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Assisted migration of the Western Swamp Turtle (*Pseudemydura umbrina*): Using eco-energetics to inform translocation decisions under climate change

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BSc. Conservation Biology, Zoology (Hons.)
2009

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Declaration

I, Sophie Arnall, certify that:

This thesis has been substantially accomplished during enrolment in the degree.

This thesis does not contain material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution.

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The research involving animal data reported in this thesis was assessed and approved by The University of Western Australia Animal Ethics Committee under approval numbers RA/3/100/966 and RA/3/100/1039, as well as under equivalent approvals from the Perth Zoo (2010–8 and 2011–5).

The research involving animals reported in this thesis followed The University of Western Australia and national standards for the care and use of laboratory animals.

The following approvals were obtained prior to commencing the relevant work described in this thesis: Regulation 4 License; Department of Biodiversity, Conservation and Attractions - Parks and Wildlife Services, and Regulation 17 License; Department of Biodiversity, Conservation and Attractions - Parks and Wildlife Services.

The work described in this thesis was funded by the Australian Research Council, the National Environmental Science Program (Threatened Species Recovery Hub), the Perth Zoo, the Department of Biodiversity, Conservation and Attractions - Parks and Wildlife Services, the University of Western Australia, the University of Melbourne, the Wildlife Preservation Society of Australia, the National Climate Change Adaptive Research Facility (Terrestrial Biodiversity node), and the Friends of the Western Swamp Tortoise community group.

This thesis contains published work and/or work prepared for publication, some of which has been co-authored.

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13/03/2018

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Sophie Arnall Dated

ABSTRACT

Assisted migration is an emerging conservation tool that serves to deliberately relocate species threatened by environmental change to areas that are predicted to be suitable in the long-term. Whilst it holds promise, it has also garnered considerable controversy, and to date there are few examples of its implementation within a climate change context. This thesis explores the general premise that Australia's rarest reptile, the western swamp turtle (*Pseudemydura umbrina*) is a suitable candidate for assisted migration, and then aims to assess potential assisted migration sites through mechanistic species distribution modelling.

To demonstrate that the species is a suitable candidate for assisted migration, I reviewed decision support tools available in literature and assessed *P. umbrina* against the considerations contained in these. The swamp turtle is an obligate summer aestivator, inhabiting swamps that fill seasonally with rain and dry annually over summer. The species is principally threatened by a reduction in rainfall which reduces the hydroperiod (the length of time swamps hold water) and thus increases the time spent in aestivation (dormancy) each year. To provide evidence of local climate change, I compiled and analysed water depth recordings 1970 to present, and showed a reduction to hydroperiod length with time. Using literature, I explain how this shortening affects the swamp turtle and also submit why reasons for its decline also make it a suitable candidate for assisted migration. I then support this idea by discussing *P. umbrina* in context of over 150 factors, in five themes useful for assessing a species' suitability for assisted migration, arguing the turtle is an appropriate candidate for a deliberate, outside-of-range translocation.

As *P. umbrina* is Critically Endangered and as its distribution is restricted, species distribution modelling is most appropriately achieved using a mechanistic (rather than correlative) approach. I used the mechanistic model NicheMapR (an R integration of the model NicheMapper^{TM}) to create a species distribution model useful for assessing assisted migration sites for *P. umbrina* under climate change. I then modelled the post-hatchling life-stage under current and future (2050 and 2070) Western Australian climate scenarios, simulating a warmer and drier environment.

To parametrise the model I measured standard metabolic rates of swamp turtles across their preferred temperature range using flow-through respirometry at nominal temperatures of 15, 20, 25 and 30°C. I estimated the energy requirements of *P. umbrina*, and produced a thermal response curve for driving the model.

Next I generated a Dynamic Energy Budget (DEB) model to better understand how translocation success might be maximised. DEB models quantify how organisms assimilate and allocate energy for maintenance, storage, growth and reproduction, and are attractive for species distribution modelling because they provide an opportunity to capture dynamics of growth, body condition, and reproduction as an explicit function of temperature (and thus, climate change). I analysed over fifty years of *P. umbrina* population records, using growth and reproduction data from wild and captive-bred turtles to parameterise a DEB model that could capture seasonal aestivation events. Using this, I was able to make predictions for lifespan and times to starvation, both elements of the turtles' biology that were previously unknown.

Finally, I integrated this DEB model with NicheMapR to produce an energetically-driven, spatially-resolved prediction of *P. umbrina* growth, maturation, reproduction, and survival within the species' current core range, and at five candidate assisted migration sites. To validate the model I compared the simulations for growth, carapace temperatures, reproduction, water temperatures, and hydroperiods against measured observations taken during the same years. It was identified that an increase in basking behaviour was able to mitigate the predicted negative impacts of climate change, and also improve the long-term suitability of the species' core range. I conclude that three of five candidate assisted migration locations will likely be suitable for *P. umbrina* if individuals are able to employ some flexibility in their current basking behaviours.

Whilst the primary emphasis of this thesis was on *P. umbrina*, this work exemplifies a range of factors necessary for evaluating an assisted migration strategy: from arguing the requirement and appropriateness of the target species, to filling knowledge gaps for distribution modelling, to assessing potential recipient sites, and discussing their appropriateness in the context of a deliberate introduction event. As such, it forms a template for other at-risk fauna.

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Over the other side, I can’t thank the members of the CAMEL lab enough for sharing the basement with me. In particular, Rocio Aguilar and Himali Ratnayake made me feel at home when I was far away from my own (I couldn’t have done it without you girls). A special thank you to Elia Pirtle for the wonderful original illustration that opens this thesis and now meaningfully decorates my office at home.

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PREFACE & PUBLICATIONS ARISING

This thesis is in agreement with the University of Western Australia Doctor of Philosophy Rules for the content and format of a thesis. In accordance with the University of Western Australia's regulations regarding Research Higher Degrees, this thesis is presented as a combination of traditional research chapters (e.g. Chapter 2), and journal papers (e.g. Chapters 3, 4, and 5). The latter may be papers that have been published, manuscripts that have been submitted for publication but not yet accepted, manuscripts that could be submitted, or any combination of these. A general introduction (Chapter 1) and discussion (Chapter 6) surrounds the core body of work. All papers are co-authored by my supervisors and others involved in the work undertaken. However, in every case I am the primary author and was responsible for the content of the chapter/papers. The relative contributions of each additional author are outlined in the statement of contribution that opens each chapter. Some repetition between chapters was unavoidable.

Conference presentations arising from this work are as follows:

Arnall, S., Hipsey, M., Kearney, M., Kuchling, G., & Mitchell, N. (2010). "Ecoenergetics of the Western Swamp Tortoise: Modelling the Translocation Viability of Australia's Rarest Reptile". *35th Meeting of the Australian Society of Herpetology*. 20th - 23rd September, Barmera, South Australia.

Arnall, S., & Kearney, M. (2011). "DEB parametrisation for the Western Swamp Tortoise". *The Second Course and Symposium on Dynamic Energy Budget Theory*. 4th – 15th April, Lisbon, Portugal (course component).

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Kearney, M., **Arnall, S.,** Kuchling, G., & Mitchell, N. (2017). “The western swamp turtle – a tortoise in a hurry?” *The Fifth Course and Symposium on Dynamic Energy Budget Theory*. 21st May – 2nd June, Tromso, Norway (symposium component).

Publications produced during my candidature that are related to (but not directly arising from) this thesis are as follows:

Martin T. G., Nally S., Burbidge A. A., **Arnall S**., Garnett S. T., Hayward M. W., Lumsden L. F., Menkhorst P., McDonald-Madden E. & Possingham H. P. (2012). “Acting fast helps avoid extinction”. *Conservation Letters,* 5: 274-280.

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

Harris S., **Arnall S**., Byrne M., Coates D., Hayward M., Martin T., Mitchell N. & Garnett S. (2013). "Whose backyard? Some precautions in choosing recipient sites for assisted migration of Australian plants and animals." *Ecological Management & Restoration*, 14: 106-111.

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

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

An authorship declaration for the remainder of this thesis is appended to this section.

AUTHORSHIP DECLARATION: CO-AUTHORED PUBLICATIONS

This thesis contains work that has been published and/or prepared for publication.

Details of the work:

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.

Location in thesis:

Chapter 3

Student contribution to work:

I was responsible for experimental conception and design, and conducted the pilot studies (Appendix C), obtained animals ethics permits and scientific licenses, made the measurements, and analysed the data. I was the primary author, and was responsible for producing the written work in the chapter/paper. A breakdown of the relative contributions of each author are provided in the 'preface and statement of contribution' that opens the chapter.

Co-author signatures and dates:

[redacted]

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02/09/2017

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I executed the DEB modelling with assistance from M. Kearney, after sourcing, transcribing, collating and analysing previously unpublished records. I also independently analysed temperature logger data for incubators at Perth Zoo, measured temperatures for turtle holding ponds and aestivation pens across 2012 and 2013, and assisted Perth Zoo staff in taking the corresponding growth measurements pre-and post-aestivation. I was the primary author, and was responsible for producing the written work in the chapter/paper. A breakdown of the relative contributions of each author are provided in the 'preface and statement of contribution' that opens the chapter.

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Chapter 5: 'Predicting the growth, reproduction, and survival of *Pseudemydura umbrina* under climate change' prepared as a manuscript for potential future journal submission
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Co-author signatures and dates: [redacted] Matt Hipsey 01/09/2017 Michael Kearney 22/08/2017 [redacted] Gerald Kuchling 02/09/2017 Nicola Mitchell 04/09/2017

Student signature: [redacted] 13/03/2018
I, Nicola Mitchell, certify that the student statements regarding their contribution to each of the works listed above are correct. Coordinating supervisor signature: [redacted] Date: 13/03/2018

The master was an old Turtle--
we used to call him Tortoise--

Why did you call him Tortoise, if he wasn't one?
Alice asked.

We called him Tortoise because he taught us.

Lewis Caroll
Alice in Wonderland
1865

CHAPTER ONE

INTRODUCTION

Habitat destruction and fragmentation means that with a rapidly changing climate, many species will be unable to disperse into areas capable of supporting them in the long-term.

Many regions are expected to undergo relatively rapid changes in climate (IPCC 2014), which follows an unprecedented history of global warming (Marcott *et al.* 2013) thought to have been anthropogenically caused (Cook *et al.* 2013). When faced with climatic challenge, species typically exhibit three core strategies to resist local extinction: shift spatially (change in range, e.g. Parmesan & Yohe 2003; Chen *et al.* 2011), shift temporally (change their phenology, e.g. Ge *et al.* 2015), and shifts in 'self' (avoidance of stressful conditions through physiological or behavioural means; e.g. Donelson *et al.* 2011; Bellard *et al.* 2012). A species' potential for acclimation, plasticity and/or evolutionary adaptation (see Angilletta 2009) has a large influence on the effectiveness of these strategies. For example, species with high reproductive rates and relatively short lifecycles (r-strategists; *sensu* MacArthur & Wilson 1967) may be able to adapt *in-situ* and indeed, there are already examples of genetic and/or plastic responses that have been attributed to climate change (e.g. Franks *et al.* 2014, but see Hoffmann & Sgrò 2011).

Impacts of climate change are magnified for longer-lived species whose slow generation times and low reproductive rates hamper a micro-evolutionary response to a changing environment (Salamin *et al.* 2010). For longer-lived species, the simplest and most strongly supported response is to shift spatially so as to track their climatic niches (Moritz & Agudo 2013). But the Anthropocene (Steffen *et al.* 2007) has brought about additional challenges; when habitats are anthropogenically (or naturally) fragmented, opportunities for dispersal are disrupted. Consequently, some species will develop a high risk of extinction due to an inability to leave climatically unsuitable habitats (Thomas *et al.* 2006). This limitation has given rise to ‘assisted migration’: the *“safeguarding [of] biological diversity through the translocation of representatives of a species or population harmed by climate change to an area outside the indigenous range of that unit where it would be predicted to move as climate changes, were it not for anthropogenic dispersal barriers or lack of time”*; Hällfors *et al.* 2014). The management concept of assisted migration was first introduced in 1985 (Peters & Darling 1985), and has since garnered both controversy and momentum (reviewed in Hewitt *et al.* 2011 and Seddon *et al.* 2015).

Examples of assisted migration are limited (Willis *et al.* 2009; Green *et al.* 2010; McLane & Aitken 2012; Castellanos-Acuña *et al.* 2015; Torreya Guardians 2015), largely due to the ethical dilemmas it creates, its untested nature, and the uncertainty surrounding costs and benefits (Javeline *et al.* 2015 and references therein). However, relatively recent research (Javeline *et al.* 2015) suggests that despite early opposition (e.g. Huang 2008; Ricciardi & Simberloff 2009; Aubin *et al.* 2011) most conservation scientists and policy makers now hold fairly neutral views on assisted migration. Many experts justify the use of assisted migration when it is designed to prevent species extinction and overcomes human-made dispersal barriers, especially if any risks to non-target species can be eliminated. Further, adopting the ‘precautionary principal’ (by delaying action due to lack of scientific certainty; O’Riordan 2014) may drive species to extinction due to inaction, given the relatively rapid rate of global change (Sax *et al.* 2009; Schwartz *et al.* 2009; Martin *et al.* 2012). Thus, assisted migration has quickly become a practicable conservation tool for some species, with focus rapidly shifting towards the creation of policies and recommendations to facilitate its implementation (e.g. Burbidge *et al.* 2011). As translocations outside of native ranges have historically shown high failure rates (Lindenmayer & Burgman 2005; Short 2009), the challenge is now to develop protocols and methods that will maximise the success of assisted migration initiatives, particularly in selecting translocation sites that are likely to support the persistence of the target species in the long-term.

Common modelling approaches have limited applications for guiding the translocation of threatened species

Any model that can predict the future distribution of a species under climate change will be a valuable tool for selecting translocation sites in the future. Species distribution models (SDMs) which can be used to predict the past, present and future distributions of species are viewed as being particularly important in climate change planning and management (e.g. Guisan *&* Thuiller 2005; Elith & Leathwick 2009; Rowland *et al.* 2011). Species distribution models can be used in three key ways to (partially) inform translocation decisions: 1) by revealing whether habitat suitability is likely to change in regions currently occupied by the target species, 2) by identifying potentially suitable recipient sites for the translocation of the target species, and 3) by detecting which local species may be at risk of impact from the introduced target species through an overlap in their predicted distributions (Guisan *et al.* 2013). Because these considerations all apply to assisted migration, SDMs have been specifically recommended in numerous decision support frameworks developed for guiding its use (e.g. Chauvenet *et al.* 2013a and others; see Chapter 2 for an extensive list).

SDMs most commonly take the form of correlative ‘climate-envelope’ models (Elith & Leathwick 2009; Dormann *et al.* 2012) which use species occurrence records to characterise a set of suitable habitats, capturing the association between the species' geographic location and its climate (Lawing & Polly 2011). These models are statistical in nature: they rely on correlation between distribution records and environmental variables to create a species' probability of occurrence across a landscape, or some index of the suitability of the area for occupation (Kearney 2006). Unfortunately, as many threatened species have restricted distributions, correlative approaches have limited value as there is insufficient occurrence data with which to draw the environmental correlations necessary for the models (Guisan & Thuiller 2005; Mitchell *et al.* 2013). Species requiring assisted migration are likely to be rare and have narrow distributions (Foden *et al.* 2013), which makes them especially poor candidates for climate-envelope modelling. Further, the inability of correlative models to produce accurate predictions in novel or non-equilibrium situations such as climate change has been noted (Dormann 2007; Fitzpatrick & Hargrove 2009; Buckley *et al.* 2010; Elith *et al.* 2010). This point is particularly pertinent in an assisted migration context, because unlike traditional translocations, assisted migrations will occur in a dynamic landscape driven by changing bioclimatic conditions (Harris *et al.* 2013).

Mechanistic models offer a promising alternative for informing assisted migration

A mechanistic (or 'process-based') modelling approach offers an alternative to climate-envelope models that can be used independently of species' distribution records. Mechanistic models are based upon a species' functional traits (morphology, behaviour, physiology) and its associated life history (development, growth, reproduction), operating independently of its geographic range and the climate it inhabits (Kearney & Porter 2009; Dormann *et al.* 2012). The output variables mapped on a site or landscape scale are not probabilities of occurrence but rather can be fitness components such as survival and reproduction (Kearney 2006). Mechanistic models offer a promising alternative to correlative models as they can be used to forecast “what if” scenarios such as climate change (Huey & Janzen 2008; Iverson & McKenzie 2013), making them particularly useful in an assisted migration context.

Underpinning all species distribution models is the niche concept (Hutchinson 1957; Kearney *et al.* 2010; but see McInerny & Etienne 2012). Because correlative models use actual records of a species’ distribution, predictions are drawn from the realised niche of that organism (Robertson *et al.* 2003). The projective power of mechanistic models is thus greater than that of their correlative counterparts because they do not model the realised niche (i.e. the space occupied by a species resulting from biotic and abiotic interactions; which reveals little in the way of causal understanding; Kearney *et al.* 2010) but the fundamental niche. The fundamental niche is based only on the functional/physiological constraints of the organism, representing all the possible space that could support viable populations of a species (and in which the species may not necessarily currently occupy; Lawing & Polly 2011). For these reasons, mechanistically-based SDMs are useful for isolating factors that could drive translocation success in novel circumstances.

Robertson *et al.* (2003) state that ‘while mechanistic models are likely to yield superior results to correlative models (particularly under climate change scenarios), they are often extremely time-consuming and more difficult to build, relying on a greater knowledge of the biology of the target organism than correlative models’. Specifically, mechanistic models have drawn criticisms over the large number of parameters required for estimation, and their reliance upon data that is often limited in availability or temporal-spatial resolution (Dormann *et al.* 2012). However, these constraints are similar to the prerequisites of assisted migration planning, which ideally requires refined knowledge on the target species' biology, its specific response/s to climatic shifts and the causative mechanisms for its decline. Whilst there are few mechanistic SDMs specifically created to inform assisted migration planning[1], there are numerous examples of these models being applied to other climatically-driven scenarios. For example, Kearney *et al.* (2008) apply mechanistic SDMs to understanding how the spread of an invasive toad species may be altered by climate change, Kearney *et al.* (2009) show how mosquito-borne disease risk may increase under warmer climates, Bartelt *et al.* (2010) show how amphibian movement patterns could be altered under future climates, and Cavallo *et al.* (2015) predict the potential for climate warming to affect offspring viability in sea turtle hatchlings.

An understanding of a species' eco-energetics will help maximise translocation success under future climates

Successful translocations programs must result in self-sustaining populations (Griffith *et al.* 1989), which can theoretically be achieved by translocating individuals into habitats that allow them to allocate adequate proportions of their energy budgets to development and reproduction, rather than simply survival and maintenance (which takes priority when energy resources are limited; Homyack 2010). Modelling the outcomes of translocations therefore depends not only on understanding where a species is capable

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[1] Mitchell *et al.* (2008) in conjunction with Miller *et al.* (2012), for tuatara in New Zealand; and Mitchell *et al.* (2013, 2016) for western swamp turtles in Australia, as reviewed in Seddon *et al.* (2015) and as directly related to this study. Conversely, numerous examples exist using correlative models, e.g. Johnson *et al*. (2007) for bighorn sheep in Sierra Nevada, Fordham *et al.* (2012) for the pygmy blue-tongue lizard in Australia, McLain & Aitken (2012) for the Whitebark pine in North America, Regan *et al.* (2012) for the Tecate cypress in Canada, and Chauvenet *et al.* (2013b) for the New Zealand hihi.

of surviving, but on understanding where its demands for growth and reproduction can be met.

Eco-energetics is the study of the mechanisms involved in the acquisition and use of energy by individuals (Kooijman 2010). Through the construction of dynamic (varying with time) energy budgets, eco-energetics can be used to investigate how individual organisms assimilate and allocate energy for maintenance, storage, growth and reproduction; collectively termed a Dynamic Energy Budget (DEB) model (e.g. Kooijman 2010). The rate of an individual's energy acquisition and energy use is a function of age, sex and size, and varies with the state of the environment (i.e. with food density and temperature; Nisbet *et al.* 2000), and hence DEB models can be particularly useful in climate change contexts. Further, as the solution of a DEB model represents the entire life history of an individual in a potentially variable environment, these models can be extended to study the dynamics of whole structured populations (Kooijman 2010).

DEB models are attractive in the context of mechanistic SDMs because they provide the opportunity to capture the dynamics of development, growth, body condition, and reproduction as an explicit function of temperature (and thus, climate change; Kearney *et al.* 2010; Kearney *et al.* 2012). DEBs have already been integrated with mechanistic SDMs (e.g. Kearney *et al.* 2010; Kearney 2012; Kearney *et al.* 2012; Kearney 2013; Kearney *et al.* 2013; Roberts 2014; Schwarzkopf *et al.* 2016), and their coupling represents two-thirds of the 'thermodynamic niche' framework (hereafter termed the 'eco-energetic niche' to make this distinction; the third component is a geometric nutritional and water axis; Kearney *et al.* 2012). The eco-energetic niche differs from the traditional fundamental niche concept by focusing only on the thermodynamic and biophysical constraints that apply to a species, providing a more targeted 'first principals' construct which excludes more general factors that may also comprise a species' fundamental niche, such as a species' genetics (Kearney *et al.* 2013). By developing a DEB model which can be coupled with a climatically-driven biophysical model of distribution, the eco-energetic niche model provides a powerful tool for forecasting the impacts of climate change on species' life histories, and for informing mitigation strategies such as assisted migration (*sensu* Kearney *et al.* 2013).

