ s.e.}$ (as compared to the average mass loss of $11.9 \text{ g} \pm 1.25 \text{ s.e.}$ recorded for the 160 individuals measured at the zoo). The largest discrepancy between observed and predicted values across all DEB models was in metabolic rate (Fig. 4d; but see Section 4 below).

The MF2 strategy greatly overestimated length even when manually minimising the zoom parameter. Any values for κ greater than 0.18 resulted in the individual not reaching puberty, and with κ set to 0.18 the procedure was able to run, but both mass and length declined with each starvation period. Turtles measured at Perth Zoo experienced a change in mass (mean decrease of $7.9 \% \pm 2.6 \text{ s.e.}$) but not in length ($0.2 \text{ mm} \pm 0.0 \text{ s.e.}$) over the aestivation period, so the predictions from MF2 were unrealistic.

Turtles had very rapid growth in their first year (Fig 5a, 5b). Wild individuals grew more slowly ($0.77 \text{ mm year}^{-1}$) than did captive *P. umbrina* ($0.97 \text{ mm year}^{-1}$) in the first seven years of life, but growth trajectories aligned after approximately eight years, with an average growth rate of 0.92 mm per year for turtles over seven years old. When growth data of wild individuals were compared to the MF3 model, the model was able to capture the long-term growth trajectories for length (Fig. 5a) but slightly overestimated mass (Fig. 5b).

The primary parameters of *P. umbrina* (as taken from MF3) were compared in Table 3 to those of five other Chelidae for which DEB models have been produced. *P. umbrina* had much higher volume-specific somatic maintenance costs ($504.1 \text{ J d}^{-1} \text{ cm}^{-3}$) than any other Chelidae (range $12.4 - 24.0 \text{ J d}^{-1} \text{ cm}^{-3}$). Their Arrhenius temperature was also much higher, being almost 2.5-fold greater than that of other Testudines in the AmP

collection ($n = 30$; typical Arrhenius temperatures are around 8000K; range for Testudines and Reptilia are 7000 - 8000K and 6750 – 14065K, respectively; *P. umbrina* 19371K). The remaining parameters did not deviate substantially from values previously derived for Chelidae. Despite being comparatively high in respect to Testudines, $[p_M]$ fell within the range of values reported for Reptilia ($n = 60$, limited to extant species; range 10.6 - 1000.0 J d⁻¹ cm⁻³). Generating a fit with $[p_M]$ reduced to values more typical of Testudines (18.96 J d⁻¹ cm⁻³) resulted in a model that underestimated the rapid first-year growth of hatchlings (mass of 14.4 g at end of first year; critical mass = 18.0 g, MF3 = 26.9 g) and that did not reflect aestivation accurately (Fig. 6a, 6b; S1).

4. Discussion

The fact that *P. umbrina* occupies an environment in which food resources fluctuate seasonally from abundant to absent makes fitting a DEB model challenging because the whole-of-life energy budget model must capture long-term growth as affected by repeated annual aestivation, and associated starvation. Aestivation is most simply defined as ‘inactivity during the dry seasons’ (Gregory 1982). It has been recorded in several Testudine species (e.g. in the *Kinosternidae*; Ligon & Peterson 2002), but it is not always accompanied by metabolic depression despite lipid and protein stores being drawn upon over the starvation period (Crawford 1994). Quiescent and burrowing behaviour, increases in body fluid concentrations, reduced rates of evaporative water loss, modified nitrogen metabolism and/or storage of excretory wastes (to minimise urinary water loss) are all alternative, or complementary traits to metabolic depression during aestivation (Ligon & Peterson 2002, and references therein). Our DEB models suggest that metabolic depression during aestivation is a required strategy for *P. umbrina* survival as when the models were run without metabolic depression, reserves

were insufficient to reach puberty (which is also when vitellogenesis takes place in *P. umbrina*; Kuchling & Bradshaw 1993). The extent to which *P. umbrina* is able to reduce its energy and water requirements during periods of starvation is yet to be experimentally quantified, but other Testudines can reduce their metabolic rate to around 0.2-0.8 of rest during aestivation (from Table 6 of Guppy & Withers 1999). Aestivation events of over one year have been recorded Testudine species, such as 480 days in the facultative aestivating *Chelodina longicollis* (Roe & Georges 2007) and two years in *Kinosternon flavescens* (Rose 1980), though both periods included overwintering where temperatures were reduced (Roe *et al.* 2008). Our DEB model predicts a maximal starvation time of around 275 days for an adult at 20 °C. Comparative DEB models for other semi-aquatic turtle species (particularly those for which metabolic depression has been quantified) would be highly informative.

The fact that *P. umbrina* embryos also aestivate addresses the disparity between the observed and expected age at birth. Embryonic arrest is widely recorded in chelonians and can take numerous forms (e.g. pre- and post-ovulatory; Rafferty & Reina 2012). Delayed hatching/embryonic aestivation is a strategy that prolongs the residence of an embryo within the egg while the external environment is unfavourable, and is perhaps best exemplified by the pignose turtle (*Carettochelys insculpta*) which has full-term embryos that go into aestivation (Doody *et al.* 2001). Cessation of aestivation is triggered by a rapid fall in oxygen availability which coincides with submersion of nests by the first floods of the wet season (Doody *et al.* 2001). Similarly, emergence of *P. umbrina* hatchlings in the wild is triggered by a drop in temperature (and pressure) that generally coincides with rainfall, signalling the commencement of the wet (and therefore, feeding) season (Burbidge 1981). Embryonic aestivation in *P. umbrina* has been inferred using heart rate monitoring, which has shown heart rates dropping to zero

in eggs that ultimately hatched (Mitchell *et al.* 2016)¹. By applying the developmental rate function developed by these authors (Figure 2 of Mitchell *et al.* 2016), it can be predicted that for the female individuals incubated at 24 °C in our model, embryonic maturity would be reached after approximately 105 days, leaving an approximately seven-week aestivation period. This is supported by an incubation study by Mitchell *et al.* (2016) where the mean aestivation period for embryos incubated at 24 °C was 62 days (\pm 23 days; range 33 – 94 days; n = 6; N. Mitchell, unpublished data), which is equivalent to an approximately 9 week aestivation period. In the DEB MF3, age at birth was estimated at 55 days. The addition of a 94-day aestivation period shifts the estimate to 149 days, which is similar to the observed value (153 days). Given the large range in the embryonic aestivation periods inferred by the heart rate drop, re-examining embryonic heart rate changes with an increased sample size would provide more confidence in the model's ability to predict age at birth precisely.