Study species

The western swamp turtle (*Pseudemydura umbrina*; known in Western Australia more commonly as the western swamp tortoise; Plate 1) is a small, semi-aquatic turtle endemic to the south-west of Western Australia. It has conservation significance due to being highly threatened (Critically Endangered; TSSC 2004; IUCN 2015), having a high-profile (largely due to conservation efforts headed by the Perth Zoo and Western Australia's Department of Biodiversity, Conservation and Attractions, Parks and Wildlife Service) and its inherent zoological novelty (Kuchling 1993). Its conservation is further supported by community members who actively raise awareness about this species' plight and recovery. Within the context of assisted migration, the western swamp turtle is an ideal species on which to devise a mechanistic SDM because:

1. Like many threatened species, the turtle has a restricted range (Burbidge *et al.* 2010) (Figure 1.1);
2. The turtle has specialised habitat requirements (characterised by the presence of ephemeral wetlands on clay-based soils, with access to nearby aestivation refuges; TSSC 2004), and this habitat is highly fragmented (Burbidge 1981);

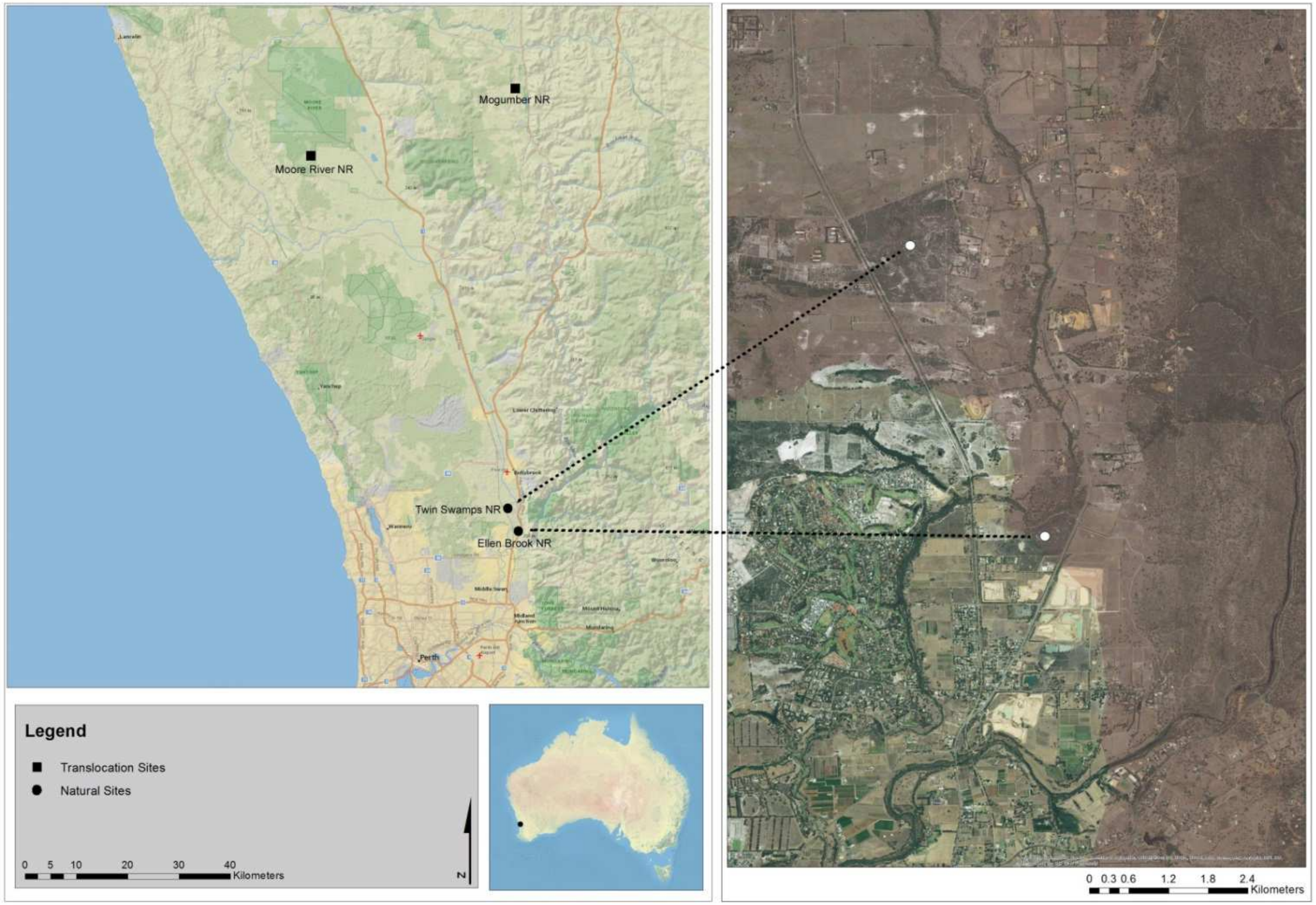

Figure 1.1- The current distribution of the western swamp turtle (*Pseudemydura umbrina*), including aerial photograph of western swamp turtle habitat, demonstrating the fragmented nature of the landscape.

3. The climate of south-west Western Australia has become notably drier and slightly hotter over the past three decades (CSIRO 2009a; CSIRO 2009b; IOCI 2012), and this has had a negative impact on available turtle habitat (see Chapter 2, Chapter 5);
4. Due to habitat fragmentation, the species has no ability to disperse from its current habitat at the pace required by contemporary climate change;
5. Translocations are technically feasible and have been practiced for at least 40 years (23 years successful when captive-bred individuals are used; Kuchling & DeJose 1989; Burbidge *et al.* 2010; G. Kuchling pers. comm.);
6. A captive population exists from which turtles can be sourced for translocations, including assisted migrations;
7. Data on growth, survival and reproduction (in captivity and in the wild) has been collected since 1963, resulting in a unique opportunity for model validation; and,
8. Sites that will remain suitable under projected future climate change are required to secure populations of *P. umbrina* in the wild (Burbidge *et al.* 2010; Mitchell *et al.* 2013).

The western swamp turtle is also an excellent candidate for DEB modelling because it has several life history thresholds that are highly sensitive to energy acquisition and use (e.g. the necessity for individuals to reach a critical mass of 18 g before their first aestivation event; expanded at Chapter 2). This means potential translocation sites can be assessed for their suitability in meeting the species’ growth, development, and reproduction needs. These latter aspects will be increasingly important for determining this species’ potential to persist within its current habitat under a less climatically-favourable future.

Scope and aims of thesis

The fundamental aims of this thesis are firstly, to evaluate the suitability of the western swamp turtle for assisted migration and secondly, to construct, explore and test an energetic model of the species. The latter is developed for aiding the selection of translocation and/or assisted migration sites.

In Chapter 2, my goal is to build a case for the assisted migration of the western swamp turtle. I begin by describing the changes to their habitat from 1970 to the present, placing a particular emphasis on the shortening of the wetland hydroperiods and describing how this influences the life history of the species. I then evaluate the western swamp turtle against decision frameworks available for appraising the suitability of species for assisted migration, arguing their appropriateness as a candidate for a deliberate, outside-of-range introduction.

I then turn my focus towards developing a physiological model of *P. umbrina* to help understand how climate change might affect growth, reproduction and survival in their current habitat, and to examine the eco-energetic constraints that might influence success at potential assisted migration sites. This was a stepwise process, commencing with the development of a DEB model, and then continuing with its integration into a mechanistic niche model explored under multiple climate scenarios.

A key component necessary for the production of a DEB model is the construction of a thermal response curve, which I achieve in Chapter 3 by measuring the standard metabolic rates of *P. umbrina* within their preferred temperature range. In Chapter 4, I incorporate this response curve into a DEB model for *P. umbrina*, and I assimilate extensive historical data in order to better parameterise the model. Here I produce several important predictions for the species, such as growth rates and times to starvation, and examine the comparative growth rates of wild and captive *P. umbrina* for the first time. In Chapter 5, I link this DEB model with a niche model developed for Ellen Brook Nature Reserve, where the single self-sustaining population of swamp turtles exists. I explore how behaviour can influence growth, maturity, reproduction, and survival here, and test this against current and historic observations. I then examine the model in context of novel climatic futures, applying it at five potential assisted migration sites to compare how these traits change under the wetter and cooler conditions predicted for these areas. I conclude by making some recommendations for the future assisted migration of *P. umbrina* in Chapter 6.

Whilst the primary emphasis of this thesis is on the western swamp turtle, this work exemplifies a range of factors necessary for testing and potentially adopting an assisted migration strategy: from arguing the requirement and appropriateness of the target species (Chapter 2), to filling knowledge gaps required for distribution modelling (Chapters 3 and 4), to exploring responses under climate change (Chapter 5) and discussing appropriateness in the context of a deliberate introduction event (Chapter 6). Whilst expansion and improvements to this process are possible, as it stands, this research provides a template for processes that could be applied to other fauna threatened by climate change. Our understanding of *P. umbrina* biology has progressed in hand with this study, but more importantly, this research raises new challenges and opportunities for the management of this iconic species in an era of rapidly changing climate.

Plate 1 – The western swamp turtle (*Pseudemydura umbrina*).

Photograph: S. Arnall

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CHAPTER TWO

BUILDING A CASE FOR THE WESTERN SWAMP TURTLE AS A CANDIDATE FOR ASSISTED MIGRATION

PREFACE AND STATEMENT OF CONTRIBUTION

The first aim of my thesis was to discuss and demonstrate the appropriateness of *P. umbrina* as an assisted migration candidate. I intended to achieve this by using decision frameworks available for assisted migration in the literature, but was not able to select a single framework that adequately captured the plight of the species. Instead, it became necessary to review and synthesise the decision tools available to provide a catalogue of considerations against which to assess the swamp turtle.

Thus, this chapter has two linked components: a synthesis of the situation facing the swamp turtle (including an original compilation and analysis of historical habitat datasets; Part A), and a review of the decision tools available to evaluate its assisted migration (Part B).

Except as noted otherwise below, the work presented in this chapter is my own original work.

The concept of employing assisted migration to better conserve the western swamp turtle was first proposed by N. Mitchell and colleagues in the Australian Research Council Linkage Project that supported my research (Mitchell *et al.* 2009).

In demonstrating local climate change, I used the unpublished raw data of G. Kuchling, A. Burbidge, and P. Fuller, which was collected solely by these individuals. All analysis and interpretation of their data is my own. The water gauge data provided by G.

Kuchling and A. Burbidge also appears in the PhD thesis of A. M. Hasnein bin Tareque whose hydrologically-focused research was conducted concurrently to my own. My analysis of these data was independent.

I used B. Jenny's 'color oracle' program to design my figures to be compatible with colour blindness (http://colororacle.org; Monash University, Australia).

I conceptualised, designed, and executed the literature review and was responsible for the written content of the chapter. I was the primary author of the chapter, and N. Mitchell, M. Hipsey, G. Kuchling, and M. Kearney provided supervisory feedback on the content.

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2.1 INTRODUCTION

Assisted migration (known variously as assisted colonisation, managed relocation, facilitated dispersal and others; see Hällfors *et al.* 2014 for review) is an often-controversial tool proposed to combat one of the largest perceived symptoms of the Anthropocene – species loss due to climate change (Steffen *et al.* 2007)[1]. In its most modern interpretation, assisted migration refers to conservation translocations that are motivated by climate change, for which currently there are few examples (Willis *et al.* 2009; Green *et al.* 2010; McLane & Aitken 2012; Castellanos-Acuña *et al.* 2015; Torreya Guardians 2015). In contrast, conservation introductions to meet other objectives have long been practised successfully (e.g. over 40 years in Australia and New Zealand; Seddon *et al.* 2015). Whilst the concept of assisted migration has grown in momentum since the resurgence of the idea in 2007, the majority of assisted migration literature has remained at the theoretical discussion and debate stage, rather than moving towards implementation (Javeline *et al.* 2015).

The reluctance to move forward with assisted migration projects is likely to do with acceptance of responsibility, given the strong emphasis on risk and its minimisation in the conservation literature (Hewitt *et al.* 2011; Javeline *et al.* 2015). An individual's perception of assisted migration will depend on their background, values, and attitudes (McLachlan *et al.* 2007). Responses can range from a readiness to implement assisted migration even if there is still debate (e.g. "Many times decisions are needed before

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[1] Here I distinguish from the definition given by the IUCN (2013) and as reviewed in Seddon *et al.* (2015), which gives 'assisted colonisation' as the "intentional movement and release of an organism outside its indigenous range to avoid extinction of populations of the focal species", and thus can include many motivators such as disease risk, and genetic management. I adopt Hällfor *et al.*'s (2014) definition for the purposes of this study as my research focuses on climate change.

scientific proof and consensus are available. In the context of assisted migration, waiting can result in a "no-choice" situation in which there is no species to save"; Ahteensuu & Lehvävirta 2014) to considering it only in the most exceptional of cases (e.g. "… assisted colonization ought to have, at most, a very minor role in the portfolio of ecosystem management practise" and "the burden for establishing an exceptional case should be substantial"; Seddon *et al.* 2009).

Despite this range in views, there appears to be consensus that assisted migration is a viable conservation option if the perceived benefits outweigh the potential costs (Seddon 2009; Albrecht *et al.* 2013). Thus, the onus falls to the end-user to justify assisted migration using a cost-benefit assessment that demonstrates a high level of knowledge at the species and ecosystem-levels (*sensu* Ahteensuu & Lehvavirta 2014), under both current and expected future climatic conditions. This is a substantial task (one which may arguably preclude some species from assisted migration; Davidson *et al.* 2008), and has prompted the development of many frameworks and decision tools to help evaluate and validate whether assisted migration should be undertaken.

Chauvenet *et al.* (2013a) suggest that "one way to minimize the risks of negative ecological impacts and to maximize the net benefit of assisted [migration] is to work within a well-defined and, ideally, widely accepted decision framework". However, currently there exists no single 'gold standard' framework with which to refer. This is likely because assisted migration is often a complex scenario for which there is no 'one size fits all' solution (Vitt *et al.* 2009). Further, some authors (e.g. Harris *et al.* 2013) have recommended assessment against general frameworks (such as those developed for weed risk assessments; e.g. Setterfield *et al.* 2010), which further broadens the considerations available to conservation managers. This can also encourage 'cherrypicking' of frameworks to best suit particular agendas, which then prevents a comprehensive assessment and may result in some factors being overlooked.

Here I take decision support frameworks available for assisted migration in the literature, and attempt to implement them as an end-user interested in assessing the appropriateness of assisted migration for the western swamp turtle (*Pseudemydura umbrina*). This Critically Endangered (TSSC 2004; IUCN 2015) species has already been identified as potentially benefitting from assisted migration (Burbidge *et al.* 2011; Mitchell *et al.* 2013; Dade *et al.* 2014; Mitchell *et al.* 2016; Bin Tareque 2017). However, there are no detailed assessments of the biological, environmental, economic, and social factors that could be relevant to deciding whether assisted migration should be implemented (Richardson *et al.* 2009). Further, an evaluation of risks, and the identification of practical strategies to minimise or eliminate these are also required in the preparatory phase of any assisted migration strategy (Gallagher *et al.* 2015), and in this regard the turtle has also not yet been assessed.

I begin by presenting the available information on the turtle and its current habitat that is relevant within an assisted migration context (Part A). I then place this information within a catalogue of considerations common to assisted migration decision tools, developed by reviewing and synthesising 24 frameworks specifically aimed at assisted migration (Part B). This approach serves two purposes. Firstly, it provides a formal evaluation of the swamp turtle's suitability for assisted migration, contributing to transparent decision making for this species' conservation (Martin *et al.* 2012; Popescue & Hunter 2012). Secondly, it provides an overview of the factors currently recommended for evaluating assisted migration, serving to simplify future decision making.

PART A – THE CANDIDATE

2.2 THE WESTERN SWAMP TURTLE

The western swamp turtle is a highly threatened freshwater turtle endemic to the south-west corner of Western Australia: one of the top 25 global biodiversity hotspots (Myers *et al.* 2000), and an area of high reptile diversity (Rix *et al.* 2015). Ancient and monotypic in its subfamily (Gaffney 1977; Gaffney & Meylan 1988; Zhang *et al.* 2017), the swamp turtle was thought to be extinct for over 100 years until its rediscovery in 1953 (Kuchling 2000). There are no localised records prior to this time, but anecdotal information suggests that in recent history the turtle was restricted to the clay soils of the region – an area encompassing no more than 150 km^2 (Cogger *et al.* 1993).

In the decade after its rediscovery, a population of around 300 individuals occurred at two adjacent wetlands, now the "Ellen Brook" and "Twin Swamps" Nature Reserves (Burbidge 1967). A population crash in the 1970s and 1980s saw this number fall to just 15-25 adults surviving in the wild (Kuchling 2000). Since this crash the species has benefitted from a captive breed-for-release program - a major undertaking at the Perth Zoo, who have now bred and reared more than 600 juveniles for release (Kuchling & DeJose 1989; G. Kuchling, pers. comm.). The wild population is currently estimated at around 200 individuals, of which just over 50 are known to be mature (G. Kuchling, pers. comm.), located across four closely-occurring sites within the swan coastal plain of Western Australia (one natural self-sustaining, one natural supplemented, and two sites founded by captive-reared individuals; Figure 1.1[2]).

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[2] As at 2016, trial translocations commenced at some locations to the south of the current range of *P. umbrina* (refer Chapter 5 for details).

Currently classified as Critically Endangered (TSSC 2004; IUCN 2015), a population of at least 50 adults persisting in the wild for a minimum of five years is required for the species to be down-listed to Endangered, which is the primary immediate goal in the species' recovery (Burbidge *et al.* 2010). The captive breeding program, coupled with continued threat abatement strategies will foreseeably see the species' conservation status improved, provided that individuals released as juveniles survive to adulthood and reproduce. The threats to the western swamp turtle which may preclude this are generally well understood, and are outlined in detail elsewhere (see Burbidge *et al.* 2010). However, one of these threats might prevent the important criterion of more than 50 adults persisting in the wild from being met. Climate change (specifically, a drying climate) has been identified as one of the most significant barriers to the ongoing persistence of this species within its natural range, and is a likely cause of limited population growth in recent years (Mitchell *et al.* 2013).

2.3 WHY WORRY? HOW THE BIOLOGY OF THE TURTLE IS INFLUENCED BY CLIMATE

Over relatively long time-scales, Australia's climate and vegetation has transformed considerably since the rainforests of the early Miocene (Travouillon *et al.* 2009), where the only fossil records similar to western swamp turtles have been found (Gaffney *et al.* 1989). The single skull fragment discovered from the Riversleigh deposits of far North-Queensland (over 2000 km from Ellen Brook Nature Reserve) is virtually identical to that of *P. umbrina*, which has prompted suggestions that the species has changed little over time (Gaffney *et al.* 1989). If so, then the *P. umbrina* lineage was presumably once more widespread, and has since adapted to meet the challenges of drought, and/or contracted to regions that provided continuous habitat throughout the drying of the continent (Georges & Thompson 2006; Gow 2009). It is within this ancient context that *P. umbrina* now inhabits the south-west of Western Australia, where it may have resided since the Cretaceous (Burbidge *et al.* 1974; Zhang *et al.* 2017).

The environmental cues that influence the behaviour of the turtle here are now generally well understood (see Burbidge 1981 for overview). *P. umbrina* does not occur in permanent water but inhabits shallow (ca. 40 cm) ephemeral wetlands that fill with winter rain and dry annually over summer. When the swamps are empty, the turtle survives by aestivating (a period of summer hibernation) under leaf litter or in natural holes underground until rainfall fills the swamps once more. Turtles mate in water mostly in winter and early spring (Kuchling & DeJose 1989), and the time when the swamps hold water also presents their only opportunity to feed as they prey upon aquatic species (Gilbert 2011; Katja Schmölz, unpublished data). It is due to this limited activity window each year that climate change has the potential to impact on the survival of wild populations. The length of time that swamps hold water (hereafter referred to as the 'hydroperiod') is correlated with turtle growth (where shorter hydroperiods result in less growth; Burbidge 1981; Mitchell *et al.* 2013) which when shortened influences reproductive success and survival in the following ways:

i) **Prevents individuals from surviving aestivation**. Energy stores can only be accumulated when the swamps hold water and contain food. Hatchlings are particularly susceptible to desiccation and death over the summer aestivation period if growth has been minimal (Mitchell *et al.* 2013). Kuchling (in Burbidge *et al.* 2010) hypothesised that a mass of 18 g was necessary for hatchlings to survive the summer aestivation period, as no hatchlings of less than 18 g are known to have emerged at Ellen Brook Nature Reserve after the aestivation period (G. Kuchling, pers. comm.).

ii) **Lengthens time to reproductive maturity**. Maturation in swamp turtles is determined in part by size, with females reaching sexual maturity at an average of 107 mm carapace length (Chapter 4). Seasons where rainfall has not been limiting result in greater growth and thus can shorten times to maturity (Chapter 5).

iii) **Prevents egg production**. In females, vitellogenesis occurs during summer aestivation and is conditional upon the females accumulating adequate energy reserves during the hydroperiod (Kuchling & Bradshaw 1993). Double-clutching can occur in captivity when food is given in excess, suggesting a strong relationship between food availability and reproductive output. After mating, if energy reserves are limited, females can abort eggs by follicular atresia (i.e. not ovulating and reabsorbing the yolk of pre-ovulatory follicles; Kuchling 1989; Kuchling & Bradshaw 1993; Kuchling 1999).

iv) **Compromises hatchling survival**. Hatching in swamp turtles is triggered by a drop in nest (incubation) temperature that typically coincides with late autumn or early winter rains (Burbidge 1981). When hatchlings emerge approximately 180 days after eggs are laid, they can feed only if the swamps hold water. The recent pattern of declining winter rainfall is resulting in a longer dry period after the emergence of the hatchlings, which places them at a higher risk of starvation, desiccation, and predation (by the European red fox, *Vulpes vulpes*; the rat, *Rattus rattus*; the southern brown bandicoot, *Isoodon obesulus;* and avian predators including birds of prey and the raven, *Corvus coronoides*; Burbidge *et al.* 2010).

v) **Disrupts biological rhythms**. The seasonal filling and drying of the swamps might be an important trigger for nesting behaviour because access to permanent water with an absence of aestivation was one of the factors thought to contribute to poor captive breeding success in the past (Kuchling & DeJose 1989).

Spring is the most important time for the accumulation of energy stores, as high-energy prey items (such as tadpoles) are usually abundant, and warmer water temperatures allow turtles to be active and forage for a larger proportion of the day (Burbidge 1981). In the wild, prey becomes concentrated in shallow pools as the swamps recede, providing optimum feeding conditions towards the end of the active season (Kuchling & DeJose 1989). When food is not limiting, higher water temperatures increase growth rates in hatchlings and juveniles (Mitchell *et al.* 2012), and adults (King *et al.* 1998). Whilst these observations suggest that warmer conditions would favour swamp turtles, this may not be the case for their prey. Freshwater ecosystems, particularly those with standing water, are especially sensitive to the effects of increased temperatures (Whitehead *et al.* 2009), and a change in prey availability could have serious long-term consequences for the persistence of the wild turtle populations. Water temperatures regulate the timing of emergence and the abundance of aquatic insect populations at different life stages (e.g. Davidson & Hazelwood 2005; Durance & Ormerod 2007), and also affect the life cycle of a wide variety of other aquatic organisms which often have a limited range of thermal tolerance (Wade *et al.* 2002). Aquatic communities can be further threatened by deoxygenation of the water, which is exacerbated when increased temperatures and lower rainfall occur in tandem (Whitehead *et al.* 2009). Even if turtle prey species are fast-reproducing ‘r’ strategists (MacArthur & Wilson 1967), which arguably may be able to adapt to warmer temperatures *in-situ* due to their high fecundity and short generation times, it is conceivable that community composition will shift some way under escalating climate change.

2.4 EVIDENCE FOR LOCAL CLIMATE CHANGE

Annual rainfall has declined in south-west Western Australia since the late 1960s, with reductions particularly marked for early winter rainfall (IOCI 2012), which has declined by 14 % since the mid-1970s (Bates *et al.* 2008; Petrone *et al.* 2010). Because winter rains are vital for filling the perched ‘Gilgai’ clay-based swamps characteristic of swamp turtle habitat, this winter reduction is particularly significant. Heavy rainfall early in the wet season is required for water to seep through the cracks in the clay, causing the clay to swell and seal, and thus allowing the swamps to pool water (Burbidge 1967). For this reason, swamp turtle growth can vary between years with similar precipitation: sheet flooding from heavy rain can fill the swamps quickly and initiate the hydroperiod, but a number of lighter falls totalling the same amount can lead to delays in swamp initiation and reduce the persistence of ponding (Burbidge 1967). Fronts in south-west Western Australia have progressively weakened since the 1940s (Raut *et al.* 2014), resulting in fewer episodes of heavy winter rainfall. In tandem, mean annual temperatures have risen by 0.4° C (Bates *et al.* 2008), and groundwater extraction for irrigation and industry have also increased (McFarlane *et al.* 2012). These trends suggest that without remedial management, current swamp turtle habitat will become increasingly unsuitable over time.

A shortening of hydroperiods within western swamp turtle reserves has been observed anecdotally, but to date not quantified. Visual depth gauges were erected in Ellen Brook and Twin Swamps Nature Reserves in the late 1960s, and have been regularly monitored since 1972. These show that hydroperiods at Twin Swamps Nature Reserve have shifted and shortened with time, with some swamps remaining essentially dry since 2006 (Figure 2.1). Hydroperiods in this habitat historically spanned from mid-June to mid-December (Burbidge 1981), with some swamps holding water until mid-January (e.g. 1964; Burbidge 1967). By comparison, at Ellen Brook Nature Reserve water is usually present from “late May, or early June until mid-November” (Burbidge 1967, pp. 26). A desirable or typical swamp depth for *P. umbrina* is 20-30 cm (Burbidge *et al.* 2010), and swamps at Ellen Brook have generally maintained this, even in low rainfall years (Figure 2.2). This may explain why the *P. umbrina* population at Ellen Brook Nature Reserve is self-sustaining, while evidence of recruitment at Twin Swamps was effectively absent until a groundwater supplementation scheme for two swamps commenced in 2010. Water temperatures have been logged continuously at Ellen Brook Nature Reserve since 2009 and whilst it is too early to detect any climate shifts, they are provided here for future comparison (Figure 2.3).

Short hydroperiods in the wild have been artificially mitigated as part of this species’ recovery actions (e.g. Plates 2 and 3; Section 2.4), which has made it difficult to assess the direct effects of recent shifts in the local climate on traits relevant to the turtles’ survival. However, Burbidge (1967) attributed low recruitment of juveniles to the effects of a “recent run of five dry years [1958-1962]” which at the time

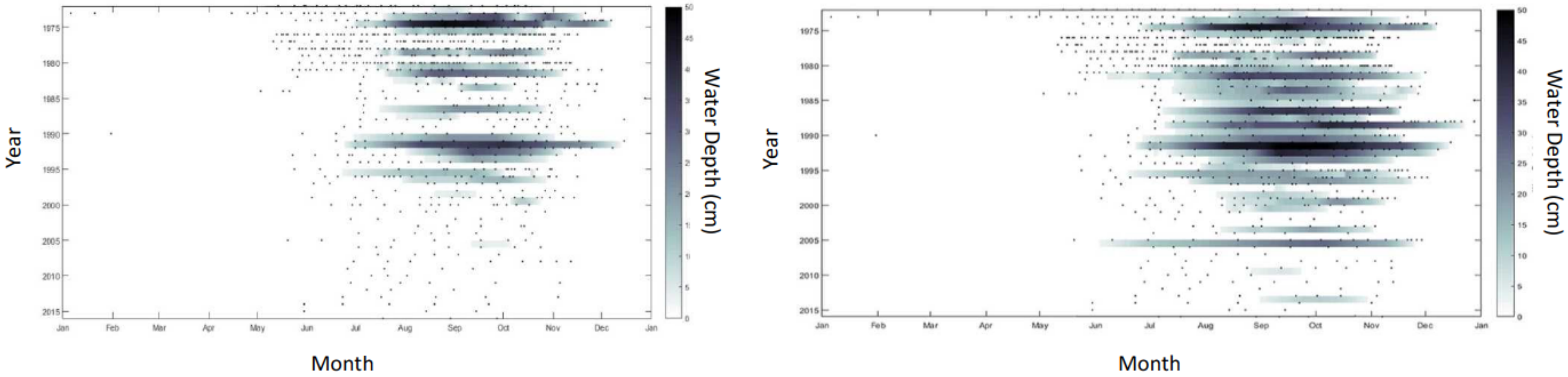

Figure 2.1 – A 45-year history of natural hydroperiods at Twin Swamps Nature Reserve (swamp "SE" left; swamp "SW" right), spanning 1972 to 2016, demonstrating a general shortening and seasonal shift in swamp hydroperiods, and a reduction in water depth with time. Black points represent individual sampling events (recording of water depth against permanent visual depth gauge).

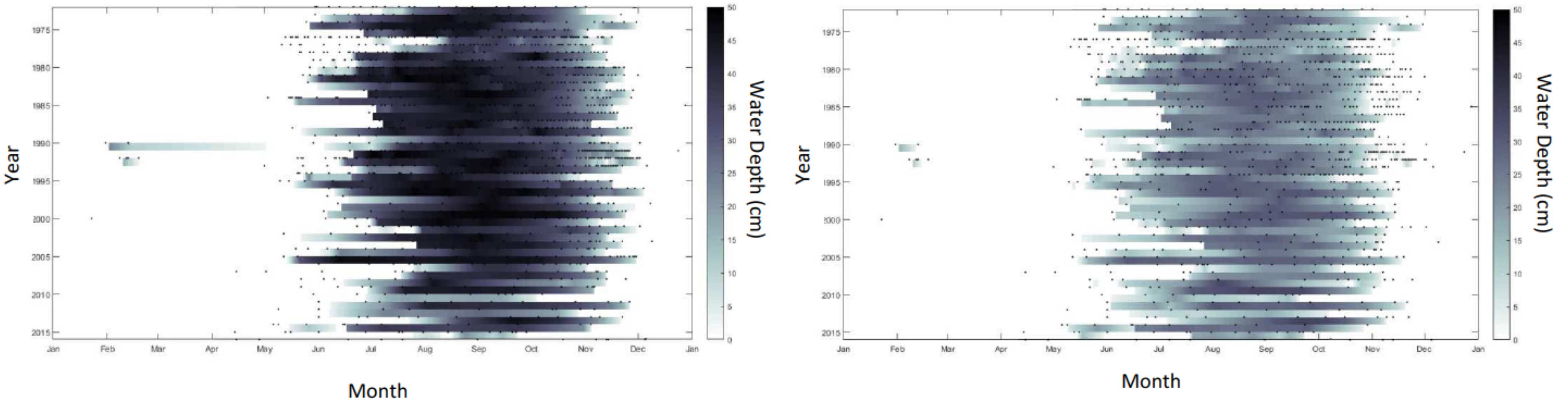

Figure 2.2 – A 45-year history of natural hydroperiods at Ellen Brook Nature Reserve, (swamp "1" left; swamp "2" right) spanning 1972 to 2016. Black points represent individual sampling events (recording of water depth against permanent visual depth gauge). Ellen Brook demonstrates a resilience to drought, with hydroperiods being similar in their duration and length over time (though depths are reduced).

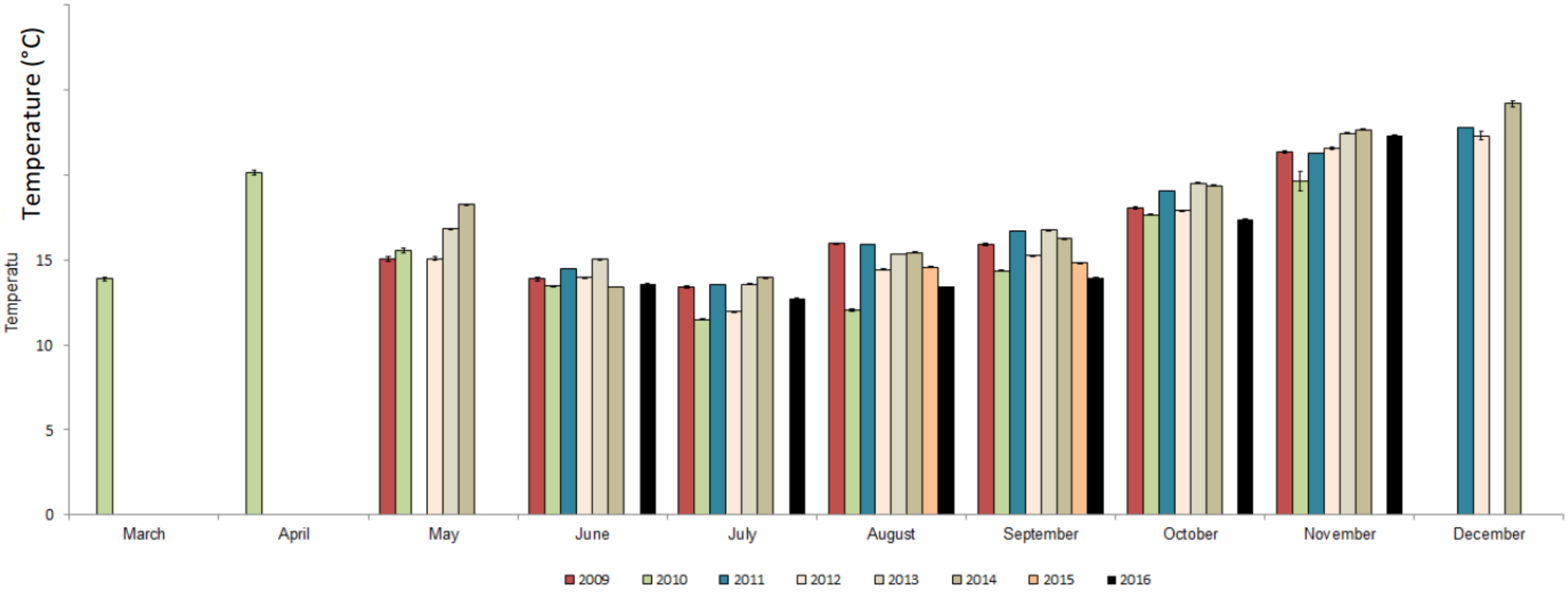

Figure 2.3 – Record of water temperatures on Ellen Brook Nature Reserve from 2009 to 2016 (December 2016 excluded due to weather station failure). Points are means ± standard error. Absence of values in some months (e.g. March 2009, 2011-2016) signifies no water in the swamps at that time (excluding December 2016).

was the longest sequence of dry years on record (Burbidge 1967, pp. 78). Additionally, in 2006, a severely reduced hydroperiod of around three months resulted in an unusual number of deceased turtles (hypothesised to be caused by starvation; Mitchell *et al.* 2013). This year was also marked by exceptionally low reproduction rates, where it was concluded that low rainfall prevented the species from breeding in three out of the four reserves (Mitchell *et al.* 2013).

Projections from global climate models predict a hotter, drier, and more unpredictable climatic future for Western Australia. Temperatures are predicted to increase up to 5 °C by 2070, with a corresponding 40 % reduction to rainfall (Pearce *et al.* 2007; Cai *et al.* 2009; CSIRO 2009a; CSIRO 2009b). With none of the most recent climate models predicting any increase in rainfall volume for south-west Western Australia between the late 20th and 21st centuries (CMIP5 models; generated in the fifth Intergovernmental Panel for Climate Change Assessment Report; Stocker *et al.* 2013; Smith & Power 2014), the climatic outlook is unfavourable for this species' recovery.

2.5 BUILDING RESISTANCE AND RESILIENCE: LIMITATIONS OF CURRENT *IN-SITU* MANAGEMENT OPTIONS

It is highly unlikely that the western swamp turtle will be able to adapt at the rate required by contemporary climate change because the species is slow to mature (in optimal conditions females reach a reproductive age at an average of ten years) and has a low reproductive rate, laying a single clutch of two to five eggs per year (Chapter 4). The lifespan of *P. umbrina* is unknown, but adult females and males collected in the 1960s are still reproducing, suggesting they are long lived *k*-strategists (*sensu*

MacArthur & Wilson 1967). Opportunities for dispersal to better habitats are limited because *P. umbrina* is restricted to a region that has lost approximately 70 % of its native vegetation due to clearing (for clay mining, viticulture, horticulture, and urban expansion). This has resulted in highly fragmented natural habitat with significant anthropogenic barriers to dispersal (Shephard *et al.* 2008; Burbidge *et al.* 2010). Thus, it is unlikely that the turtle would be able to adapt or disperse naturally at a rate that could keep pace with climate change (Mitchell *et al.* 2013). Without mitigation, it is "doubtless a long sequence of dry winters… followed by long hot summers would see the extinction of the species [in the wild]" (Burbidge 1967, pp. 86).

Assisted migration is typically presented as a 'last resort' management option (e.g. Schwartz 2005; Richiardi & Simberloff 2009; Burbidge *et al.* 2011; but see Richardson *et al.* 2009), once possibilities for climatic resilience and resistance have been explored (Hansen *et al.* 2003; Millar *et al.* 2007). Climatic resilience refers to the overall resources available to a system to withstand climatic stressors, while resistance refers to processes that stall and/or protect the ecosystem from climatic stressors (Millar *et al.* 2007). Under these definitions, resilience has been addressed in swamp turtle management by focusing on other threats (e.g. predation) and augmenting existing population numbers (see Burbidge *et al.* 2010). Although failure rates are often high when captive reared individuals are translocated (Seddon *et al.* 2015), the reintroductions of turtles into Twin Swamps Nature Reserve, as well as introductions to two new habitats to the north, have demonstrated that these individuals successfully survive in the wild. Unfortunately, whilst these 'resilience' strategies are effective at buffering the cumulative impacts of threats on the species, they do not prevent the problems arising from climate change. Other potential strategies to enhance resilience are also generally not appropriate or feasible. For example, because swamp turtle habitat is surrounded by a mosaic of agricultural land and urban development, the potential for acquisition and restoration of land is limited, and this prevents any large expansion or connection of reserves. As local *in-situ* management options are generally preferable to the translocation of species (Griffith *et al.* 1989; Lindenmayer & Burgman 2005; Godefroid *et al.* 2011), climate-change resistance strategies will be particularly important for securing wild populations of *P. umbrina*.

Climate change resistance in *P. umbrina* habitat has focused on the extension of swamp hydroperiods via human intervention. Three methods have been employed: pumping of bore water, deepening and bunding of swamps (Plate 2), and installation of shallow pools (Plate 3). Whilst these have been successful at extending the temporal extent of the swamps, they have not been straightforward to implement (Table 2.1). For example, pumping of ground bore water at Twin Swamps Nature Reserve was initiated in 1994 to supplement the swamps during times of insufficient rainfall. Whilst this was intended to be in operation only in years and months where rainfall was limiting (G. Kuchling, pers. comm.), since 2003 the pump has been essentially running for the entire ‘wet’ season and required an upgrade in 2010 to meet the higher flow rates necessary for its continued use (Burbidge *et al.* 2010). The pumping of bore water is now regarded as essential in Twin Swamps Nature Reserve and is likely to continue indefinitely. There are no specific strategies to safeguard against potential increases in temperature due to climate change. Instead, mitigation of increased temperatures is facilitated through revegetation (provision of additional shade via planting of native species) which is achieved during habitat restoration (Burbidge *et al.* 2010). These approaches may be effective at delaying the effects of climate change, but ongoing implementation (in particular of pumping ground water) is subject to external factors and political vagaries.

Table 2.1 – Climate change resistance strategies built into current western swamp turtle reserves.

Action	Description	Pros	Cons
Pumping of bore water	Artificial supplementation of swamp water	Provides reliable source of water independent of season or weather conditions	Needs significant planning and infrastructure Usage requires electricity Usage requires high quality water (water with low dissolves salts; Burbidge *et al.* 2010) Requires routine maintenance Requires operation staff May influence invertebrate and macroinvertebrate communities (sampling studies recommended)
Mechanical deepening and bunding	Artificial modifications made to swamp morphology	Prevents drainage of water to adjacent low-lying areas, extending natural swamp hydroperiods	Requires heavy machinery (e.g. Durrell 2003), so installation is season-sensitive (complete in dry season) High equipment and personnel costs Temporarily destructive to surrounding natural vegetation Mixed results: hydroperiods are extended, but use of these 'disturbed' swamps by turtles seems conditional upon the retention of the original top-soil layer
Installation of ponds	Small plastic-lined depressions, strategically placed at boundary of reserves to mitigate fencing effects	Inexpensive Requires only hand tools Effective at reducing desiccation and predation deaths of turtles trapped along fence-lines (also mitigated through two-way gates that facilitate turtle movements)	Radio-tracking data suggests use of ponds by turtles is limited Heat-pools (small surface area, heat quickly) Invertebrate and macro-invertebrate community composition thought to be different to natural swamps

Recovery of the western swamp turtle is overseen by a recovery team – a group comprised of government and non-government experts, scientists, and local community members who together prepare (and occasionally, implement) a formal recovery plan that delineates, justifies, schedules, and costs management actions necessary to support the recovery of the turtle. In Australia, recovery plans are executed under state and Commonwealth legislation (Ortega-Argueta *et al.* 2011). The western swamp turtle is now on its fourth recovery plan (Burbidge *et al.* 2010; succeeding Burbidge & Kuchling 2004, Burbidge & Kuchling 1994, and Burbidge *et al.* 1990). The continued execution of recovery objectives is subject to funding and other constraints such as ongoing cooperation with landholders, the absence of political obstacles, and the need to address other priorities (Ortega-Argueta 2008).

Ellen Brook Nature Reserve currently supports the single self-sustaining, breeding population of swamp turtles, but is fenced to provide protection from predators and is too small to accommodate a large population (Burbidge *et al.* 2010). Whilst there has been some evidence of recent recruitment at Twin Swamps Nature Reserve, this reserve is still regarded as marginal and requires targeted management for the existing population to persist (Burbidge *et al.* 2010). Additionally, whilst it is too early to determine whether self-sustaining populations will establish at the two northern introduction sites (Burbidge *et al.* 2010), preliminary analyses suggest that the current population is at the northern-most margin of a large area where the climatic niche is similar, and that translocations beyond this area are likely to be unsuitable under future climate scenarios (Mitchell *et al.* 2013*;* Mitchell *et al.* 2016; Bin Tareque 2017). The identification of additional reserves that will remain suitable long-term under the much lower rainfall environments expected in the future are required to promote the long-term persistence of *P. umbrina* populations in the wild. Accordingly, there is strong rationale for the assisted migration of this species.