There are two plausible explanations for why the DEB model was able to capture growth well, but failed to reproduce the observed metabolic rates. The first is that the measurements in Arnall *et al.* (2015) could have been confounded by aestivation (i.e. the turtles were commencing aestivation in the absence of water and as a result of being fasted; but refer to discussion in Arnall *et al.* 2015 for why this is unlikely). The second is that the disparity could represent the difference between resting metabolic rates, as measured in Arnall *et al.* 2015, and long-term average metabolic rates incorporating activity costs (but not the heat increment of feeding), as predicted by the DEB model.

The predicted metabolic rates were approximately at the values expected for foraging

¹ Here we make the distinction between 'embryonic aestivation' and 'embryonic diapause' which have been used interchangeably when discussing egg development in *P. umbrina* (e.g. Mitchell *et al.* 2016). Embryonic diapause concerns arrest after oviposition, prior to somite and vitelline membrane formation (Rafferty & Reina 2012). Conversely, arrest during the final stages of development prior to hatching is termed aestivation (Rafferty & Reina 2012). Data from Mitchell *et al.* 2016 shows that eyespot development precedes the heart rate drop in *P. umbrina*. As eyespot development occurs after the formation of membranes, embryonic *P. umbrina* undergo aestivation rather than diapause in this context.

chelids (after Gatten 1974), and swamp turtles at Perth Zoo are quite active during the wet periods, especially during late afternoon (S. Arnall, pers. obs.). Further, turtles in the wild at Ellen Brook Nature Reserve spend almost 60% of their time in warm water, at which time they are likely active (calculated from Table 2 in King *et al.* 1998).

Western swamp turtles had the highest Arrhenius temperature, and second highest somatic maintenance costs for the reptiles in the AmP collection. Although there is considerable variation in $[p_M]$ across taxa, *P. umbrina*'s high somatic maintenance costs might be explained by elements of the 'waste to hurry' hypothesis (Kooijman 2013). This proposes that by increasing both assimilation and somatic maintenance, species waste resources, and in doing so remain small, but can grow fast and respond rapidly to the transient availability of food. Somatic maintenance has priority over growth, and growth ceases when all reserves are required for somatic maintenance (Sara *et al.* 2013). Thus, to grow and reproduce fast during periods of blooming resources, individuals would need to eat rapidly. However, this would result in a large body size which, in turn, would require higher maintenance costs (as these are proportional to structural body length). Such high maintenance costs would be problematic during periods of low resource availability (e.g. in the dry season in the western swamp turtle). By increasing somatic maintenance costs, growth and reproduction are boosted independently of size (i.e. ultimate structural length) and this, when coupled with metabolic depression, provides a mechanism for surviving periods of low resource availability (Kooijman 2013).

The Labord's chameleon (*Furcifer labordi*) has the highest $[p_M]$ in the AmP collection presently ($1000 \text{ J d}^{-1} \text{ cm}^{-3}$) and similar to *P. umbrina*, this species also hatches in synchrony with the onset of the annual rain season (Karsten *et al.* 2008), after which

juveniles grow very rapidly (reaching maturity after only two months; Eckhardt *et al.* 2017). In a deciduous forest with a rainy season of about five months, *F. labordi* has an obligate year-long lifespan, and consequently it is regarded as a ‘waste to hurry’ species. Unlike the Labord’s chameleon, turtles are renowned for their longevity, delayed reproduction and iteroparity (Kuchling 1999). While *P. umbrina* does not display the typical characteristics of ‘waste to hurry’ species such as the chameleon, copepods and salps (i.e. a small age at first maturation, and a large reproduction rate), they are small in comparison to other Testudines (which can be several hundred kilograms; Iverson 1992), and rely on the presence of abundant food within a short seasonal growth period, which resembles a blooming resource (Kooijman 2013). *P. umbrina* is the only turtle endemic and restricted to ephemeral wetlands in a Mediterranean climate where low temperatures in cool wet winters restrict energy acquisition to a short period in the spring, and no food or water is available during long hot dry periods from late spring to autumn. The long-lived *P. umbrina* has a life span similar to that of humans (Burbidge *et al.* 2010; approximately 90 years predicted in MF3) and hatchlings have to grow very rapidly to survive their first summer, which cannot be achieved following dry winters. A ‘waste to hurry’ strategy, rather than increasing the fraction of reserve that is allocated to κ , might be an adaptation to being long-lived while inhabiting ephemeral wetlands where resource availability varies from year to year.

A mechanism that also appears to facilitate survival in a resource-dynamic habitat is the labile control of reproduction, in which energetically demanding reproductive processes (such as gravidity and/or oviposition) can be curtailed until conditions become more favourable, or can be aborted entirely (Kuchling 1999). Vitellogenesis (the allocation of resources to reproduction) starts in *P. umbrina* during aestivation, over half a year prior

to oviposition (Kuchling and Bradshaw 1993). At the time when vitellogenesis commences, food availability in the following spring is not guaranteed and so it is impossible to predict whether a resource bloom during the wet season will allow reproduction to proceed. In contrast to most other turtles which ovulate once preovulatory follicles have developed (a pre-programmed mechanism), *P. umbrina* can abort eggs by follicular atresia (i.e. not ovulating and reabsorbing the yolk of preovulatory follicles) in years when blooming fails and resources are scarce (Kuchling and Bradshaw 1993; Kuchling 1999). In these years, this labile control conceivably allows the energy allocated to the yolk to be relegated to somatic maintenance and survival. In chelonian reptiles, species inhabiting predictable environments typically have reproduction that relies heavily on pre-programmed mechanisms (closed control), while labile control often operates in species living in unpredictable habitats where exogenous cues play a more important role (Kuchling 1999). This distinction may be particularly relevant within the context of uncertain environmental futures (such as climate change).