Plate 2 – Bunding technique, used to prevent water flowing to adjacent low-lying areas and in doing so, promoting lengthened hydroperiods. Photograph: S. Arnall

Plate 3 – Pond installed at the boundary of a fenced reserve (Ellen Brook Nature Reserve), implemented to mitigate fencing effects (e.g. to reduce the desiccation risk to individuals seeking to exit the reserve and move onto neighbouring agricultural land, which they are likely to attempt towards the end of the wet season as swamps begin to dry). Two-way gates also allow turtles to move in and out of Ellen Brook Nature Reserve at will. Photograph: S. Arnall

PART B - ASSISTED MIGRATION: ASSESSING THE APPROPRIATENESS AND RISKS

2.6 IDENTIFYING EXISTING DECISION TOOLS FOR ASSISTED MIGRATION AND ASSESSING *P. UMBRINA*

To locate decision support tools developed for assisted migrations, I used the Web of Science (Science Citation Index Expanded, Social Sciences Citation Index, and Arts and Humanities Citation Index), and Google Scholar, searching articles in English from 1975 to present (accessed 18/08/2015). I used the search terms “assisted” OR “managed” OR “facilitated” OR “human assisted” OR “artificial” OR “benign” OR “conservation” OR “transformative” AND “migration” OR “coloni*ation” OR “relocation” OR “introduction” OR “translocation” OR “dispersal” OR “restoration” with the additional search string “decision” OR “risk” AND “tool” OR “framework” OR “assessment” OR “making” OR “analysis”, AND “climate change” OR “changing climate” OR “global warming”. This resulted in 554 articles, which were reduced to 54 after discarding those that were clearly irrelevant, and those that did not refer to assisted migration (or its synonyms) in the title or abstract. This served to eliminate general decision support tools, leaving only those that were presented within an assisted migration context. These were then reviewed for author, title, keywords, and content. An addition, seven articles were included by cross-referencing during this process, or through notifications of new literature published between the original search date and the 26th of January, 2017.

In their rhetorical analysis of debate over assisted migration, Klenk and Larson (2013) show proponents use decision tools in three ways to support arguments: firstly, for evaluating species, secondly for evaluating sites, and thirdly for determining the expected risks and benefits. Here I addressed two of these factors, as the final one (site evaluation) was not applicable for the assessment of assisted migration for potential candidate species. Accordingly, I eliminated articles that focused on site objectives (e.g. the identification of recipient sites; e.g. Harris *et al.* 2013) and I also eliminated those that were aimed at achieving specific objectives after assisted migration was identified as appropriate (such as for deciding on the timing of movements, e.g. McDonald-Madden *et al.* 2011).

The resultant literature spanned 2007 to 2017 (n = 59). These were divided into three categories: those that provided decision tools in table or figure formats (e.g. flow charts, n-dimensional plots, and Venn diagrams; n = 17), those that specifically discussed selection criteria within the text (e.g. where considerations were listed and discussed; n = 7), and those that met the literature selection criteria but were not aimed at facilitating the evaluation of species for assisted migration (i.e. not the above; n = 35; Figure 2.4). The latter category was excluded from further consideration.

Factors were transcribed verbatim to reduce interpretation bias. I then grouped similar factors together by keywords and summed the number of times they appeared in the literature. For example, “The species either has poor intrinsic dispersal ability or faces anthropogenic dispersal barriers” (Hällfors *et al.* 2016), “Can species move quickly enough?” (Shoo *et al.* 2013), “What evidence suggests that species are absent from climatically suitable locations because of dispersal limitations that could be addressed by assisted migration?” (Schwartz *et al.* 2012), “Species traits: lacking dispersal ability” (Gallagher *et al.* 2015), “Poor dispersal ability: intrinsic and extrinsic dispersal

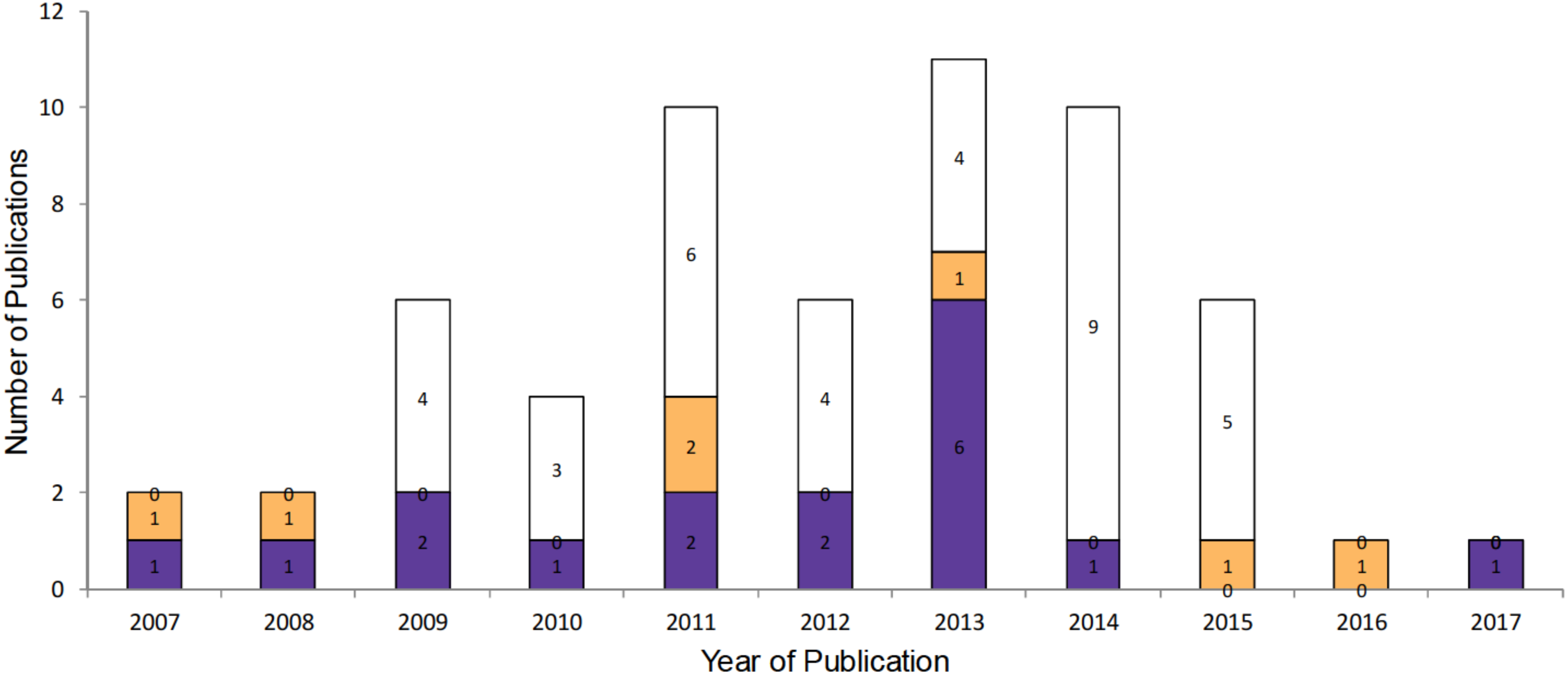

Figure 2.4 – Decision frameworks published between January 2007 and January 2017, that were assessed as applicable for facilitating the appropriateness of assisted migration for threatened species (refer Section 2.5). Purple denotes publications that produced decision tools in table or figure formats, orange denotes those publications that produced decision tools and/or criteria in text format, and white categorises those publications that met the literature selection criteria but were not aimed at facilitating species evaluations (peripheral publications). Numbers represent the volume of publications in each category.

limitations” (Foden *et al.* 2013), “Will [taxa] arrive at new habitats unassisted?” (Winder *et al.* 2011), “Prioritise collection of taxa with poor dispersal ability” (Vitt *et al.* 2009), and “All other things being equal, species that appear unlikely to disperse and colonize on their own because of limited vagility will be prime candidates for assistance” (Hunter 2007) were all pooled into the category ‘Vagility’, and this was given a score of eight. I subjectively nested each category within one of five major themes based upon how they were predominantly discussed in the literature assessed. Where broad statements were given (e.g. “Consideration must be given to minimizing the risks”; Gallagher *et al.* 2015) these were placed into “In General” categories within each relevant theme (e.g. within the ‘Risks’ theme in the aforementioned example).

The frameworks included here often operate with the caveat of being guides only, and do not provide an exhaustive list of all considerations. Furthermore, I recognise that these frameworks were designed to be used in their specified ways, such as by taking an *a-priori* approach, answering stepwise questions, or by simultaneously scoring factors. Nevertheless, the inclusion of each factor within individual tools implies decisional importance, and the approach adopted resulted in a comprehensive set of 158 assessment factors within 25 categories, nested into five themes (Figure 2.5).

I used the categories created to facilitate the evaluation of *P. umbrina* towards its suitability for assisted migration. Any instances where categories could not be addressed were explicitly identified as knowledge gaps. References to relevant themes or categories in Figure 2.5 are bolded in parentheses in the text below, and numbers in parentheses refer to the corresponding sections in Part A.

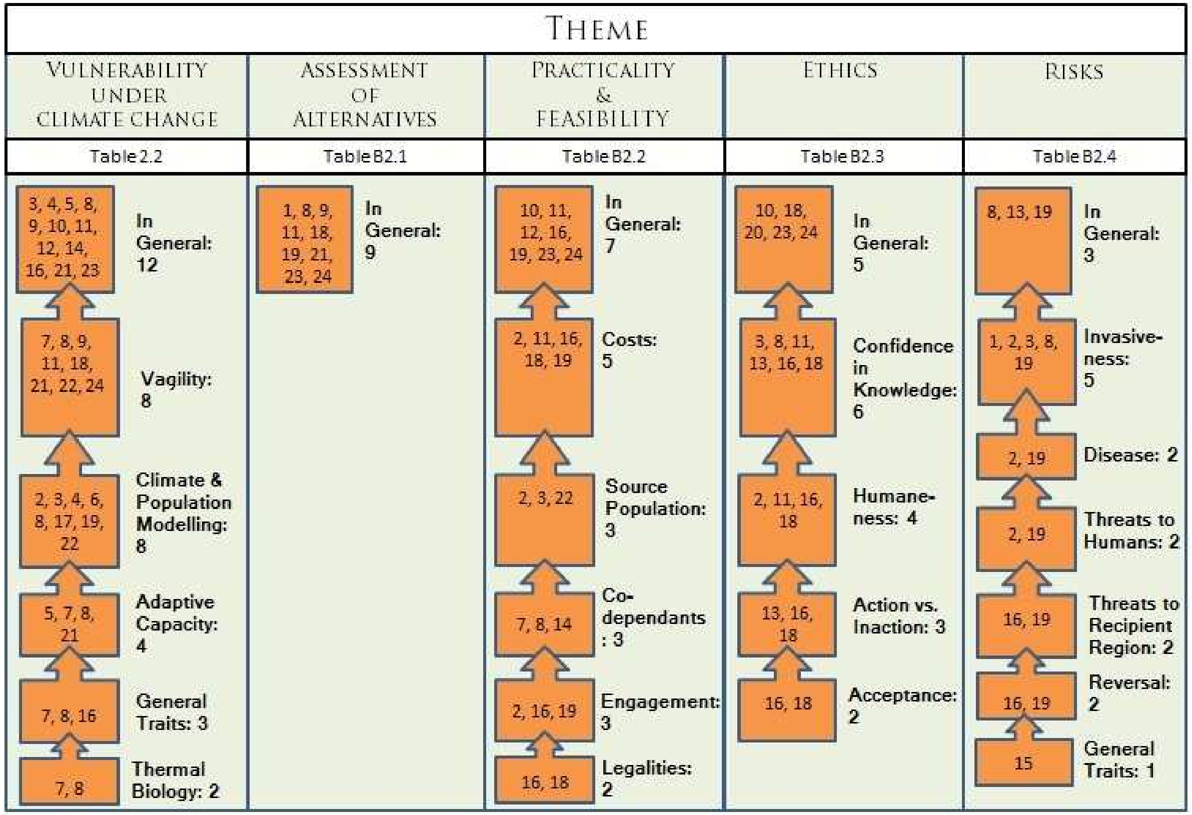

Figure 2.5 – Themes (light green boxes) with categories (orange boxes) resulting from a literature review into factors for assessing the suitability of species for assisted migration (and conversely, the suitability of assisted migration for individual species). Numbers given within the category boxes correlate to references as follows: 1) Abeli *et al.* 2014; 2) Burbidge *et al* . 2011; 3) Chauvenet *et al.* 2013a; 4) Chauvenet *et al.* 2013b; 5) Dawson *et al.* 2011; 6) Ferrarini 2016; 7) Foden *et al.* 2013; 8) Gallagher *et al.* 2015; 9) Hällfors *et al.* 2016; 10) Hoegh-Guldberg *et al.* 2008; 11) Hunter 2007; 12) McIntyre 2011; 13) McLachlan *et al.* 2007; 14) Moir *et al.* 2012; 15) Mueller & Hellmann 2008; 16) Richardson *et al.* 2009; 17) Rout *et al.* 2013; 18) Schwartz *et al.* 2012; 19) Schwartz & Martin 2013; 20) Shirey & Lamberti 2009; 21) Shoo *et al.* 2013; 22) Vitt *et al.* 2010; 23) Williams & Dumroese 2013; and 24) Winder *et al.* 2011.

2.7 RESULTS

2.7.1- THEME 1: VULNERABILITY UNDER CLIMATE CHANGE

A requirement to demonstrate a species' probability of extinction under climate change was the highest occurring general requisite (n = 12/36; 33.3%), and was the most heavily emphasised aspect throughout the literature reviewed. For example, Hunter (2007) suggested it would be more acceptable to prioritise those species that were definitely in decline because of climate change, than those that were only affected mildly, and Schlaepfer *et al.* (2009) suggested there would be little resistance to assisted migration if imminent extinction was expected. This theme had the highest number of factors (n = 51/158; 32.3%), nested within five categories that were identified to assist in evaluating a species' risk of decline or extinction under climate change. These were 'vagilty' (n = 8 tools, with a score of 8), the use of 'climate and population modelling' (n = 8 tools, with a score of 13), an evaluation of a species' 'adaptive capability' (n = 4 tools, with a score of 5), an assessment of selected 'general traits' that correlate with increased extinction risk (n = 3 tools, with a score of 5) and an assessment of thermal biology (n = 2 tools, with a score of 6; Table 2.2).

For P. umbrina, *evidence for climate change in both the broader region, and within their specific habitats has been demonstrated (2.3). The principal effect of climate change is reduced rainfall which shortens swamp hydroperiods, directly reducing the annual activity windows of the turtles. These reduced hydroperiods then affect the capacity of the turtle to survive, grow and reproduce, as described in Section 2.1.2 (and in Chapter 4,* ***In General****).*

Whilst the species is capable of dispersing (movements of up to 600 m in two days have been recorded; Burbidge & Kuchling 2004), the lack of suitable connecting habitat

Table 2.2 – Factors assigned to the theme 'vulnerability under climate change', as derived from the assessment of 24 decision tools on assisted migration. 'General traits' and 'thermal biology' refer to those aspects that increase a species' vulnerability to decline under climate change. Refer to Figure 2.5 for reference key. Comparable tables for the remaining four themes are provided in Appendix B.

Category	Ref	Factor
In General	3	Is the species threatened by the impact of climate change?
	4	How will climate change impact the spatial distribution of the [taxa's] suitable habitat?
	4	How does climate influence the [taxa's] vital rates?
	5	Exposure to climate change.
	8	Loss of suitable climatic habitat within the current range.
	9	Climate change (e.g. changes in temperature and precipitation regimes) is predicted to render (part of) the species' current distribution area unsuitable.
	10	Is there a high risk of decline or extinction under climate change?
	11	Probability of extinction due to climate change.
	12	Anticipated need for response to change and depletion of habitat [climate].
	14	Will ex-situ dependant species decrease greatly in abundance or go extinct?
	16	Likelihood of extinction/decline in geographic distribution and/or decline in abundance within geographic distribution.
	21	Is there a high risk that environmental suitability will decline under climate change?
	23	What is the risk of decline or extinction under climate change?

Category	Ref	Factor
Vagility	7	Poor dispersal ability: Intrinsic and/or extrinsic dispersal limitations.
	8	Species traits: Lacking dispersal ability.
	9	Migration inability (the species either has poor intrinsic dispersal ability or faces anthropogenic dispersal barriers).
	11	Candidate Species: Vagility (all other things being equal, species that appear unlikely to disperse and colonize on their own because of limited vagility will be prime candidates for assistance).
	18	What evidence suggests that species are absent from climatically suitable locations because of dispersal limitations that could be addressed by assisted migration?
	21	Can species move quickly enough?
	22	Prioritise collection of taxa with dispersal limitations.
	24	Will [taxa] arrive at new habitat unassisted?
Climate & Population Modelling	2	Current and predicted future climate of taxon's range (describe modelling used and provide an estimate of reliability of predictions, state why the future climate at current site will not be suitable).
	3	[Use of] species distribution models.
	3	[Use of] population models.
	4	How will climate change impact [the taxon's] population dynamics?
	6	How long will the assisted colonization be successful under climate change scenarios?
	8	Species distribution models [will be a factor of] successful assisted migrations.
	17	Species Assessment: Population viability assessment.
	19	Species Assessment: Climate change vulnerability assessment.
	19	Spatial Planning: Species distribution modelling.
	19	Spatial Planning: Spatial population performance.
	22	Undertake species distribution modelling at range edges.
	22	Undertake species distribution modelling outside future climate envelope.
	22	Undertake GIS based habitat matching protocols.

Category	Ref	Factor
Adaptive Capacity	5	Inherent capacity to adapt to change.
	7	Low adaptive capacity (poor evolvability).
	8	Species traits: Long generation times.
	8	Species traits: Small effective population size; reduced genetic variation.
	21	Genetics: Enough population genetic variation for evolutionary response; enough geographic genetic variation.
General Traits	8	Higher trophic level species.
	8	Body size.
	8	Species traits: Specialist species (including mutualistic relationships)
	7,16	Rare species.
	8, 16	Narrow distributions.
Thermal Biology	7	Thermally sensitive species: Specialised habitat and or microhabitat requirements.
	7	Environmental tolerances or thresholds (at any life stage) that are likely to be exceeded due to climate change.
	7	Thermally sensitive species: Dependence on interspecific interactions that are likely to be disrupted by climate change.
	7	Dependence on environmental triggers that are likely to be disrupted by climate change.
	8	Species traits: Physiological limits.

*hinders their dispersion. Some reserves (e.g. Ellen Brook Nature Reserve) are fenced to prevent the entry of predators, and others are situated within a mosaic of horticultural, agricultural, and residential land which presents an anthropogenic dispersal barrier. Therefore, it is highly unlikely that turtles would arrive at suitable new habitats unassisted. Where reserves are unfenced, the vagility of the species appears to be low as females return to familiar nesting sites over many years (G. Kuchling, unpublished data). Homing behaviour in other reptile species is common (e.g. Sullivan et al. 2004) and this should not be discounted when evaluating which distances at which to translocate swamp turtles. This should also be considered when selecting source individuals as turtles can have strong spatial memory (Roth II & Krochmal 2016) which can influence navigation success in new environments (Krochmal et al. 2015). For this reason, the movement of captive-bred individuals from captive conditions is likely to be preferable to the movement of resident individuals in the establishment and stocking of an assisted migration population (**Vagility**).*

*Population modelling for the species is yet to be completed, and this is identified as a knowledge gap. However, climate modelling indicates that current populations are at the northernmost limit of climatic suitability (Mitchell et al. 2013) and that at least one population is at risk of decline from climate change by 2050, without remedial management (Ellen Brook Nature Reserve population; Mitchell et al. 2016; Chapter 5), with another population already deemed marginal due to a shifting climate (Twin Swamp Nature Reserve population; 2.4; Bin Tareque 2017). Confidence in these model predictions is subjectively assessed as medium to good (**Climate and Population Modelling**).*

The capacity for the swamp turtle to adapt in-situ is considered to be poor: population size is small, reproductive rate is low, and the species has a long generation time (2.4, Chapter 4). However, the evolutionary potential of the species has not been formally evaluated, and this is identified as a knowledge gap, especially given the reports of a historic bottleneck in the population from which many wild individuals have been sourced (Kuchling & DeJose 1989; ***Adaptive Capability****).*

The swamp turtle has three of five general traits that may increase its vulnerability to climate change (the species is rare, it has a narrow distribution, and it has a comparatively small body size; ***General Traits****). It is also climatically sensitive, and is especially vulnerable to heat stress and desiccation during times when it is active but the swamps do not hold water (e.g. after hatching, and when seeking aestivation sites; 2.3; Burbidge 1981). Specifically, the species has a high Arrhenius temperature associated with its physiological rates which suggests a high sensitivity to temperature (Chapter 3, Chapter 4). Its reliance on environmental triggers that are likely to continue to be disrupted by climate change places it at an increased risk of extinction;* ***Thermal Biology****).*

2.7.2- THEME 2: EXPLORATION OF ALTERNATIVES

The second most frequently cited requirement (n = 9/36; 25% of the 'in general' factors) was the requisite to evaluate the potential of less extreme alternatives to assisted migration (Table B1). This included addressing questions such as "Can habitat be created to accommodate natural altitudinal or latitudinal shifts?" (Winder *et al.* 2011), as well as considering the prospect of future change (e.g. "Are … barriers predicted to disappear under the effect of climate change?"; Abeli *et al.* 2014). Consideration of both *in-situ* (e.g. provision of local climatic refugia) and *ex-situ* (e.g. improving habitat connectivity along the gradient of change) options were required when evaluating alternatives.

The potential for ex-situ restoration around P. umbrina *habitat is limited. The natural distribution of the turtle is very small, with reserves separated by a highly-modified landscape, and the potential to reclaim or rehabilitate this connecting habitat is low primarily due to cost and tenure (2.5). Within the boundaries of the current reserves, some localised internal refugia exist (e.g. in the form of artificial ponds). In addition, swamp hydroperiods can be artificially lengthened (e.g. through pumping bore water or construction of bunding). These present some viable in-situ solutions, but can be affected by logistical factors, such as access and cost, and do not address limiting issues such as reserve size (2.5;* ***In General****).*

2.7.3- THEME 3: PRACTICALITY AND FEASIBILITY

Theme 3 considered the practicalities of implementing assisted migration in general (n = 7/36, 19.4%), and in terms of 'costs' (n = 5 tools, with a score of 5), the identification of a suitable 'source population' (n = 3 tools, with a score of 4), the explicit recognition of 'co-dependents' (n = 3 tools, with a score of 5), the necessity for social and stakeholder 'engagement' (n = 3 tools, with a score of 10), and an assessment of 'legalities' (n = 2 tools, with a score of 7). There were a total of 38 criteria within this theme (24.1% of all criteria; Table B2). In general, there was a requirement to explicitly identify the degree to which the focal species could be captured, transported, released, and monitored (Richardson *et al.* 2009), with a general agreement that if the practical knowledge for moving a species safely could be demonstrated, the project would likely be considered acceptable (Hunter 2007).

Translocations of animals and plants for conservation reasons have been practised in Australia for several decades (Short 2009; Seddon et al. 2015) and there are well-established guidelines and approval processes in most States and Territories, including for introductions (Burbidge et al. 2012, and references therein). Translocation of captive-bred P. umbrina *is technically, legally, and financially feasible, having been demonstrated since 1994. The captive breeding protocols for this species are well established, with 20-30 individuals bred by Perth Zoo for release annually (Mitchell et al. 2013). The costs and financial responsibilities associated with both captive breeding and translocations are reported in the recovery plan that guides the conservation efforts for this species (Burbidge et al. 2010;* **In General, Costs, Legalities***).*

Assisted migration would have little impact on the captive source population as releases already occur under existing translocation protocols, and the removal of individuals from the captive population is factored into the breeding program. Wild populations can only persist if the current in-situ management to compensate for low rainfall is continued (2.5), and should it be ceased, it is likely these source populations would be extirpated. Current management preference is to continue in-situ options into the foreseeable future, with in-situ management being prioritised over the movement of local individuals. Should local individuals be moved, population resilience and genetic variation would be reduced (especially if older individuals with rare genotypes were removed) and therefore, conservation managers will need to carefully consider what level of future threat will be sufficiently large to trigger relocation from existing reserves, if any, and in what configuration these will be executed (Schwartz et al. 2012; **Source Population***).*

P. umbrina *is not known to be a co-dependent. It is a mid-trophic level predator, consuming aquatic macroinvertebrates and small tadpoles (Burbidge 1981; Gilbert 2011; Katja Schmölz, unpublished data). Native predators are principally water-birds, but eggs or hatchlings may also be consumed by bandicoots, foxes, and rats (Burbidge et al. 2010). There are no known species that specialise on* P. umbrina*, and the turtle is not thought to be a major component of any species' diet. Further, it does not exclusively limit invertebrate/macroinvertebrate prey, sharing this role with other co-inhabiting predators (i.e. it is not functionally unique), and so any potential for mesopredator release (Crooks & Soule 1999) is reduced (****Codependents****).*

The Western Swamp Tortoise recovery team is identified as being the responsible body for guiding and implementing translocations, and this also presents an opportunity for managers, stakeholders, and scientists to work collaboratively towards decision making. The species receives considerable community support (a "Friends of the Western Swamp Tortoise" community group exists, with over 250 active members and 900 general supporters) and the translocations of swamp turtles is also met with public support, with many community members attending release events (J. Bant, pers. comm.). This suggests a community willingness to support assisted migration. There does not appear to be any cultural contraindications, but there may be a social cost related to those individuals whose properties border populations of P. umbrina*, and to which some regulations may be imposed (e.g. limitations of fertiliser use within 100 m of property boundaries; G. Kuchling, pers. comm.). Engagement with specific stakeholders will be required once recipient sites have been identified and assessed as suitable (****Engagement****).*

2.7.4- THEME 4: ETHICS

An assessment of ethics was frequently identified as a necessary component of any assisted migration plan, with the general consensus being to expect little resistance if broad public support could be demonstrated (Hulme 2005; Schlaepfer *et al.* 2009; n = 5/36; 13.9%). Four major categories were identified to support an evaluation of ethics, and these were an assessment of the 'confidence in knowledge' (n = 6 tools, with a score of 8), a consideration of 'humaneness' (n = 4 tools, with a score of 6), an evaluation of the willingness to support action(s) (i.e. an assessment of 'action versus inaction'; n = 3 tools, with a score of 6), and an evaluation into the 'acceptance' of outcomes (n = 2 tools, with a score of 3). The 30 factors in this theme encompassed a wide range of considerations (Table B3). For example, in justifying a species' value (within 'action vs. inaction'), Richardson *et al.* (2009), Vitt *et al.* (2010) and Schwartz *et al.* (2012) all suggested higher priorities should be given to species that were keystones, flagships or iconics, and/or were conservationally, culturally or commercially significant. Similarly, Vitt *et al.* (2010) suggested ranking species based on their importance within their communities. In the same theme, Schwartz *et al.* (2012) encouraged users to question ethical responsibilities regarding the implementation of assisted migration, and Richardson *et al.* (2009) suggested users consider what affect assisted migration would have on existing conservation efforts.

From a 'species rescue' approach, the benefits of assisted migration for P. umbrina *appear to outweigh the potential costs. While the consequences of assisted migration may be irreversible, the risks are generally believed to be low (refer 2.7.5). Costs are likely to relate primarily to the financial requirements for establishing new reserves (including stakeholder engagement), releasing individuals, and population monitoring – some of which already occur under Burbidge et al. (2010). The potential benefits of* *assisted migration (specifically, the future persistence of wild populations) will arguably outweigh the potential costs (as argued below,* ***In General****).*

Trust in the ecological understanding of P. umbrina *is high, particularly as some members of the species' recovery team have worked closely with the turtle since its rediscovery over fifty years ago, meaning decisions are based upon a strong foundation of knowledge. However, trust in climatic projections is lower given that these represent hypotheses rather than observations (Tomlinson et al. 2014). Therefore, movements should be carried out in an adaptive management framework with compulsory ongoing monitoring (****Confidence in Knowledge****).*

Ethical considerations that pertain to the act of translocating P. umbrina *are somewhat negated by the fact that translocations for this species have been occurring for over 30 years, and there is no evidence of harm to individuals being moved. As assisted migration would seek to introduce individuals into more benign environments than those in which they currently occur, it is unlikely that the wellbeing of individual animals would be compromised (****Humaneness****).*

While P. umbrina *has no commercial significance (i.e. there would be no financial loss if the species were to become extinct) the turtle is charismatic, phylogenetically and biologically unique (see Chapter 1), and it has strong community support, being widely recognised as Australia's rarest reptile; all factors that would support its ongoing conservation. Without assisted migration and without current in-situ management, it is unlikely that the species would be capable of recovering from their Critically Endangered status. Assisted migration is unlikely to redirect resources away from the other recovery management actions that are in place to protect extant populations (e.g.*

*weed control, fence and firebreak maintenance, predator baiting; Burbidge et al. 2010). Twin Swamps and Ellen Brook Nature Reserves are identified as 'threatened ecological communities' and so would likely continue to receive the current level of management, and as all swamp turtle populations are considered highly valuable and necessary for the persistence of the species (IUCN 2015), it is highly unlikely that current management actions would cease (**Action vs. Inaction**).*

*The Western Swamp Tortoise recovery team would inherit the responsibility for the outcomes (both negative and positive) resulting from assisted migration. The captive population at Perth Zoo (and insurance population at Adelaide Zoo in South Australia) provide contingency should assisted migration protocols fail (**Acceptance**).*

2.7.5- THEME 5: RISKS

Whilst the focus of much assisted migration literature is on the need to minimise risks (Hewitt *et al.* 2011), only 8.3% of the factors in the decision tools reviewed related to risk evaluation (n = 22/158), and only one published decision tool cited characteristics that may constitute a species belonging to a high risk group (Mueller & Hellmann 2008). Thus drawing upon taxa-specific knowledge and literature has been identified as being important in arguing risks and their minimisation (Gallagher *et al.* 2015). Categories of 'invasiveness' (n = 5, with a score of 5), 'disease' (n = 2, with a score of 2), 'threats to humans' (n = 2, with a score of 2, 'threats to the recipient region' (n = 2, with a score of 4), the degree of 'reversibility' (n = 2, with a score of 2), and 'general traits' (n = 1, with a score of 2) were identified for assessing a species risk potential and evaluating contraindications (Table B4).

Olden et al. (2011) provide characteristics for assessing the extirpation and invasion probabilities for freshwater species. Of the 12 characteristics listed by Olden et al., P. umbrina *have a high likelihood of extirpation (displaying ten of the 12 characteristics suggested to relate with freshwater species vulnerability) and two characteristic likely to make them invasive (these being a wide breadth of diet, and no parental care). In addition, the turtle's life history (low clutch sizes with a maximum of five eggs, long generation times, slow times to maturity; Chapter 4) also suggest they are unlikely to become invasive, as rapid reproduction is biologically constrained. By contrast, the highly invasive red eared slider (*Trachemys scripta elegans*), which is listed as one of the top 100 most invasive alien species globally (Lowe et al. 2000) and poses an extreme establishment risk in Australia (Csurhes & Hankamer 2016), can produce clutches of 2-30 eggs up to six times per year (Scalera 2007) and can reach maturity in two years (Dundee & Rossman 1989). Based on this, and on the information presented below, the assisted migration of* P. umbrina *is assessed as being relatively low risk in terms of invasive potential* (***Invasiveness***).

P. umbrina *is historically sympatric with another larger turtle,* Chelodina (Macrodiremys) colliei. *However, there has been no evidence of either species posing a disease risk to the other, and assisted migration is unlikely to alter this. A skin condition can affect captive-bred individuals, but this relates to husbandry practise and is treatable (Ladyman et al. 1998;* ***Disease***). P. umbrina *does not represent any threat to human safety* (***Threats to Humans***), *and as swamp turtles play no discernible role in the aesthetics of a landscape, have a benign role within their habitat, and do not provide a strong ecosystem service (i.e. they are not an ecological engineer, keystone species, or similar) the potential risks to the recipient sites are likely to be low* (***Threats to Recipient Region***).

While P. umbrina *does not possess the traits linked to increased invasive potential under assisted migration (****General Traits),*** *because it is semi-aquatic, the turtle presents a potential dispersal/invasion risk, especially if released from anthropogenic barriers to dispersal. However, the species' reliance on ephemeral wetlands limits their invasive potential because the turtles are immobile (in aestivation) for approximately six months each year when the swamps are dry. In a worst-case scenario, this offers some opportunity to collect and reverse an introduction, providing that aestivating animals can be located (translocated individuals are typically radio-tracked; Burbidge et al. 2010). Further, although western swamp turtles are rare, they are well studied and have a long history of monitoring, which further reduces risks and improves post-release management (Huang 2008) (****Reversibility****).*

2.7.6-SUMMARY OF KNOWLEDGE GAPS

Gallagher *et al.* (2015) was the only example specifically identifying the need to fill knowledge gaps (to the best extent possible) before proceeding with an assisted migration plan. In working through the considerations from Figure 2.5, it is straightforward to identify which components are lacking, and thus set them aside to be addressed.

Knowledge gaps identified for P. umbrina *during assessment were 1) the need for population modelling, 2) a lack of knowledge of the species' genetic diversity and evolutionary potential, and 3) a requirement for an improved understanding of home ranges and homing behaviour.*

2.8 DISCUSSION

A well-conceived, holistic approach to assisted migration includes documentation that changes in the climate are contributing to a species' decline, an assessment of invasive risk, a guarantee that adequate resources are available (and that these have not been reallocated from protecting extant populations), the identification of recipient sites, experimental evidence that the recipient site has a low probability of being harmed, and a confirmation that assisted migration is legal (Haskins & Keel 2012). The considerations compiled here cover the majority of these elements, but do not include factors that consider recipient sites. For *P. umbrina*, and perceivably many other assisted migration candidates that are narrowly-endemic, the identification of sites requires a significant investment of effort and time. This is because many candidates for assisted migration will not have sufficient distribution points with which to construct correlative species distribution models (SDMs) such as the 'climate-envelope' models recommended in Theme 1. Instead, evaluators will need to rely on mechanistic (physiologically-based, non-statistical) models, and these represent a far greater investment of time and data than their correlative counterparts (Dormann *et al.* 2012). Whilst many of the factors listed above will need to be reassessed once a recipient site is identified (in particular ethical, logistical, and risk-assessment considerations are likely to require revaluation), it is not useful to assess sites early in the selection process unless it is possible to construct SDMs rapidly. Specifically, it would be counterintuitive to invest effort in identifying sites without first having evaluated the source population, or having demonstrated the feasibility of translocations.

This catalogue provides a comprehensive approach for evaluating candidate assisted migration species, by highlighting factors considered to be important by conservation practitioners, and by encouraging end-users to use these to inform decision making.

However, it does not provide a quantitative framework to more formally evaluate a species or compare assisted migration options. Whilst it would be possible to ascribe weightings to each particular theme or factor (e.g. Richardson *et al.* 2009), it would be difficult to do so in a way that equally evaluates all species, given that the relative importance of factors is likely to differ based upon the taxa being evaluated, and on the specific circumstances motivating their assisted migration. Instead, assisted migration protocols should be evaluated on a case-by-case basis (Javeline *et al.* 2015). However, in the scenario where multiple potential candidates require comparison by the same user, weightings could be assigned to each factor based upon the availability of resources, the information available, the relative importance of each theme, and the user's own individual value system (Sandler 2010). Because each evaluator is likely to place emphasis on different aspects, this catalogue provides a means to ensure factors for evaluating assisted migration are not overlooked, and helps users identify species-level knowledge gaps that may have otherwise been undetected.

In developing this review and in evaluating the turtle, I acknowledge assessment from a 'species rescue' point of view, rather than a functional persistence one (Parker *et al.* 2010). The latter is more likely to encompass newer motivations for assisted migration, such as the 'push-pull' approach outlined in Lunt *et al.* (2013) which addresses ecosystem functioning as a whole resulting from the removal, and receipt, of the target species. Species that have limited ecological roles (such as *P. umbrina*), are suggested to be better candidates for assisted migration due to a separation from co-dependents or a functional role (Vitt *et al.* 2010). However, this also highlights their lack of ecosystem service and therefore may reduce their inherent value for assisted migration, meaning cultural or commercial aspects become more heavily emphasised given the reality of limited conservation dollars (Shoo *et al.* 2013).

For *P. umbrina*, assisted migration appears to be a good conservation strategy, and on balance the species is well-suited to this approach, although some knowledge gaps need to be addressed in order to optimise translocation success. Though the process of evaluating a species this way is lengthy, it is also not exhaustive. Literature from the field of invasion biology demonstrates the vast number of factors and considerations that might be useful for predicting the potential invasiveness of a species, which are continually evolving and improving (Lockwood *et al.* 2013). Unfortunately, assisted migration needs to progress in concert with rapid environmental and climate change, and so at some point it becomes necessary to accept the potential consequences of not conducting an exhaustive evaluation. Instead, it may be necessary to accept what information is available as a foundation, and to move forward under an adaptive management framework which employs strategies to minimise risks once translocations are underway.

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CHAPTER THREE

A THERMAL PROFILE OF METABOLIC PERFORMANCE IN *P. UMBRINA*

PREFACE AND STATEMENT OF CONTRIBUTION

Having argued that the western swamp turtle is a strong candidate for assisted migration (Chapter 2), my focus shifted towards identifying suitable sites for the assisted migration of the species.

Theoretically, assisted migration sites could be identified from correlative species distribution models (SDMs). However, as discussed in Chapter 1, construction of correlative SDMs are not possible for species with very restricted distributions. Instead, mechanistic SDMs provide a much more suitable approach, but require detailed behavioural and physiological data, and in particular are driven by a known biological rate-response to temperature (the Arrhenius temperature response). These models are ideally informed by temperature vs. biological rate measurements, for which no suitable dataset exists for the western swamp turtle.

Here my aim was to create a dataset which could be used to calculate an Arrhenius temperature, which would in turn inform physiological-based models (Chapters 4 and 5). I chose to measure standard metabolic rates in the turtle as metabolic rates provide a robust index of a species response to environmental temperatures, largely due to tightly controlled factors (e.g. digestive state) and the independence of measurements from behaviour (Withers 2001).

Except as noted otherwise below, the work presented in this chapter is my own original work.

S. Tomlinson assisted me in writing the data acquisition software which was used to record metabolic data, as based on original unpublished software written by P. Withers.

I was responsible for experimental conception and design, and conducted the pilot studies (Appendix C), obtained animals ethics permits and scientific licenses, made the measurements, analysed the data, and was the primary author for the chapter and paper. N. Mitchell, G. Kuchling, M. Hipsey, and M. Kearney provided supervisory feedback on the content.

Experimental work was conducted under approved University of Western Australia animal ethics protocols RA/3/100/966 and RA/3/100/1039, as well as under equivalent approvals from the Perth Zoo (2010–8 and 2011–5).

I used B. Jenny's 'color oracle' program to design my figures to be compatible with colour blindness (http://colororacle.org; Monash University, Australia).

This chapter is presented as published (Arnall *et al.* 2015), with the exception of plural pronouns (we, us, our) which have been replaced by individual terms.

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3.1 INTRODUCTION

The western swamp tortoise (*Pseudemydura umbrina*; hereafter referred to as the western swamp turtle) is Australia's rarest reptile, currently surviving in four locations within the Swan Coastal Plain of Western Australia (Burbidge *et al*. 2010). This species is the only extant member of the subfamily Pseudemydurinae (Gaffney 1977) and is the smallest of all Australian chelids (Burbidge 1967; Burbidge *et al*. 1974). Once thought to be extinct, it is now known to occur in a small number of ephemeral wetland swamps where it spends the wet winter/spring season feeding, growing and mating, and the dry summer/autumn season aestivating under leaf litter or in natural tunnels formed in the ground (Burbidge 1981).

Primarily threatened by land clearing and habitat change, clay mining, predation by exotic animals, and wildfire (Burbidge *et al*. 2010) there are growing concerns over the species' ability to withstand climate change (Burbidge *et al*. 2010; Mitchell *et al*. 2013). Activity of *P. umbrina* is contingent upon water availability and temperature: the turtle is able to grow and reproduce only when the swamps it inhabits are filled with water warm enough for it to be active. The south-west of Western Australia has experienced a 15% reduction in rainfall since the mid-1970s with the greatest decline in May, June and July (IOCI 2012), a time that historically signalled the filling of the swamps within *P. umbrina* habitat (Burbidge 1981). A shortening and shifting of the swamp hydroperiod (i.e. the length of time the swamps hold water) reduces the turtles' capacity to feed and accumulate energy for body maintenance over the dry summer aestivation period. This is especially concerning for hatchlings, as individuals failing to meet a critical mass of 18 g in their first year are unlikely to survive aestivation (Mitchell *et al*. 2013). Furthermore, in females, vitellogenesis occurs over the summer aestivation months and is conditional upon the accumulation of adequate energy reserves over the active period (Kuchling & Bradshaw 1993).

Despite their Critically Endangered status, the physiology of *P. umbrina* has remained relatively unstudied (Lucas *et al.* 1963; Burbidge 1967; Burbidge 1981). Recent research on its habitat requirements (Dade *et al.* 2014) indicated that food availability for *P. umbrina* is an important factor for selecting future translocation sites for this species, due to the critical link between energy acquisition and the capacity for the turtle to survive, grow and reproduce. A dynamic energy budget (DEB) model (Kooijman 2010) has been proposed to better understand the effects of energy limitation on egg production and hatchling survival, and to predict how recruitment may be influenced by future variations in temperature and rainfall (Mitchell *et al.* 2013). Yet despite the importance to its conservation of its energy demands being met, the baseline energy requirements of *P. umbrina* have not been quantified.

Accordingly, here I measure the metabolic rates of *P. umbrina* within its known thermal tolerance range to assess its potential energetic needs. I also create a thermal response curve to predict how the species may respond to extremes in temperature, and discuss how the metabolic physiology of *P. umbrina* differs from that of other chelids.

3.2 METHODS

3.2.1 STUDY ANIMALS AND MAINTENANCE

Eight adult male *P. umbrina* from the captive breeding population at Perth Zoo (South Perth, Western Australia) were used for repeated measurements of standard metabolic rate (SMR). These individuals were housed outdoors in groups under a natural photoperiod, in polyethylene-lined ponds ~3.9 m long x 1.2 m wide, with a maximum depth of 0.4 m. In between measurement cycles, turtles were fed a maintenance diet of 2.5 g of ‘turtle pudding’ (minced beef, skinned rat, crayfish, white fish, egg yolk, gelatine, calcium carbonate and Herptivite™; Rep-Cal Research Laboratories) between 13:30 and 15:30 hours daily, and had opportunistic access to live prey (brine shrimp, blood worms, mosquito larvae and tadpoles). Five of the turtles were fed standard turtle pudding whilst the remaining three were given a trial diet in accordance with an ongoing study by Perth Zoo (as per standard turtle pudding recipe, with beef and rat replaced by herring).