A pressing challenge for conservation managers is to predict the responses of species to novel environments. Quantifying responses at scales that capture the interaction between the biophysical traits of a species, and the environmental constraints on ecosystem energetics is both challenging and critical (Tomlinson *et al.* 2014). This study presents the first set of bioenergetic information for *P. umbrina*, and the DEB model produced offers a tool to explore how changing environmental conditions might affect growth and reproduction in this species, particularly under novel conditions such as climate change. This information is especially relevant in the context of seeking additional translocation sites for this species, which is a goal in the recovery plan that guides the turtles' conservation (Burbidge *et al.* 2010). Existing models developed for informing translocation site selection (Mitchell *et al.* 2013; Dade *et al.* 2014; Mitchell *et*

al. 2016, Bin Tarque 2017) currently lack the ability to predict key life history parameters such as development times, growth rates, and potential reproductive outputs. Therefore, once spatially-resolved (e.g. Kearney *et al.* 2013; Schwarzkopf *et al.* 2016), our DEB model can contribute to conservation decision making by facilitating the evaluation of potential translocation sites in terms of their suitability for meeting the species' ecological energetic needs.

The energetics of individual organisms and the flow of energy through ecosystems drives many important processes that define ecological niches, community structure, and ecosystem dynamics (Tomlinson *et al.* 2014). While not explored here, our DEB model of *P. umbrina* could form the basis for future population modelling (e.g. van der Meer *et al.* 2011) which would be especially useful for predicting how resilient populations of *P. umbrina* may be to the hotter and drier climates predicted for the region it inhabits (CSIRO & BOM 2007; IOCI 2012). It could also inform carrying capacity questions (e.g. Filgueira *et al.* 2014) to ensure ecosystem health is preserved and populations are stocked appropriately. Additionally, our DEB model could be used to perform spatially-explicit 'virtual experiments' to explore how the species responds to new environments and conditions (e.g. Kolbe *et al.* 2010). This approach would allow managers to test numerous 'what-if' scenarios, without compromising the wellbeing of individuals. Under novel futures, managers will increasingly require a mechanistic understanding of what drives a species' persistence and success, and these potential applications are prime examples of how DEB modelling might be used to inform conservation and management objectives.

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References

AmP. (2017). Online database of DEB parameters, implied properties and referenced underlying data. Available at http://www.bio.vu.nl/thb/deb/deblab/add_my_pet [last accessed 1/12/2017].

Arnall, S. G., Kuchling, G., and Mitchell, N. J. (2015). A thermal profile of metabolic performance in the rare Australian chelid, *Pseudemydura umbrina*. *Australian Journal of Zoology*, 62: 448-453.

Bin Tareque, A. M. H. (2017). An integrated eco-hydrological approach for assessing critical wetland habitats and conservation reserves in a changing climate. PhD Thesis. University of Western Australia, Crawley, Australia.

Bunn, S.E., Thoms, M.C., Hamilton, S.K., and Capon, S.J. (2006). Flow variability in dryland rivers: boom, bust and the bits in between. *River Research and Applications*, 22: 179-186.

Burbidge, A. A. (1981). The ecology of the western swamp tortoise *Pseudemydura umbrina* (Testudines: Chelidae). *Wildlife Research*, 8: 203-223.

Burbidge, A. A., Kuchling, G., Olejnik, C., and Mutter, L. (2010). Western Swamp Tortoise (*Pseudemydura umbrina*) Recovery Plan, 4th Edition. Department of Environment and Conservation, Perth, Australia.

Crawford, K.M. (1994). Patterns of energy substrate utilization in overwintering painted turtles, *Chrysemys picta*. *Comparative Biochemistry and Physiology Part A: Physiology*, 109: 495-502.

CSIRO and BoM. (2007) Climate change in Australia. Technical Report, 2007. (Eds K.B. Pearce, P.N. Holper, M. Hopkins, W.J. Bouma, P.H. Whetton, K.J. Hensessy, and S.B. Power). CSIRO Marine and Atmospheric Research Division, Victoria, Australia.

Dade, M. C., Pauli, N., and Mitchell, N. J. (2014). Mapping a new future: using spatial multiple criteria analysis to identify novel habitats for assisted colonization of endangered species. *Animal Conservation*, 17: 4-17.

Doody, J.S., Georges, A., Young, J.E., Pauza, M.D., Pepper, A.L., Alderman, R.L., and Welsh, M.A. (2001). Embryonic aestivation and emergence behaviour in the pig-nosed turtle, *Carettochelys insculpta*. *Canadian Journal of Zoology*, 79: 1062-1072.

Eckhardt, F., Kappeler, P. M., and Kraus, C. (2017). Highly variable lifespan in an annual reptile, Labord's chameleon (*Furcifer labrodi*). *Scientific Reports*, 7: 1-5.

Filgueira, R., Guyondet, T., Comeau, L. A., and Grant, J. (2014). A fully-spatial ecosystem-DEB model of oyster (*Crassostrea virginica*) carrying capacity in the Richibucto Estuary, Eastern Canada. *Journal of Marine Systems*, 136: 42-54.

Gatten, R. E. (1974). Effects of temperature and activity on aerobic and anaerobic metabolism and heart rate in the turtles *Pseudemys scripta* and *Terrapene ornata*. *Comparative Biochemistry and Physiology Part A – Physiology*, 48: 619–648.

Gregory, P.T (1982). Reptilian hibernation. In 'Biology of the Reptilia', Vol. 13. (Eds C. Gans and F. H. Pough). pp. 53–154 (Academic Press: USA).

Guppy, M., and Withers, P. (1999). Metabolic depression in animals: Physiological perspectives and biochemical generalizations. *Biological Reviews of the Cambridge Philosophical Society*, 74: 1-40.

IOCI. (2012). Western Australia's weather and climate: a synthesis of Indian Ocean climate initiative stage 3 research. CSIRO and BoM, Canberra, Australia.

Iverson, J.B. (1992). Correlates of reproductive output in turtles (Order Testudines). *Herpetological Monographs*, 6: 25-42.

Jusup, M., Sousa, T., Domingos, T., Labinac, V., Marn, N., Wang, Z., and Klanjšček, T. (2017). Physics of metabolic organization. *Physics of Life Reviews*, 20: 1-39.

Karsten, K. B., Andriamandimbiarisoa, L. N., Fox, S. F. and Raxworthy, C. J. (2008). A unique life history among tetrapods: An annual chameleon living mostly as an egg. *Proceedings of the National Academy of Science*. 105: 8980–8984.

Kearney, M. (2012). Metabolic theory, life history and the distribution of a terrestrial ectotherm. *Functional Ecology*, 26: 167-179.

Kearney, M. (2013). Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology Letters*, 16: 1470-1479.

Kearney, M. R., Simpson, S. J., Raubenheimer, D., and Kooijman, S. A. L. M. (2013). Balancing heat, water, and nutrients under environmental change: a thermodynamic niche framework. *Functional Ecology*, 27: 950-966.

King, J. M., Kuchling, G., and Bradshaw, S. D. (1998). Thermal environment, behavior, and body condition of wild *Pseudemydura umbrina* (Testudines: Chelidae) during late winter and early spring. *Herpetologica*, 54: 103-112.

Kolbe, J. J., Kearney, M., and Shine, R. (2010). Modeling the consequences of thermal trait variation for the cane toad invasion of Australia. *Ecological Applications*, 20: 2273-2285.

Kooijman, S. A. L. M. (1993). 'Dynamic Energy Budgets in biological systems: Theory and applications in ecotoxicology' (Cambridge University Press: USA).

Kooijman, S. A. L. M. (2004). Add My Pet. Unpublished guide to DEBtool. Distributed at the *Second Symposium on Dynamic Energy Budget Theory*, 13/4/2011- 15th/4/2011, Lisbon, Portugal.

Kooijman, S. A. L. M. (2010). 'Dynamic Energy Budget Theory for Metabolic Organization.' (Cambridge University Press: USA).

Kooijman, S. A. L. M. (2013). Waste to hurry: Dynamic energy budgets explain the need of wasting to fully exploit blooming resources. *Oikos*, 122: 348-357.

Kooijman, S. A. L. M. (2014). Add My Pet. VU University, Amsterdam, 44p. Available from DEB Lab: <https://www.bio.vu.nl/thb/deb/deblab/>

Kooijman S. A. L. M. and Lika K. (2014). Resource allocation to reproduction in animals. *Biological Reviews*, 89: 849–859.

Kooijman, S. A. L. M., Sousa, T., Pecquerie, L., van der Meer, J., and Jager, T. (2008). From food-dependent statistics to metabolic parameters, a practical guide to the use of dynamic energy budget theory. *Biological Reviews*, 83: 533-552.

Kuchling G. (1999). The Reproductive Biology of the Chelonia. Zoophysiology Vol. 38. (Springer Berlin Heidelberg New York).

Kuchling, G., and Bradshaw, S. D. (1993). Ovarian cycle and egg production of the western swamp tortoise *Pseudemydura umbrina* (Testudines: Chelidae) in the wild and in captivity. *Journal of Zoology*, 229: 405–419.

Kuchling, G., Dejose, J. P., Burbidge, A. A., and Bradshaw, S. D. (1992). Beyond captive breeding: the western swamp tortoise *Pseudemydura umbrina* recovery programme. *International Zoo Yearbook*, 31: 37-41.

Letnic, M., and Dickman, C. R. (20016). Boom means bust: interactions between the El Niño/Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodiversity and Conservation*, 15: 3847-3880.

Ligon, D.B., and Peterson, C.C. (2002). Physiological and behavioral variation in estivation among mud turtles (*Kinosternon spp.*). *Physiological and Biochemical Zoology*, 75: 283-293.

Lika, K., Kearney, M. R., Freitas, V., van der Veer, H. W., van der Meer, J., Wijsman, J. W. M., Pecquerie, L., and Kooijman, S. A. L. M. (2011a). The ‘covariation method’ for estimating the parameters of the standard Dynamic Energy Budget model I: philosophy and approach. *Journal of Sea Research*, 66: 270–277.

Lika K., Kearney M. R., and Kooijman S. A. L. M. (2011b). The ‘covariation method’ for estimating the parameters of the standard Dynamic Energy Budget model II: properties and preliminary patterns. *Journal of Sea Research*, 66: 278–288.

Marn N, Kooijman S.A.L.M., Jusup M., Legović T., and Klanjšček T. (2017). Inferring physiological energetics of loggerhead turtle (*Caretta caretta*) from existing data using a general metabolic theory. *Marine Environmental Research*. 126:14-25.

Mitchell, N. J., Hipsey, M. R., Arnall, S., McGrath, G., Tareque, H. B., Kuchling, G., Vogwill, R., Sivapalan, M., Porter, W. P., and Kearney, M. R. (2013). Linking eco-energetics and eco-hydrology to select sites for the assisted colonization of Australia’s rarest reptile. *Biology*, 2: 1-25.

Mitchell, N. J., Rodriguez, N., Kuchling, G., Arnall, S. G., and Kearney, M. R. (2016). Reptile embryos and climate change: Modelling limits of viability to inform translocation decisions. *Biological Conservation*, 204: 134–147.

Nisbet, R. M., Muller, E. B., Lika, K., and Kooijman, S. A. L. M. (2000). From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology*, 69: 913-926.

Nisbet, R. M., McCauley, E., and Johnson, L. R. (2010). Dynamic energy budget theory and population ecology: lessons from *Daphnia*. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365: 3411–3590.

Orchard, T. J. (1975). Calculating constant temperature equivalents. *Agricultural Meteorology*, 15: 405-418.

Rafferty, A. R., and Reina R. D. (2012). Arrested embryonic development: a review of strategies to delay hatching in egg-laying reptiles. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20120100.

Roe, J. H., and Georges, A. (2007). Heterogeneous wetland complexes, buffer zones, and travel corridors: landscape management for freshwater reptiles. *Biological Conservation*, 135: 67-76.

Roe, J. H., Georges, A., and Green B. (2008). Energy and water flux during terrestrial estivation and overland movement in a freshwater turtle. *Physiological and Biochemical Zoology*, 81: 570-583.

Rose, F.L. (1980). Turtles in arid and semi-arid regions. *Bulletin of the Ecological Society of America*, 61: 89-89.

Sara, G., Palmeri V., Montalto V., Rinaldi A., and Widdows J. (2013). Parametrisation of bivalve functional traits for mechanistic eco-physiological dynamic energy budget (DEB) models. *Marine Ecology Progress Series*, 480: 99–117.

Schwarzkopf, L., Caley, M. J., and Kearney, M. R. (2016). One lump or two? Explaining a major latitudinal transition in reproductive allocation in a viviparous lizard. *Functional Ecology*, 30: 1373–1383.

Sharpe, P. J. H., and DeMichele, D. W. (1977). Reaction kinetics of poikilotherm development. *Journal of Theoretical Biology*, 64: 649–670.

Sousa T., Domingos T., and Kooijman S. A. L. M. (2008). From empirical patterns to theory: A formal metabolic theory of life. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363: 2453–2464.