3.2.2 MEASUREMENT OF SMR

Measurements of SMR took place over eight weeks during the austral spring of 2012 at Perth Zoo in a controlled-temperature room set at 23 °C (± 2 °C). Following Bennett and Dawson (1976) SMR was defined as metabolic rate measured during the inactive part of the day in resting and fasted animals. Accordingly, turtles were fasted for a minimum of 100 h (average approximately five days) before each measurement of SMR. For fasting, turtles were housed individually in a controlled-temperature room set to 21.5 °C, within 0.5 m x 0.7 m x 0.4 m plastic tubs consisting of 15 cm of water and a shallow gravel landing area. Water was exchanged daily, and faeces were screened for the presence of indigestible markers (round-edged craft glitter) that were fed to turtles in their last feed before fasting. Turtles reliably defecated before 10:00 hours on each day, and were considered to have a clear gut on the morning upon which they were no longer producing faeces, after visualisation of the markers.

On the day of measuring, turtles were removed from their holding containers and placed in the dry metabolic chamber for a minimum of 8 h to equilibrate to the test conditions.

Metabolic rates (volumetric oxygen consumption, $\dot{V}O_2$; volumetric carbon dioxide production, $\dot{V}CO_2$) of *P. umbrina* were measured at nominal temperatures of 15, 20, 25 and 30 °C, in random order using standard open-circuit flow-through respirometry (e.g. Withers 2001). Animals were measured during their rest phase in dry conditions from 20:00 hours, for 4–8 h, until $\dot{V}O_2$ and $\dot{V}CO_2$ had become stable and minimal. Ethical constraints prevented us from conducting wet measurements (it was necessary to eliminate any risk of drowning). Individuals were weighed to ± 0.1 g at the start and end of each experiment, and each turtle was measured once at each test temperature.

3.2.3 METABOLIC SYSTEMS

To alleviate time constraints, two metabolic systems ran concurrently at Perth Zoo; these were otherwise identical except for the analysers used. Outside atmospheric air was regulated by mass flow controllers at a flow rate of 200 mL min^{-1}, dried and passed into a sealed 3 L metabolic chamber placed inside a controlled-temperature cabinet set at ambient temperatures (T_a) of 15-30 °C. As *P. umbrina* is an obligate summer aestivator, it was possible that awake and fasted turtles would seek water when confined to the metabolic chambers. Pilot studies showed that *P. umbrina* failed to rest in the absence of cover, so 25 g of artificial plastic leaves were placed in each chamber into which the turtles could hide during measurement. This not only effectively prompted turtles to be inactive (reducing the effects of rising lactate: Jackson 2011) but also improved gas washouts across the duration of the traces (Lighton 2008).

Excurrent air was dried by Drierite columns (anhydrous calcium sulfate; W. A. Hammond Drierite), and analysed for O_2 and CO_2 content (David Bishop 280 Combo gas analyser; David Bishop Instruments, or Sable Systems Foxbox-C; Sable Systems International). Temperature was monitored real-time using temperature probes (Vaisala

HMP45A; Vaisala Oyj and Sable Systems Foxbox-C; Sable Systems International) and logged using precalibrated iButtons (Thermocron DS1921G; Maxim Integrated) set to record ambient temperature within the chambers at 60 s intervals. The gas analysers and temperature probes were interfaced to a PC directly by a data-acquisition board (DataQ DI-710-UL; DataQ Instruments Inc.). Custom-written Visual Basic (v6) software (Microsoft) was used to record O_2, CO_2 and T_a every 20 s throughout the experimental period. $\dot{V}O_2$ and $\dot{V}CO_2$ were calculated after Withers (2001) for the period (at least 20 min) when they were stable and minimal. Baseline recordings of background O_2, CO_2 and T_a were obtained for at least 60 minutes before and after the animals were placed into the metabolic chamber for measurement.

A precalibrated infrared thermometer (ZyTemp TN425LC; Radiant Innovation Inc.; dry skin surface temperature against cloacal temperature) was used to measure body temperature (T_b) immediately after removing the turtle from the chamber. This was preferred to repeated cloacal measurements as it was more reliable for obtaining immediate measurements. All measures of T_b were taken in triplicate within 15 s of the turtle being removed from the chamber. Skin surface measurements were taken from the inguinal depression behind the hind limbs.

Two-point calibrations were performed on all analysers. Oxygen analysers were calibrated using an electronic zero function (Foxbox) or with nitrogen (0% O_2; David Bishop combo analyser) and dry industrial air (20.95% O_2). Carbon dioxide analysers were calibrated with nitrogen (0% CO_2) and a 0.53% calibration gas (BOC gases). Temperature probes were checked against a calibrated thermometer at each experimental temperature. Finally, mass flow controllers were calibrated using a volumetric meter corrected to standard temperature and pressure.

3.2.4 CALCULATIONS AND DATA ANALYSIS

Energy requirements were calculated from the conversion factors for O_2 to kilojoules following Withers (1992), using the average measured respiratory exchange quotient (RQ; RQ= $\dot{V}CO_2$ / $\dot{V}O_2$) for that experiment. Statistical analyses were performed using StatistiXL (ver. 1.8, statistiXL). Individual variability was compared using repeated-measures ANOVA, or *t*-tests for dual temperature comparisons. I fitted a thermal response curve by following the quantitative formulation described in Kooijman (2010; after Sharpe & DeMichele 1977) for the reduction of physiological rates at low and high temperatures, as follows:

$$s(T)/s(T_1) \text{ with } s(T) = (1 + exp\,(\frac{T_{AL}}{T} - \frac{T_{AL}}{T_L}) + exp\,(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T}))^{-1}$$

where s represents the 'stress' value, T represents temperature, T_L and T_H are the lower and upper boundaries of the tolerance range respectively and T_{AL} and T_{AH} are the Arrhenius temperatures for the rate of decrease at both boundaries (all in temperature, K). To complete the curve, I plotted $\dot{V}O_2$ as zero at 42.5 °C, after Burbidge (1981), who established the critical thermal maximum for *P. umbrina* at this temperature. The critical minimum was estimated as 5 °C after Leung (in Lucas *et al.* 1963) who reported that *P. umbrina* withdrew into its shell and became torpid at ~10 °C. Values are presented as mean ± standard error, with *N* = number of animals and *n* = number of observations.

3.3 RESULTS

The average body mass of turtles at the time of measurements was 302.3 g ± 5.7 g (*N* = 8, *n* = 32; range = 261–364 g). Fasting before measurement resulted in an average individual mass loss of 4.6 g ± 0.3%. Turtles regained mass during the interval between measurements, resulting in no significant change to body mass at the time of measurements across all temperature treatments ($F_{3,28} = 0.046$, $P = 0.987$). There was no significant influence of diet on $\dot{V}O_2$ ($F_{1,6} = 0.149$, $P = 0.712$), hence data for individuals fed both types of diet were pooled for all analyses.

Body temperature was significantly influenced by ambient temperature ($F_{1,27} = 649.16$, $P < 0.001$), with $T_b = 2.6\ (\pm\ 0.8) + 0.9\ (\pm\ 0.0)\ T_a$ ($R^2 = 0.96$). Mass-specific oxygen consumption at 20 °C (0.007 ± 0.000) and 30 °C (0.030 ± 0.002) is shown in Table 3.1 alongside the Q10 (Van't Hofft 1884) for the same interval. Oxygen consumption rates at 15 °C and 25 °C were 0.002 (± 0.000) and 0.018 (± 0.000) respectively. RQs at 20 °C and 30 °C were 0.957 (± 0.092) and 0.711 (± 0.010), and were significantly higher at 20 °C than at 30 °C ($T_{1.89} = 2.53$, $P = 0.020$). The RQs at 15 °C and 25 °C were 0.959 and 0.845. The Q10s for $\dot{V}O_2$ were 9.21 and 4.60 at 15-25 °C, and 20-30 °C respectively. The Q10s for $\dot{V}CO_2$ across the same intervals were 7.99 and 3.50. The calculated resting energy requirements for *P. umbrina* were 0.087, 0.318, 0.885 and 1.560 J g^{-1} h^{-1} at 15 °C, 20 °C, 25 °C and 30 °C respectively. The thermal response curve for $\dot{V}O_2$ was best fit using values of 70 000 and 60 000 for T_{AL} and T_{AH}, 280 and 306 for T_L and T_H, and 15977 for the Arrhenius temperature (Figure 3.1).

3.4 DISCUSSION

The thermal performance (and fitness) curves of ectothermic species are asymmetric and non-linear (Huey & Stevenson 1979; Huey & Berrigan 2001; Bulté & Blouin-Demers 2006; Martin & Huey 2008) and there are numerous opinions on the best method for describing them (e.g. Angilletta 2006; Krenek *et al*. 2011). I adopted the

Table 3.1 - Q10 values based on metabolic rates (oxygen consumption, $\dot{V}O_2$) of turtles between 20 °C and 30 °C, modified after Litzgus and Hopkins (2003). Studies included here are those that reported the measurements of standard metabolic rates or resting metabolic rates of fasted turtles as mass-specific metabolic rates.

Species	**Common name**	**Life stage**	**Mean mass (g)**	**Range (g)**	**SMR at 20°C ml O2 g^{-1} h^{-1}**	**SMR at 30°C ml O2 g^{-1} h^{-1}**	**Q10**	**Reference**
Pseudemydura umbrina	Western swamp tortoise	Adult	302	261–364	0.0065	0.0288	4.41	This study
Chelydra serperntina	Common snapping turtle	Juvenile	72	57–73	0.0209	0.0521	2.49	Steyermark & Spotila (2000)
Homopus arcolatus	Parrot-beaked tortoise	Adult	155	Not Reported	0.0124	0.0315	2.54	Brown *et al.* (2005)
Gopherus agassizii	Desert tortoise	Juvenile	166	Not Reported	0.0112	0.0337	3.01	Brown *et al.* (2005)
Kinosternon subrubrum	Common mud turtle	Adult	170	97–220	0.0127	0.0557	4.39	Litzgus & Hopkins (2003)
Tachemys scripta	Red-eared slider	Adult	305	257–353	0.0109	0.0313	2.87	Gatten (1974)
Terrapene ornata	Ornate box turtle	Adult	354	180–538	0.0093	0.0149	1.60	Gatten (1974)
Kinixys spekii	Speke's hinge-back tortoise	Adult	695	244–1383	0.0116	0.0389	3.35	Hailey & Loveridge (1997)

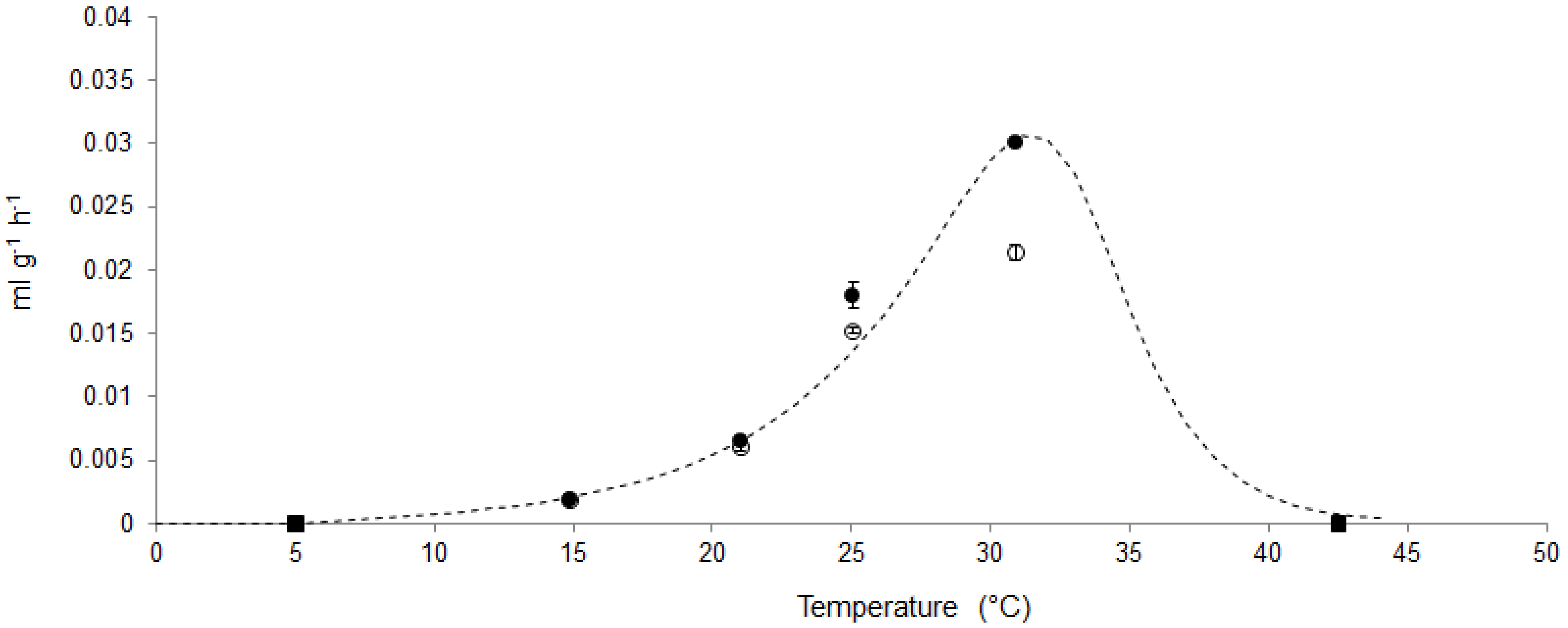

Figure 3.1 - Volumetric carbon dioxide production (open circles) and oxygen consumption (filled circles) of the Australian chelid turtle *P. umbrina*, measured at average temperatures of 14.9 °C (±0.0 °C), 21.0 °C (±0.1 °C), 25.1 °C (±0.1 °C) and 30.9 °C (±0.1 °C). The dotted line represents the predicted thermal performance curve of *P. umbrina*, with the upper and lower critical values (squares) derived from the literature (Lucas *et al*. 1963; Burbidge 1967). Values are means ± s.e. ($N = 32$, $n = 8$).

formulation from Kooijman (2010) so as to remain consistent with future intentions to integrate a DEB model into existing mechanistic models for the species (Mitchell *et al.* 2013). The leading phase of this curve is ascribed to the Arrhenius effect, whilst the declining side is attributed to the denaturation of enzymes once beyond the thermal optimum of the species (Sharpe & DeMichele 1977; Schulte *et al.* 2011). It was not possible to measure metabolic rates at either end of the critical thermal spectrum because *P. umbrina* is Critically Endangered (Burbidge *et al.* 2010) and it was important not to compromise the survival of turtles that were part of Perth Zoo's successful captive breeding program. Therefore, I constrained the curve at the lower and upper extremes by presuming instantaneous metabolic rate was zero at these points, based on information obtained from the literature (Lucas *et al.* 1963; Burbidge 1967). Whilst the critical thermal maximum for *P. umbrina* has been estimated (Burbidge 1981), the critical thermal minimum is not known and so the nominal critical minimum may have been overestimated. Many species of freshwater turtles are active at low temperatures (Ultsch 2006), and water temperatures in *P. umbrina* habitat have dropped below 10 °C on several occasions since 2009 (S. Arnall, unpublished data).

Behavioural observations support the suggestion that physiological performance declines beyond 30 °C, and that physiological performance is optimal between 25 °C and 30 °C. For example, using a water bath experiment, Leung (in Lucas *et al.* 1963) reported that when water temperatures were cooler than 14 °C or warmer than 30 °C *P. umbrina* would exit the water, and that rates of activity were highest at 26-28 °C. Similarly, using an ambient thermal gradient, Lucas (in Lucas *et al.* 1963) suggested that the preferred body temperature was likely to be between 28 °C and 32 °C. Moreover, the thermal response curve for adult *P. umbrina* described here was similar to a curve fitted to development rate data for *P. umbrina* embryos (N. Mitchell, unpublished data), providing confidence that my measurements and the resulting curve captured the peak performance temperatures and critical thermal limits of the species.

Despite spending most of its time in water, *P. umbrina* occasionally leaves water to bask, or to traverse land in order to move between swamps or seek out aestivation sites. In the case of females, turtles also leave the water to select suitable nesting locations and dig several ‘test’ nests before egg laying (Kuchling & DeJose 1989). While it is possible that my study animals may have commenced aestivation at higher test temperatures (e.g. 30 °C), it is unlikely as the metabolic response of *P. umbrina* closely resembled that of other turtle species for which data are available, including *Terrapene ornata* (Gatten 1974), *Chelydra serpentina* (Steyermark & Spotila 2000) and *Chersina angulata* (Setlalekgomo 2011) (Table 3.1). Field observations also show that animals may move location several times over the course of two or three days before settling into aestivation so it is likely that the test conditions were too brief to induce aestivation, even at higher temperatures. Comparative water-based measurements would be required to determine whether the reported standard metabolic rates were overestimated, particularly at 20 °C and 30 °C.

The calculated energetic requirements of *P. umbrina* were also consistent with those measured in other freshwater turtles (Litzgus & Hopkins 2003, and references therein). On the basis of the $\dot{V}O_2$ reported here, the total daily energy requirements for a 500 g (fasted) western swamp turtle at rest would be 3.8 kJ at 20 °C, which is similar to the requirements of another shortnecked semiaquatic Australian turtle, *Emydura macquarii* (5.4 kJ per day at 20 °C: Spencer *et al*. 1998). At 30 °C the estimate rises to almost 20 kJ per day, which would be further increased by the costs of swimming or walking (e.g. by 2.27 J $kg^{-1}m^{-1}$ and 5.97 J $kg^{-1}m^{-1}$, respectively, in *E. macquariii*; Baudinette *et al*.

2000). While the costs of feeding may be reduced towards the end of the wet season when swamps recede and prey concentrates in warm shallow water, patchy rainfall at the commencement of the wet season is likely to increase the energy demands of the turtle as they traverse land in order to move between swamps or aestivation sites. Therefore it is conceivable that under a warmer and drier climate the energy demands of *P. umbrina* will increase.

By redressing a key knowledge gap for *P. umbrina*, this study provides a foundation upon which to base a detailed mechanistic model that aims to define the thermodynamic niche of *P. umbrina* under future climates (Mitchell *et al*. 2013). DEB models have recently been integrated with standard biophysical models for terrestrial ectotherms, considerably expanding their predictive power (Kearney 2012). Importantly, this data facilitates the calculation of an Arrhenius temperature correction, which is vital in linking DEB and biophysical models. The spatially explicit predictions of the thermodynamic niche that are currently available (Mitchell *et al*. 2013) can now be expanded to encompass growth and reproduction, facilitating the determination of how survival and recruitment may be affected by future climates. For a species that is highly sensitive to abiotic factors across its entire life cycle, a coupled biophysical/DEB model will be a powerful tool for predicting the future impacts of climate change on population viability.

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CHAPTER FOUR

A DYNAMIC ENERGY BUDGET FOR THE WESTERN SWAMP TURTLE

PREFACE AND STATEMENT OF CONTRIBUTION

The construction of a dynamic energy budget (DEB) model (Kooijman 2010) represents a highly generalised approach for predicting the life history of species under different thermal, hygric, and nutritional conditions. Having obtained a rate-response curve in Chapter 3, my next aim was to produce a DEB model for *P. umbrina*. This chapter covers the development of the DEB model for the western swamp turtle, while validation (at the species' core habitat, Ellen Brook Nature Reserve) is presented in Chapter 5.

There have been several spatially-explicit models developed for the purpose of predicting the performance of the western swamp turtle under future climates (Mitchell *et al.* 2013; Dade *et al.* 2014, Mitchell *et al.* 2016; Bin Tarque 2017). These models (specifically those in Mitchell *et al.* 2013 and Bin Tarque 2017) have been useful for projecting hydrological periods and understanding how these periods, in conjunction with water temperature, affect the turtles' capacity to be active under a range of current and future climate scenarios. However, these models lack predictions of key life history parameters such as developmental times, growth rates, and potential reproductive outputs; each of which could be valuable for evaluating and predicting translocation success in novel locations.

The purpose of applying a DEB model to the western swamp turtle was thus, in part, to meet this shortfall. Motivated by the swamp turtles' sensitivity to energy availability (see Chapter 2), DEB modelling provided a formal way to quantify the mechanisms for the uptake and use of material by individuals, and to explore the energetic constraints of growth, development, and reproduction. This in turn could inform a biophysical model for *P. umbrina*, and be explored in relation to the novel thermal and hygric conditions generated by climate change (at Chapter 5). In addition, it also allowed predictions to be made about the species' biology that were previously unknown, such as maximal starvation time and lifespan.

Whilst there were numerous DEB models that could serve as a template for *P. umbrina* (add-my-pet 2017), none captured the unique life history of this species (i.e. the habitation of seasonally drying ephemeral wetlands, and associated aestivation). Thus this chapter aimed to describe and apply a modified DEB model that was able to capture periods of aestivation in the juvenile and adult.

Except as noted otherwise below, the work presented in this chapter is my own original work. The records used in the DEB model were collected by the Department of Biodiversity, Conservation and Attractions, Parks and Wildlife Service and the Perth Zoo during routine husbandry and monitoring of *P. umbrina* populations from 1963 to present. G. Kuchling, A. Burbidge and P. Fuller collected the historic data on wild individuals, and G. Kuchling and Perth Zoo staff (principally D. Burford, B. Durell and L. Shaw) collected the data for captive individuals. Any records not previously published were sourced, transcribed, collated, and analysed solely by me.