Tomlinson, S., Arnall, S. G., Munn, A., Bradshaw, S. D., Maloney, S. K., Dixon, K. W., and Didham, R. K. (2014). Applications and implications of ecological energetics. *Trends in Ecology and Evolution*, 29: 280-290.

van der Meer, J. (2006). Metabolic theories in ecology. *Trends in Ecology and Evolution*, 21: 136–140.

van der Meer, J., van der Veer, H., and Witte J. I.J. (2011). The disappearance of the European eel from the western Wadden Sea. *Journal of Sea Research*, 66: 434–439.

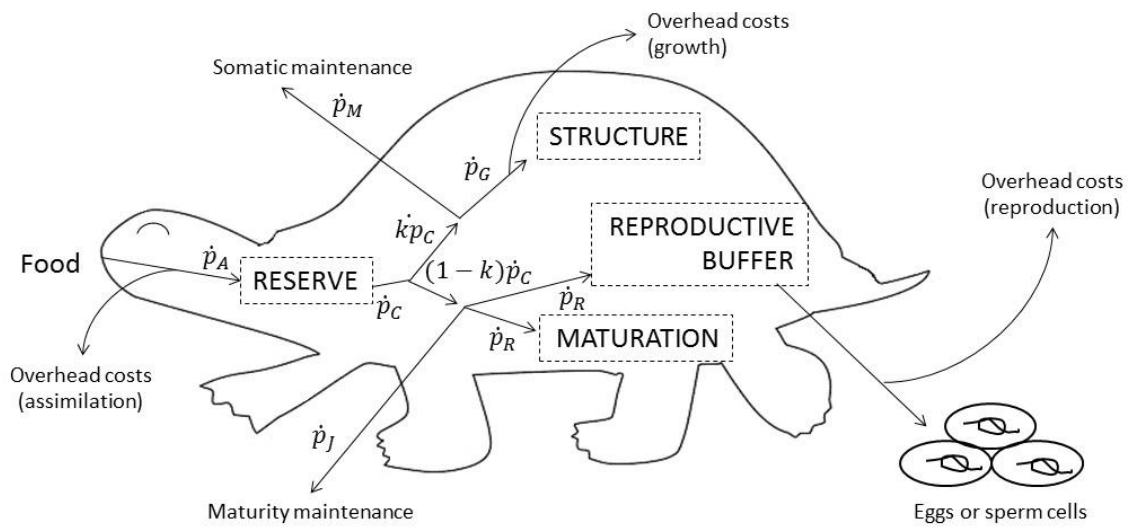


Fig. 1

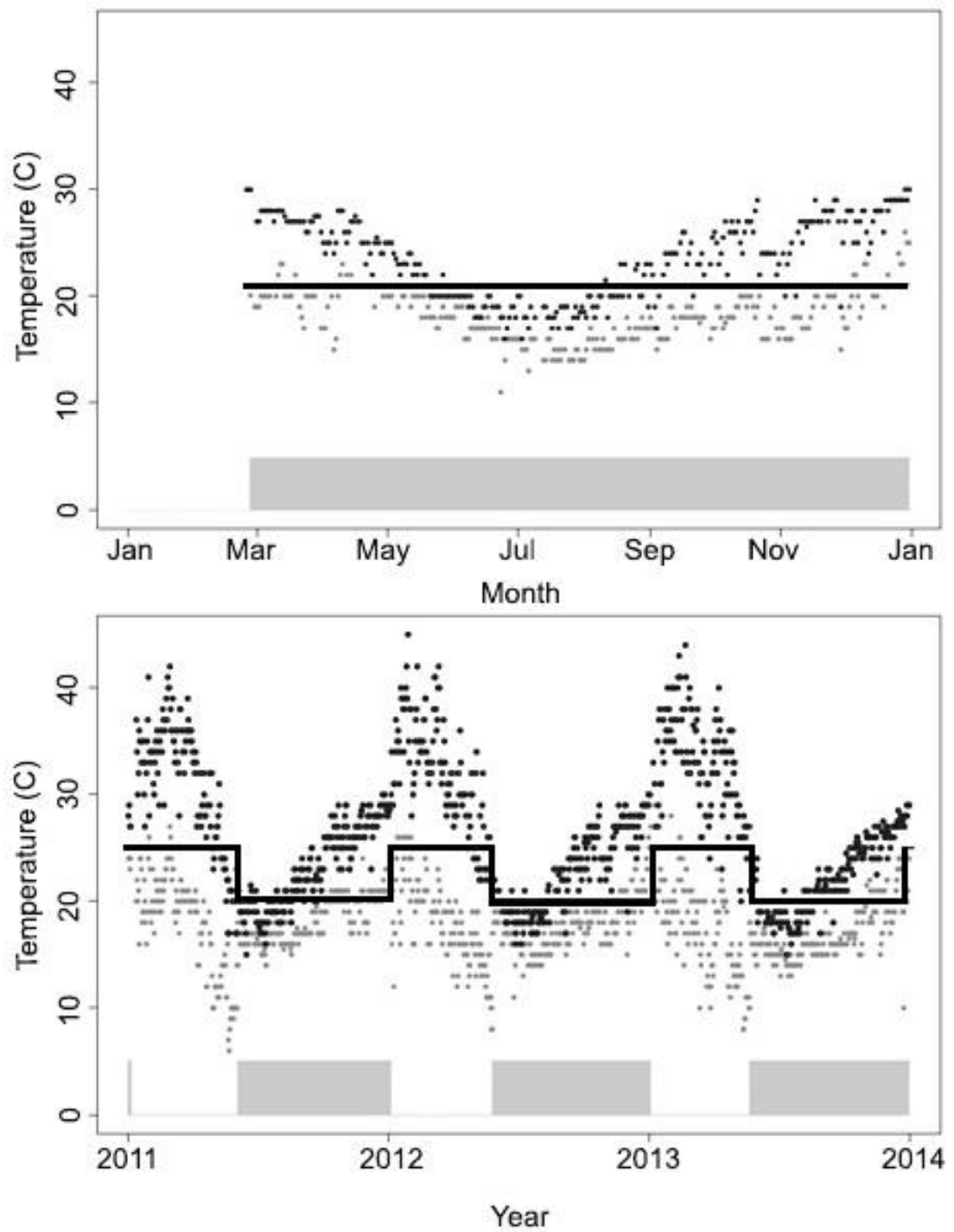


Fig. 2

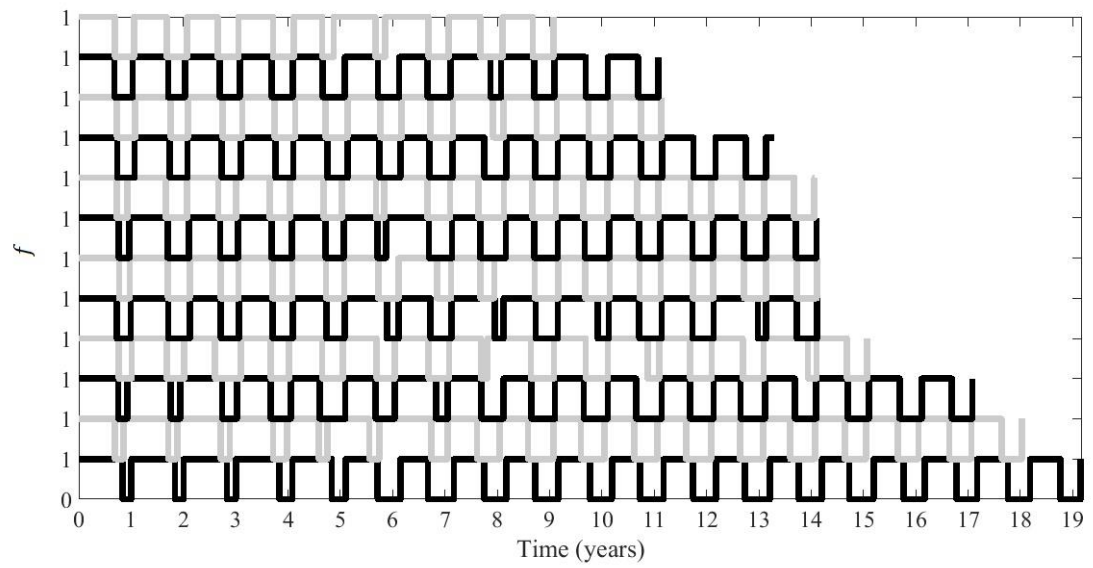


Fig. 3

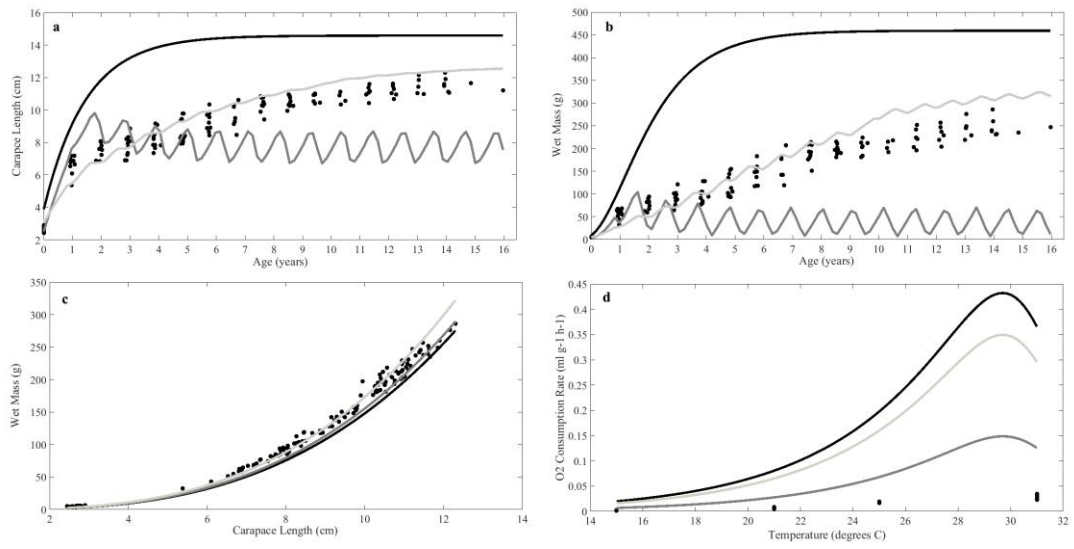


Fig. 4

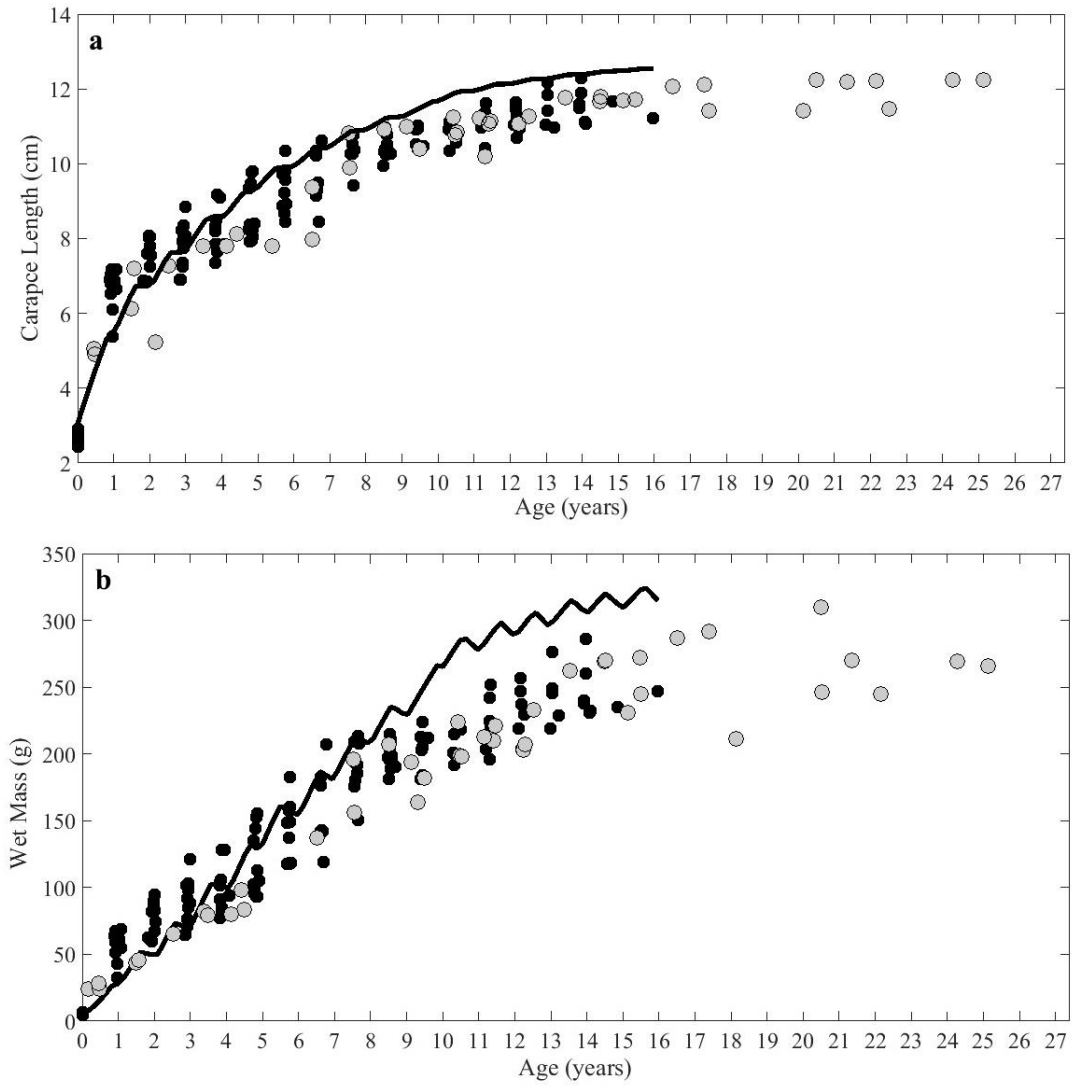


Fig. 5

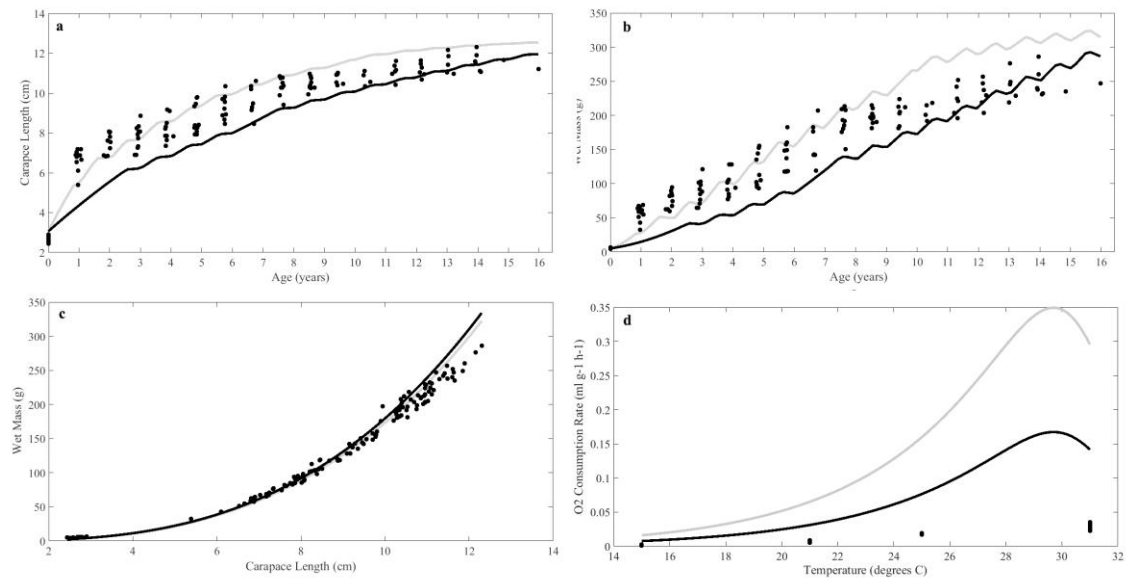


Fig. 6

Table 1 – Observed and estimated zero-variate data for *P. umbrina*, including assigned weightings, obtained through the covariation method of the estimation procedure (Lika *et al.* 2011a). MF1 refers to a model fit with an f of 0.5 (taking the midpoint f to approximate the yearly fluctuations between an f of 1 during wet periods, and 0 during aestivation periods). MF2 refers to a model fit with a splining function to explicitly derive f and c_T across time, and MF3 refers to a variation of MF2 in which a factor for metabolic depression was applied during aestivation (refer 2.4 main text). The weighting choice ('Wt.') was applied after Kooijman *et al.* (2008) to combine the accuracy of the measurement, and the effect the numerical value would have on the result. Equation and section numbers refer to Kooijman (2010), after van der Meer *et al.* (2011).

Zero-variate Data	Observed	Expected			Wt.	Refer
		MF1	MF2	MF3		
a_b , age at birth (d)	153	179.3	26.4	55.0	-	Eq. 2.39
a_p , age at puberty (d)	3767	1443	4775	2960	-	Eq. 2.53
a_m , life span (d)	36500	45300	30310	32920	-	Sn 6.1.1
L_b , length at birth (cm)	2.6	3.57	2.52	3.06	10	Eq. 2.46
L_p , length at puberty (cm)	10.7	5.68	5.87	10.10	10	Eq. 2.54
L_i , ultimate length (cm)	13.8	13.46	20.77	13.68	5	Eq. 2.21
W_b , wet weight birth (g)	5.2	8.55	2.50	4.92	1	Sn 1.2.3; Eq. 3.3
W_p , wet weight puberty (g)	236.5	34.46	31.56	178.60	1	Sn 1.2.3; Eq. 3.3
W_i , ultimate wet weight (g)	417.0	458.1	1393.0	443.6	5	Sn 1.2.3; Eq. 3.3
R_i , max. reproduction rate (# d^{-1})	0.0137	0.01063	0.0000	0.0089	-	Eq. 2.58

Table 2 – The primary DEB parameters obtained through the covariation method of the estimation procedure (Lika *et al.* 2011a). MF1 refers to a model fit with an f of 0.5 (taking the midpoint f to approximate the yearly fluctuations between an f of 1 during wet periods, and 0 during aestivation periods). MF2 refers to a model fit with a splining function to explicitly derive f and c_T across time, and MF3 refers to a variation of MF2 in which a factor for metabolic depression was applied during aestivation (refer 2.4 main text).