S. A. L. M. Kooijman provided the dynamic energy budget routine (DEBtool; freely available online[1]), and M. Kearney modified the standard DEB model to suit *P. umbrina*. I played only a minor role in writing the raw DEB model code, but I provided the datasets on which it was based and, together with M. Kearney, parametrised and ran

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[1] http://www.bio.vu nl/thb/deb/deblab/debtool/

the models. S. A. L. M. Kooijman provided feedback and guidance on various versions of these models, and assisted in the parameterisation of the ‘typical p_M’ model.

N. Mitchell provided temperature logger data for incubators at Perth Zoo, and these were analysed independently by me. I also measured temperatures for turtle holding ponds and aestivation pens across 2012 and 2013, and assisted Perth Zoo staff in taking the corresponding growth measurements pre-and post-aestivation.

I used B. Jenny’s ‘color oracle’ program to design my figures to be compatible with colour blindness (http://colororacle.org; Monash University, Australia).

I was the primary author of the chapter, with N. Mitchell, G. Kuchling, and M. Hipsey and M. Kearney providing supervisory feedback on its content.

This chapter is presented as submitted for publication (Arnall *et al.* 2018), with the exception of plural pronouns (we, us, our) which have been replaced by individual terms.

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4.1 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). 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 stochiometrically fixed pools. These three abstract pools are reserve (E, J), structure (structural volume; V, cm^3), 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 $\varkappa$ of the continually mobilised reserve is used to fuel somatic maintenance and growth (i.e. to build and maintain structure). The remaining energy ($1 - \varkappa$) 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 $1 - \varkappa$ allocation switches towards reproduction (and maturity maintenance). Henceforth, the majority of the $1 - \varkappa$ is allocated to a biomass component within the organism called the reproductive buffer, which has the same composition as reserve, and which empties periodically as gametes are released to the environment (Figure 4.1). Freshly-laid eggs are considered pure reserve, drawn from the reproduction buffer of the mother (Kooijman 2010).

This ‘$\varkappa$-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.* 2016; 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 I aim to produce a whole-of-life energy budget for the western swamp turtle using the $\varkappa$-rule DEB model, and explore what this implies about their capacity to face periods of starvation. Additionally, I 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.

4.2 METHODS

I 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

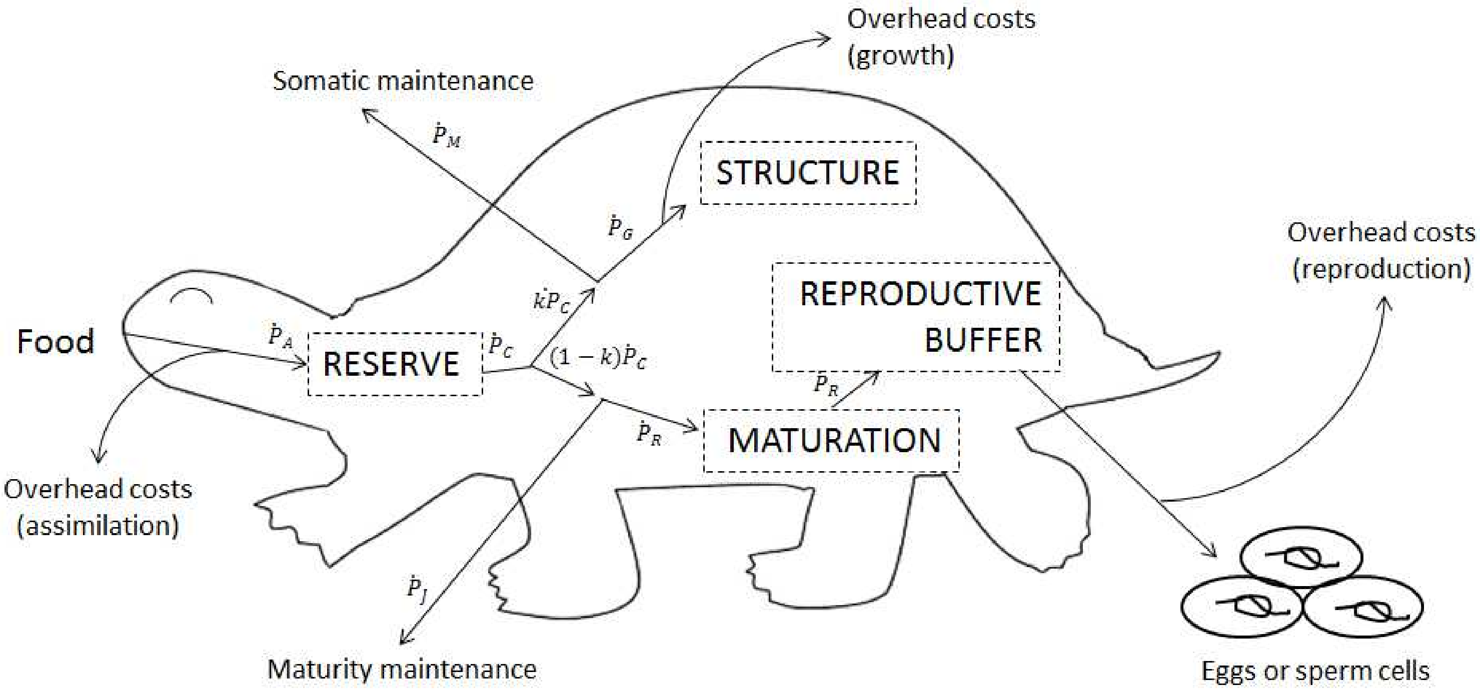

Figure 4.1 – Conceptual representation of the $\varkappa$-rule Dynamic Energy Budget model in *P. umbrina*, where arrows represent energy fluxes (in J day^{-1}) towards state variables (denoted by boxes). Notation is as follows: $\dot{P}_A$, assimilation rate; $\dot{P}_C$, mobilization rate; $\dot{P}_G$, structural growth; $\dot{P}_J$, maturity maintenance; $\dot{P}_R$, maturation; $\dot{P}_M$, somatic maintenance; $\varkappa$, kappa. Refer van de Meer (2006) and Sousa *et al.* (2008) for comprehensive descriptions of the standard DEB model.

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). I obtained these observations from individuals maintained in captivity since 1963 (Kuchling *et al.* 1992; Section 4.2.1). I then generated temperature corrections for these data (Section 4.2.2) 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 4.2.3 and 4.2.4). All modelling was completed in MATLAB® (The MathWorks™ Inc. USA) and I refer the reader to Kooijman (2010) for detailed particulars of the underlying DEB theory.

4.2.1 DATA OBSERVATIONS

I 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 (days) 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} (days) were sourced from captive husbandry records for 12 females that had hatched at Perth Zoo and had laid at least one clutch of eggs prior to 2012. 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 (SonoSite M-Turbo, and Toshiba SSA-320A/UI IM-320A). 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). 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} (days), 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, I 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.

To understand the effects of aestivation on turtle body condition and size, I 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 (± 0.01g).

4.2.2 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, I 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 4.2.3). To obtain a constant temperature equivalent (CTE; Orchard 1975) I 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 (Figure 4.2). I then converted the mean Arrhenius temperature correction factor to the respective temperature, and used this latter value as the CTE.

4.2.3 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

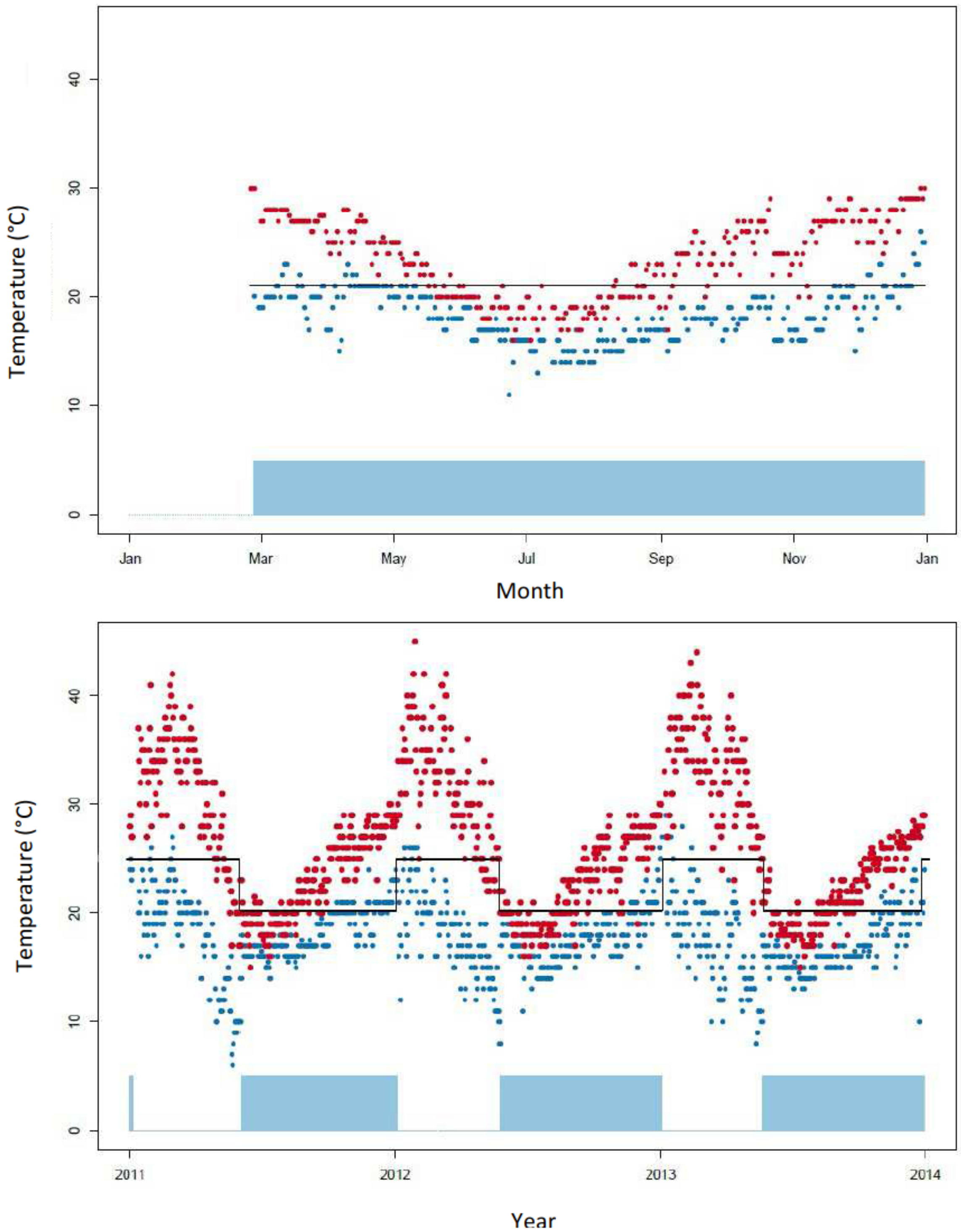

Figure 4.2 – Typical daily minimum (blue) and maximum (red) temperatures experienced by *P. umbrina* at the captive breeding facility at Perth Zoo (South Perth, Western Australia). The top panel shows the water temperatures of hatchling ponds in 2011 (commencing in March, when eggs typically hatch), while the bottom panel shows temperatures experienced by juveniles and adults. The blue bars show the wet season where the corresponding temperatures are daily maximum (red) and minimum (blue) water temperatures; in all remaining cases the temperatures are the air temperatures recorded in aestivation pens. Solid black lines depict the mean constant temperature equivalents.

sum of squared differences between the real observed values and the estimates through regression (Lika *et al.* 2011a, b). Completeness and mean relative error (MRE) were scored after Lika *et al.* (2011a), and I used the Nelder Mead simplex method (implemented in the ‘nmregr’ DEBtool routine) to search the parameter space.

I fitted the DEB model using the observational data from Section 4.2.1, giving all measures of length a greater weighting than measures of mass because turtles occasionally void their bladder on handling (Table 4.1a). I fitted the model in three ways, progressively altering the mechanisms for accommodating aestivation. In the first instance (model fit 1, hereafter termed ‘MF1’), I set f to 0.5 for all processes except egg development and oxygen consumption, to reflect the approximately half year where turtles are without food (where f is the scaled functional response, with values of 0 and 1 representing an absence of food, and saturated feeding conditions, respectively). Second, I 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, I 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, I 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}; Chapter 3) as follows:

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

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 °C = 20 + 273.15 K).

I estimated the T_A from the exponential phase of measurement (i.e. only 12 to 30 C; refer Figure 3.1 of Chapter 3) 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.

4.2.4 INCORPORATING AESTIVATION AND METABOLIC DEPRESSION INTO THE PARAMETER ESTIMATION PROCEDURE

For MF2 and MF3, I 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. Figure 4.3; where 10 of the 12 females used to fit the DEB model were

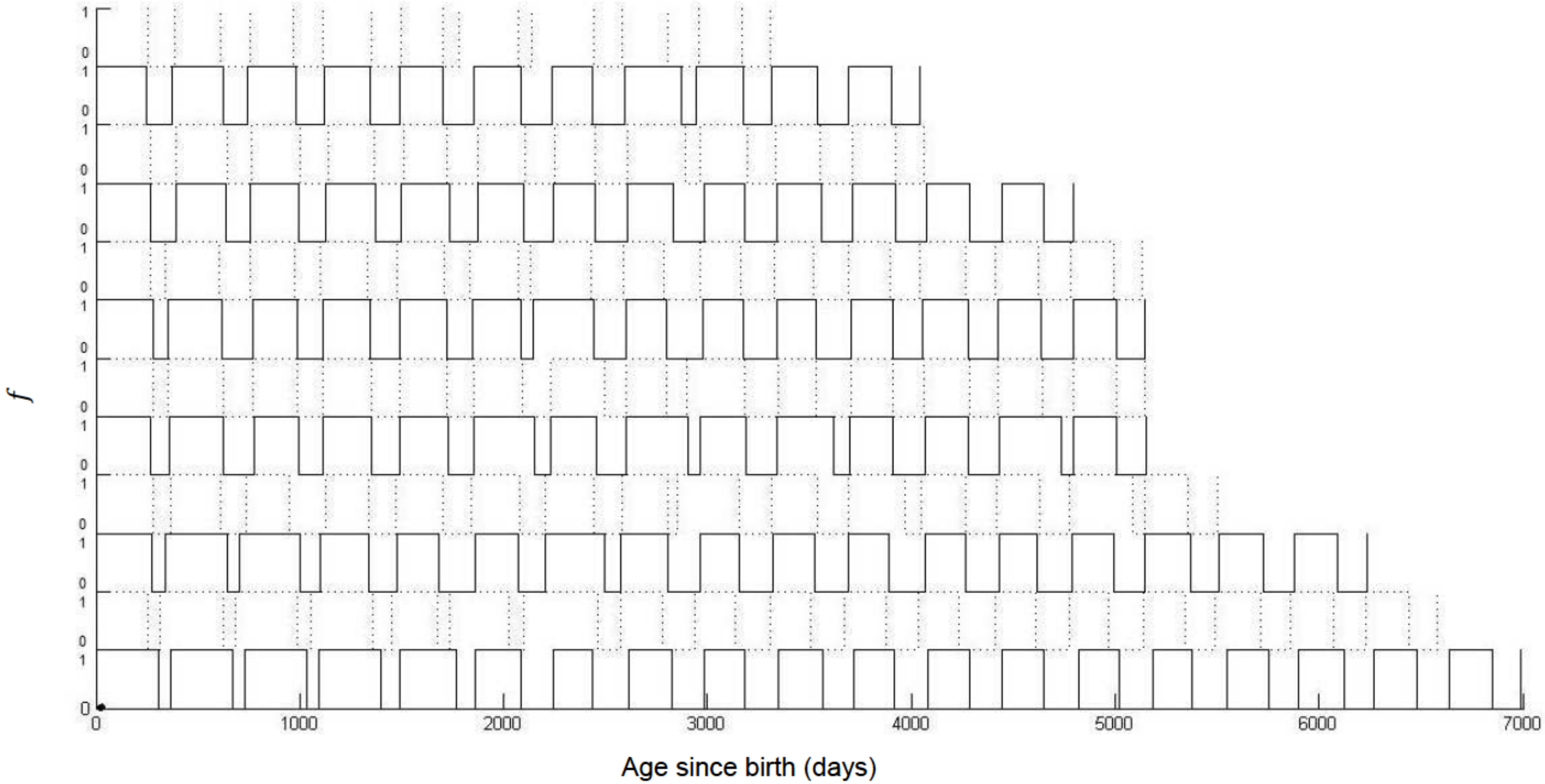

Figure 4.3 – Typical aestivation periods for *P. umbrina* at Perth Zoo. Each individual fluctuates between *f* of 0 and 1, denoting periods of starvation (during aestivation) and feeding *ad libitum* (during time spent in rearing ponds), respectively. Data for 12 female turtles are presented, with the switch days between *f* of 0 and 1 being shown by solid or dotted black lines for each alternate individual.

placed on public display at least once). For simplicity, I 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 ± 2.74 s.e.) and wild (mean 164.65 days ± 6.72 s.e.; S. Arnall, unpublished data) aestivation periods.

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, I 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, I 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:

$$\frac{de}{dt} = c_T v_2 \, \frac{(f - e)}{L}$$

where c_T is the temperature correction factor (see section 4.2.3), v_2 = v (where 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:

$$r = c_T v_2 \, \frac{(\frac{e}{L - 1})}{(\frac{L_m}{e + g})}$$

where L_m is the maximum structural length, and g is the energy investment ratio ($[E_G]/\varkappa[E_m]$; with $[E_G]$ being the volume specific cost of structure and $\varkappa$ 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:

$$\frac{de_H}{dt} = c_T(1-\varkappa)e\left(\frac{v_2}{L-r}\right) - e_H\left(k_{J_2} + r\right)$$

where e_H is the scaled maturity density, and $k_{J_2} = k_J$ (with k_J being the maturity maintenance rate coefficient).

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

$$\frac{de_R}{dt} = c_T\ \frac{(1-\varkappa)e\left(\frac{v_2}{L-r}\right) - e_H^p\ k_{J_2}\, {L_p}^3}{L^3 -\ re_R}$$

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, I 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, I additionally applied a metabolic depression factor to conductance and the maturity maintenance rate coefficient during the 182-day aestivation period such that:

$$v_2 = v\, s_M$$

and

$$k_{J_2} = k_J\, s_M$$

where s_M is the metabolic depression factor (0 to 1). It was not necessary to apply the depression factor to the rate parameters $\{\dot{p}_{Am}\}$ (maximum surface-area-specific assimilation rate) and $[\dot{p}_M]$ (volume-specific somatic maintenance rate) because they remained in a constant ratio within the parameters 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/.

4.2.5 COMPARISONS TO WILD *P. UMBRINA* AND OTHER SPECIES

I 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, I 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, I 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, I 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).

4.3 RESULTS

Primary DEB parameters for *P. umbrina* as derived from the estimation procedures are compared in Tables 4.1a and b. The MF1 and MF2 model fitting strategies failed to capture the dynamics of *P. umbrina* growth, and overestimated length and mass in both cases. The MF3 strategy best captured the growth of western swamp turtles in terms of both mass and length. 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. The MF3 strategy was also able to replicate mass

Table 4.1 – **a)** Observed and estimated zero-variate data for *P. umbrina*, including assigned weightings, and **b)** 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). 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).

a) Zero-variate Data	**Observed**	**Expected**			**Wt.**	**Refer**
		MF1	**MF2**	**MF3**		
a_b, age at birth (days)	153	179.3	26.4	55.0	-	Eq. 2.39
a_p, age at puberty (days)	3767	1443	4775	2960	-	Eq. 2.53
a_m, life span (days)	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 (# day^{-1})	0.0137	0.01063	0.0000	0.0089	-	Eq. 2.58

b) Parameter Values	**Unit**	**MF1**	**MF2**	**MF3**	**Source**
z, zoom factor	-	10.5	2.7	2.7	Estimated
δM, shape coefficient	-	0.39	0.13	0.20	Estimated
v, energy conductance	cm d^{-1}	0.01	0.10	0.01	Estimated
$\varkappa$, allocation fraction to soma	-	0.70	0.18	0.72	Estimated
$\varkappa_R$, reproduction efficiency	-	0.95	0.95	0.95	Default
$[\dot{p}_M]$, specific somatic maintenance	J d^{-1} cm^{-3}	20	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	J cm^{-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	Chapter 3
T_L, lower bound for T_A	K	278.15	278.15	278.15	Chapter 3
T_H, upper bound for T_A	K	304.15	304.15	304.15	Chapter 3
T_{AL}, value of T_A below lower bound	K	50000	50000	50000	Chapter 3
T_{AH}, value of T_A above upper bound	K	90000	90000	90000	Chapter 3
s_M, metabolic depression factor	-	NA	NA	0.0518	This study

loss over aestivation well, with an average loss of 7.73 ± 0.89g (as compared to the average mass loss of 11.9 ± 1.25 g recorded for the 160 individuals measured at Perth Zoo). The largest discrepancy between observed and predicted values across all DEB models was in metabolic rate (Figure 4.4; but see Section 4.4 below).

The MF2 strategy greatly overestimated length even when manually minimising the zoom parameter. Any values for $\varkappa$ greater than 0.18 resulted in the individual not reaching puberty, and with $\varkappa$ 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% ± 2.6 s.e.) but not in length (0.2 mm ± 0.0 s.e.) over the aestivation period, so the predictions from MF2 were unrealistic.

Consistent with their ecology (i.e. a necessity to reach a suitable size to survive their first summer aestivation event), turtles had very rapid growth in their first year. Wild individuals grew more slowly (0.77 mm year^{-1}) than did captive *P. umbrina* (0.97 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 (Figure 4.5b) but slightly overestimated mass (Figure 4.5a).