Parameter Values	Unit	MF1	MF2	MF3	Source
z , zoom factor	-	10.5	2.7	2.7	Estimated
δ_M , shape coefficient	-	0.39	0.13	0.20	Estimated
ν , energy conductance	$\frac{c}{m \cdot d^{-1}}$	0.01	0.10	0.01	Estimated
κ , allocation fraction to soma	-	0.70	0.18	0.72	Estimated
κ_R , reproduction efficiency	-	0.95	0.95	0.95	Default
$[\dot{p}_M]$, specific somatic maintenance	$\frac{J}{c \cdot m^3 \cdot d^{-1}}$	20.0	449.6	504.1	Estimated
k_J , maturity maintenance rate coefficient	d^{-1}	0.002	0.002	0.002	Default
$[E_G]$, specific cost for structure	$\frac{J}{c \cdot m^3}$	8000	7620	7965	Estimated
E_H^b , energy maturity at birth	J	9833	2554	2275	Estimated
E_H^p , energy maturity at puberty	J	4.12E+04	5.10E+05	5.57E+05	Estimated
h_a , Weibull aging acceleration	d^{-1}	9.09E-11	7.25E-11	6.30E11	Estimated
T_A , Arrhenius temperature	K	19731	19731	19731	Arnall <i>et al.</i> (2015)
T_L , lower bound for T_A	K	278.15	278.15	278.15	Arnall <i>et al.</i> (2015)
T_H , upper bound for T_A	K	304.15	304.15	304.15	Arnall <i>et al.</i> (2015)
T_{AL} , value of T_A below lower bound	K	50000	50000	50000	Arnall <i>et al.</i> (2015)
T_{AH} , value of T_A above upper bound	K	90000	90000	90000	Arnall <i>et al.</i> (2015)
s_M , metabolic depression factor	-	NA	NA	0.0518	Estimated

Table 3 – Comparison of the western swamp turtle (*Pseudemydura umbrina*) DEB MF3 to other Chelidae for which DEB models exist (AmP 2017).

Parameter	Unit	Murray River Turtle (<i>Emydira macquarii</i>)	Matua Matua (<i>Chelusia fibriata</i>)	Brazilian Snake-necked Turtle (<i>Hydromedusa maximiliani</i>)	Northern Snapping Turtle (<i>Elseya dentata</i>)	Northern Snake-necked Turtle (<i>Chelodina oblonga</i>)	Western Swamp Turtle (<i>Pseudemydura umbrina</i>)
v , energy conductance	cm d^{-1}	0.061	0.014	0.016	0.019	0.016	0.0125
κ , allocation fraction to soma	-	0.736	0.64	0.826	0.731	0.820	0.722
$[\dot{p}_M]$, vol-specific somatic maintenance	$\text{J d}^{-1} \text{cm}^{-3}$	16.40	23.96	12.41	17.58	17.18	504.10
k_j , maturity maintenance rate coefficient	d^{-1}	0.000	0.002	0.000	0.002	0.000	0.002
$[E_G]$, spec cost for structure	J cm^{-3}	7858	7833	7857	7842	7846	7965
E_H^b , energy maturity at birth	J	13,660	4505	7704	17,790	8870	2275
E_H^p , energy maturity at puberty	J	1.17e07	1.62e06	6.02e05	5.02e06	1.95e06	5.57e05
h_a , Weibull aging acceleration	d^{-1}	1.21e09	2.08e10	1.22e11	7.34e10	2.93e06	6.30e11
δ_M , shape coefficient	-	0.6172	0.2899	0.5563	0.3990	0.3413	0.1968
T_A , Arrhenius temperature	K	8000	8000	8000	8000	8000	19,730
z , zoom factor	-	13.200	13.341	6.507	11.885	9.893	2.693

Fig. 1 – Conceptual representation of the κ -rule Dynamic Energy Budget model in *P. umbrina*, where arrows represent energy fluxes (in J day⁻¹) towards state variables (denoted by boxes). Notation is as follows: \dot{p}_A , assimilation rate; \dot{p}_C , mobilization rate; p_G , structural growth; \dot{p}_J , maturity maintenance; \dot{p}_R , maturation; \dot{p}_M , somatic maintenance; κ , kappa. Refer van de Meer (2006) and Sousa *et al.* (2008) for comprehensive descriptions of the standard DEB model.

Fig. 2 – Typical daily minimum and maximum temperatures experienced by *P. umbrina* at the captive breeding facility at Perth Zoo (South Perth, Western Australia). The top panel shows the water temperatures of hatchling ponds in 2011 (commencing in March, when eggs typically hatch), while the bottom panel shows temperatures experienced by juveniles and adults. The grey bars show the wet season where the corresponding temperatures are daily maximum (black dots) and minimum (grey dots) water temperatures; in all remaining cases the temperatures are the maximum (black dots) and minimum (grey dots) air temperatures recorded in aestivation pens. Solid black lines depict the mean constant temperature equivalents.

Fig. 3 – Typical aestivation periods for *P. umbrina* at Perth Zoo. Each individual fluctuates between f of 0 and 1, denoting periods of starvation (during aestivation) and feeding *ad libitum* (during time spent in rearing ponds), respectively. Data for 12 female turtles are presented, with the switch days between f of 0 and 1 being shown by solid black or grey lines for each alternate individual.

Fig. 4a-d – Comparisons between model predictions (solid lines) and observed data (dots) for *P. umbrina* under the three different model fitting strategies. MF1 is shown as

the black line, MF2 is shown as the medium grey line, and MF3 is shown as the light grey line. (a) presents carapace length as a function of age, (b) shows wet mass as a function of age, (c) presents the length-weight relationship, and (d) shows metabolic rate with temperature.

Fig. 5 – Comparisons of wild *P. umbrina* growth (grey dots) to the DEB model predictions (black solid line; model fitting strategy ‘MF3’) and observed data for captive-bred *P. umbrina* (black dots). **a)** shows carapace length as a function of age, and **b)** shows wet mass as a function of age.

Fig. 6a-d – Western swamp turtle DEB MF3 parameterised with a somatic maintenance value typical of Testudines ($18.96 \text{ J d}^{-1} \text{ cm}^{-3}$; black lines; MRE = 0.542), against the corresponding results from MF3 ($500.4 \text{ J d}^{-1} \text{ cm}^{-3}$; grey lines; MRE = 0.781). **(a)** shows carapace length as a function of age, **(b)** shows wet mass as a function of age, **(c)** shows the length-weight relationship, and **(d)** shows metabolic rate with temperature. Further details and outputs are provided in Appendix A.