The primary parameters of *P. umbrina* (as taken from MF3) were compared in Table 4.2 to those of five other Chelidae for which DEB models have been produced. *umbrina* had much higher volume-specific somatic maintenance costs (504.1 J d^{-1} cm^{-3}) than any other Chelidae (range 12.4 - 24.0 J d^{-1} cm^{-3}). Their Arrhenius temperature was

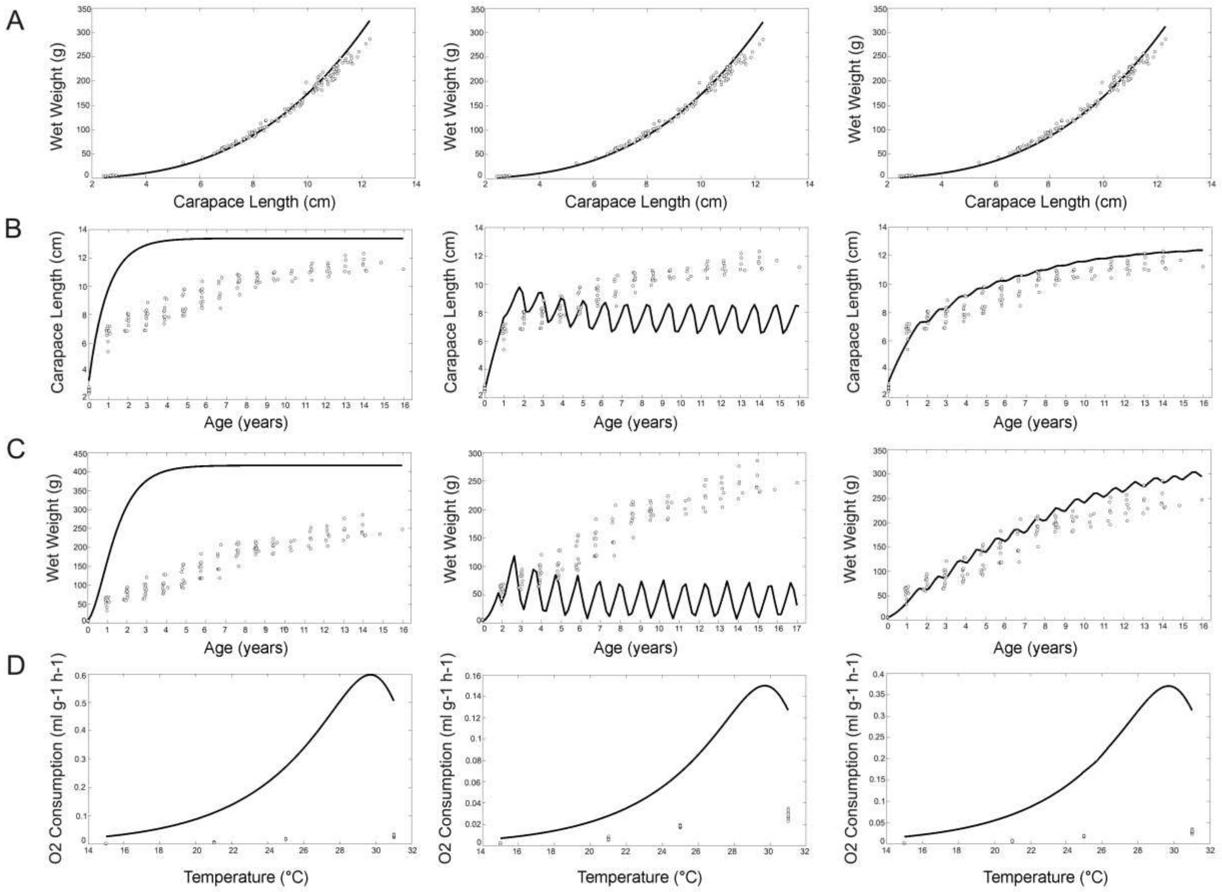

Figure 4.4a-d – Comparisons between model predictions (solid lines) and observed data (dots) for *P. umbrina* under the three different model fitting strategies. **(a)** shows the length-weight relationship, **(b)** shows carapace length as a function of age, **(c)** shows wet mass as a function of age, and **(d)** shows metabolic rate with temperature. The left, middle and right columns show MF1, MF2 and MF3, respectively. Higher resolution outputs are provided in Appendix D.

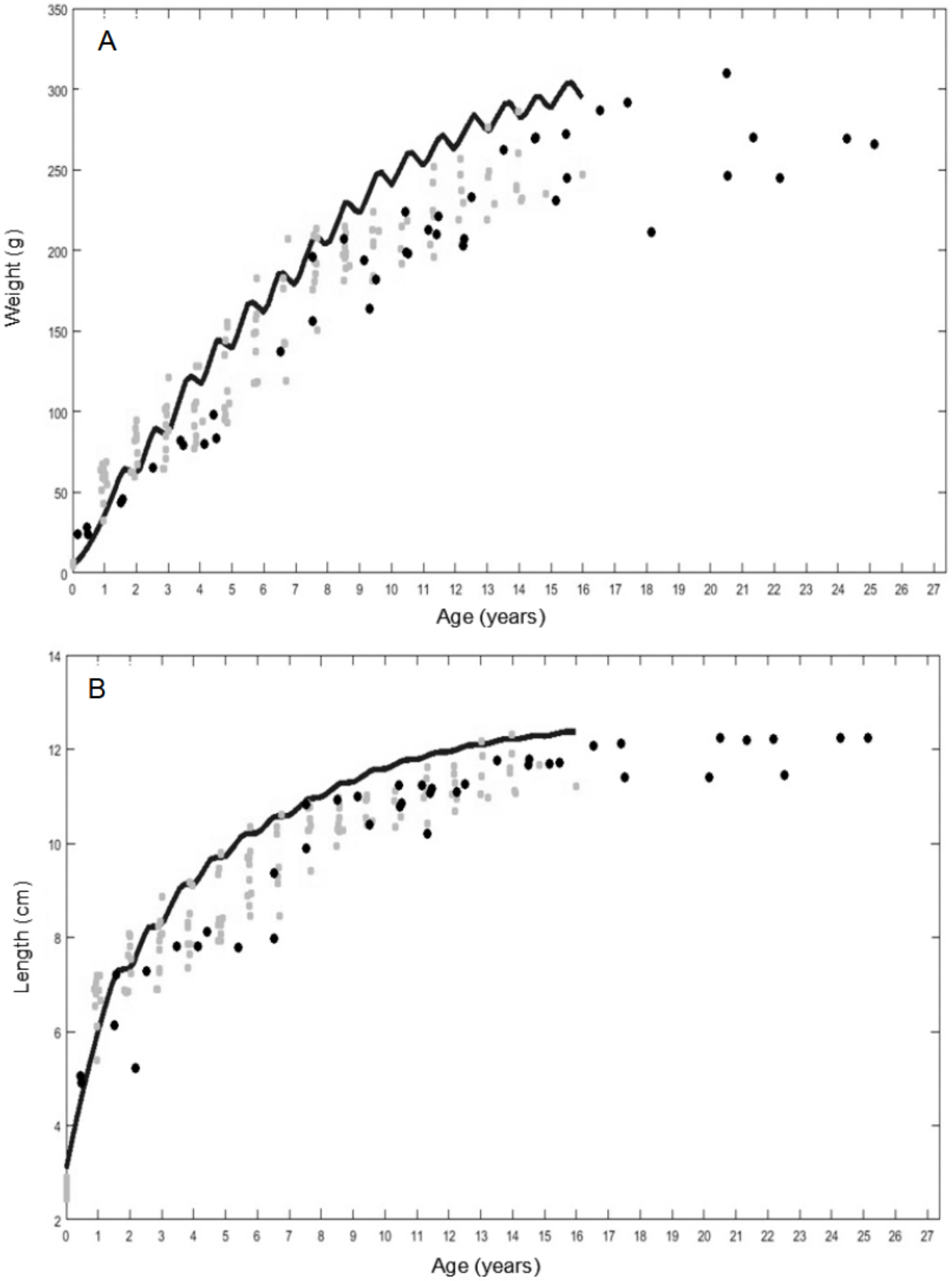

Figure 4.5 – Comparisons of wild *P. umbrina* growth (black dots) to the DEB model predictions (solid line; model fitting strategy MF3) and observed data (grey dots) for captive-bred *P. umbrina*. **a)** shows wet mass as a function of age, and **b)** shows carapace length as a function of age.

Table 4.2 – 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 (Emydura macquarii)*	*Mata Mata (Chelus fimbriata)*	*Brazillian Snake-necked Turtle (Hydromedusa maximiliani)*	*Northern Snapping Turtle (Elseya dentata)*	*Northern Snake-necked Turtle (Chelodina oblonga)*	*Western Swamp Turtle (Pseudemydura umbrina)*
v, energy conductance	cm d^{-1}	0.061	0.014	0.016	0.019	0.016	0.0125
$\varkappa$, allocation fraction to soma	-	0.736	0.864	0.826	0.731	0.820	0.722
$[\dot{p}_M]$, vol-specific somatic maintenance	J d^{-1} 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

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, $[\dot{p}_M]$ 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 $[\dot{p}_M]$ 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 (Figure 4.6; Appendix D).

4.4 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

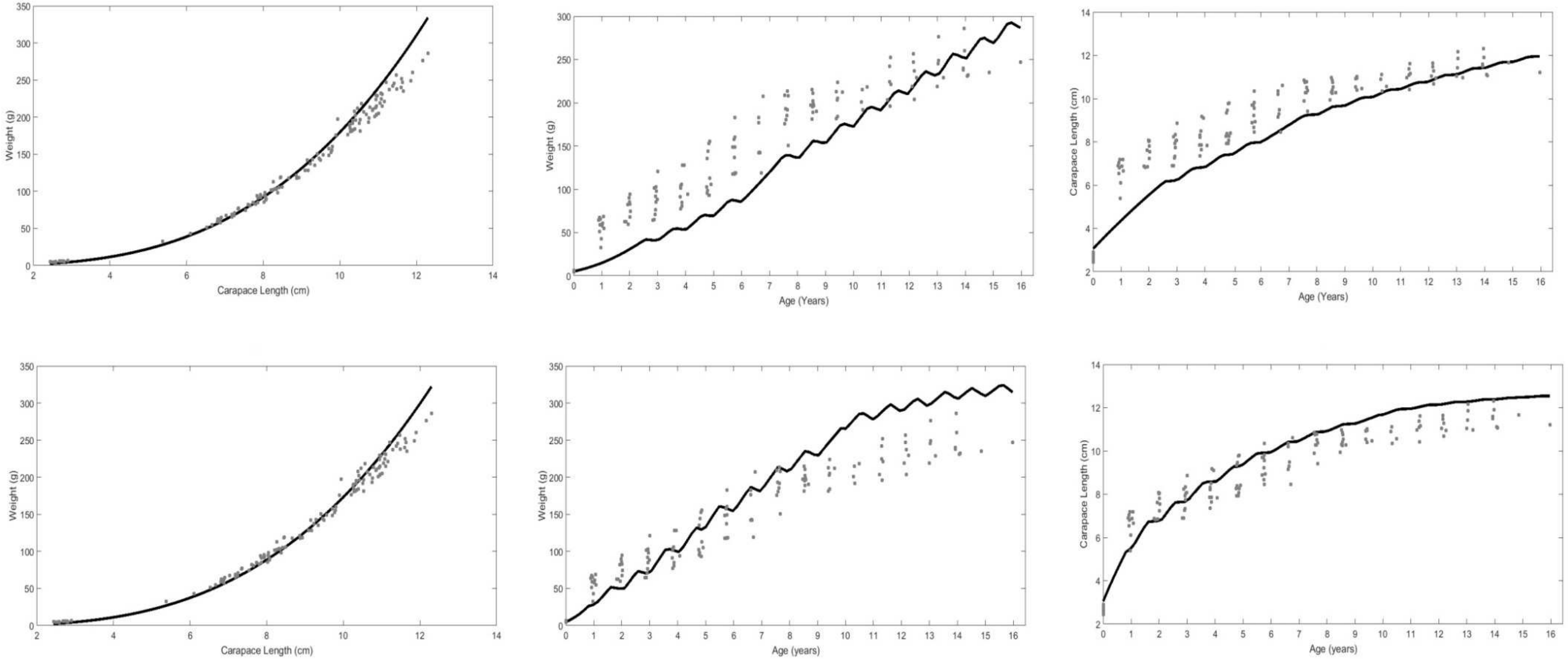

Figure 4.6 – Western swamp turtle DEB MF3 parameterised with a somatic maintenance value typical of testudines (18.96 J d^{-1} cm^{-3}; top panels; MRE = 0.542), showing the mass length relationship (left), wet mass with time (middle), and carapace length with age (right). The corresponding results from MF3 ($[\dot{p}_M]$ of 500.4 J d^{-1} cm^{-3}) are provided for comparison (bottom panels; MRE = 0.781). Further outputs are provided in the supplementary materials (Appendix D).

during aestivation (Ligon & Peterson 2002, and references therein). My 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 under warm summer conditions (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 unknown, but other semi-aquatic species that inhabit ephemeral wetlands can reduce their metabolic rate by around 50 – 70 % during dry aestivation events (from Table 6, Guppy & Withers 1999). A value of around 50 % was a satisfactory match to the observed life history data for *P. umbrina*. Aestivation events of over one year have been recorded in other 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). My 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[2]. This suggests that, for the female individuals incubated at 24 °C in my model, embryonic maturity would be reached after approximately 105 days, leaving an approximately seven-week aestivation period (from Figure 2, Mitchell *et al.* 2016). 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 (± 23 days; range 33 – 94 days; n = 6; N. Mitchell, unpublished data), which is equivalent to an approximately 9 week aestivation period. As age at birth was estimated at around 50 days in my model, the addition of a 94-day aestivation period shifts the estimate to 144 days, which is similar to the observed value of 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 Chapter 3 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 Chapter 3 for why this is unlikely). The second is that the disparity

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[2] Here I 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.

could represent the difference between resting metabolic rates, as measured in Chapter 3, 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 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 $[\dot{p}_M]$ 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 $[\dot{p}_M]$ in the AmP collection presently (1000 J d^{-1} 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 $\varkappa$, might be an adaptation to being long-lived while inhabiting ephemeral wetlands where resource availability varies from year to year.

With individual survival over decades of high importance for the species, how are energetic needs balanced with the costs of reproduction? Vitellogenesis, the allocation of resources to reproduction, takes many months in turtles (Kuchling 1999) and starts in *P. umbrina* during aestivation, over half a year prior to oviposition (Kuchling and Bradshaw 1993). At that time it cannot be predicted if a resource bloom (food availability in early spring) 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 pre-ovulatory 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.

This study presents the first set of bioenergetic information for *P. umbrina*. The DEB model offers a tool to explore how changing environmental conditions might affect growth and reproduction in this species, particularly under novel environments. 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 its conservation (Burbidge *et al.* 2010). Existing models developed for this purpose (Mitchell *et al.* 2013; Dade *et al.* 2014; Mitchell *et al.* 2016, Bin Tarque 2017) lack spatially-explicit predictions of key life history parameters such as development times, growth rates, and potential reproductive outputs. Integration of this DEB model with a mechanistic biophysical modelling platform (e.g. Kearney *et al.* 2013; Schwarzkopf *et al.* 2016) should help optimise future translocation programs for this endangered turtle. While not explored here, this DEB model could also 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).

Validation of the DEB model, ideally by hindcasting growth against historic wetland periods in the wild, is recommended before its potential integration with either population-level, or mechanistically based niche models – the latter of which have already been developed for the species (e.g. Mitchell *et al.* 2013; Mitchell *et al.* 2016).

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CHAPTER FIVE

PREDICTING THE GROWTH, REPRODUCTION, AND SURVIVAL OF *P. UMBRINA* UNDER CLIMATE CHANGE

PREFACE AND STATEMENT OF CONTRIBUTION

The aim of this final data chapter was to predict the performance of the western swamp turtle under climate change, to assist in developing an assisted migration strategy for the species, and to better understand the mechanisms of their vulnerability to climate change. Correlative species distribution models would be inappropriate for assessing future assisted migration sites for *P. umbrina*, principally because of the restricted distribution of this species, and thus the limited statistical power from which to draw inferences (refer Chapter 1). Instead, here I parametrise and explore an energetically-coupled, (mechanistic) biophysical niche model to examine how growth, survival, and reproduction might progress under climate change – both within *P. umbrina*'s current range, and at five potential assisted migration sites.

The stepwise outputs from previous chapters (specifically the thermal performance curve from Chapter 3, and the dynamic energy budget model from Chapter 4) formed the basis for this modelling work. Validation was performed by examining temperature, growth, and reproduction data from individuals at Ellen Brook Nature Reserve (from 1972 to present), alongside the environmental data presented at Chapter 2. Predictions for *P. umbrina* growth, reproduction, and survival are presented in this chapter for current, 2050, and 2070 climates, while recommendations resulting from these predictions are provided in Chapter 6.

Except as noted otherwise below, the work presented in this chapter is my own original work.

M. Kearney developed the microclimate, ectotherm, and DEB modules of the mechanistic modelling software NicheMapR (as modified from W. Porter's 'Niche Mapper™'), which was the platform used for generating the predictions in this chapter. Importantly, M. Kearney created the wetland microclimate module, and optimised its performance against the wetlands of Ellen Brook Nature Reserve. I played no role in the generation or parametrisation of the wetland model other than providing the temperature and hydroperiod plots against which it was tested (as at Chapter 2). M. Kearney provided supervisory advice on how to parametrise the ectotherm model, but I ran all the ectotherm models and explored the outputs independently.

In testing the model, I used unpublished data collected by the Department of Biodiversity, Conservation and Attractions, Parks and Wildlife Service from 1972 to 2015. G. Kuchling, A. Burbidge and P. Fuller collected the historic data on these wild individuals. Any records not previously published were sourced, transcribed, collated, and analysed solely by me.

The map shown in Figure 5.2 originated from the honours thesis of N. Rodriguez (Rodriguez 2015). This map was generated by N. Rodriguez, and subsequently modified by me to appear in this thesis. I used B. Jenny's 'color oracle' program to design my figures to be compatible with colour blindness (http://colororacle.org; Monash University, Australia).

I was the primary author of the chapter, and N. Mitchell, G. Kuchling, M. Kearney and M. Hipsey provided supervisory feedback on the content.

Reference

Rodriguez N. (2015). Modelling embryonic development under climate change to select sites for the assisted colonisation of the western swamp turtle (Pseudemydura umbrina). Honours thesis. School of Animal Biology, University of Western Australia, Crawley, Australia.

5.1 INTRODUCTION

In ectotherms, the speed at which an individual grows can have an enormous influence on fitness because traits associated with reproduction can be size-dependent (Abrams *et al.* 1996; Gotthard 2001; Schluter 2001). For example, reproduction occurs earlier in larger Eastern fence lizards than smaller ones (*Sceloporus undulatus*; Aldolph & Porter 1996), the onset of sexual maturity is determined by size in the common toad (*Bufo bufo;* Reading 1991), and in years of poor rainfall, small female desert tortoises (*Gopherus agassizii*) are less likely to lay eggs than larger ones (Curtin *et al.* 2009). Unlike endothermic species that maintain thermal homeostasis independent of their surroundings, ectotherms rely on microclimatic heterogeneity to regulate their body temperature (Deutsch *et al.* 2008; Kearney *et al.* 2009). This makes them vulnerable to climate change in a different manner to endotherms, because their ability to gain energy is dependent on their surrounding environment (Buckley *et al.* 2015). For example, if the immediate environment of an ectothermic species does not allow it to reach a body temperature that permits foraging, its time available for feeding is reduced because it must thermoregulate to a temperature that permits feeding (if suitable microclimates are available) or rest (if they are not; Seebacher 1999; Buckley *et al.* 2015). This is why, in part, so many ectothermic species face declines or extinction under climate change: as suitable microclimates become limiting, individuals will find it increasingly difficult to meet their energetic needs, which in turn will have negative impacts on species' growth, reproduction, and survival rates.

For ectothermic species that are unable to track their preferred climatic niches due to dispersal barriers (i.e. species that can only remain *in-situ* under future climates), phenotypic plasticity (changes in physiological or morphological traits within a life span), microevolution (genetic changes over many lifespans), or human intervention (e.g. implementation of conservation measures) can improve chances of local persistence under a changing climate (Fuller *et al.* 2010). Of these strategies, human intervention is likely to be of most benefit to those species with life history traits that impede rapid adaptation (e.g. slow maturation and long generation times; Salamin *et al.* 2010), and/or those species that have poor or unknown phenotypic flexibilities. Human-facilitated dispersal of individuals into climatically suitable habitats (an intervention strategy termed 'assisted migration'; Hällfors *et al.* 2014) aims to assist species with these characteristics (see Hewitt *et al.* 2011, Seddon *et al.* 2015 and Javeline *et al.* 2015 for review). Ectotherms, which constitute a large portion of global terrestrial biodiversity (Wilson 1999), are likely to be key recipients of assisted migration due to the high thermal sensitivity of their physiological needs, and thus their high vulnerability to rapid climate change (Gibbons *et al.* 2000; Huey *et al.* 2009; Huey *et al.* 2012).

Assisted migration has been proposed for the Critically Endangered western swamp turtle (*Pseudemydura umbrina*), which is threatened by climate change, is unable to disperse due to loss of connecting habitat, and is unlikely to adapt *in-situ* (Chapter 2). This species is thermally sensitive (Chapter 4), and climate change is predicted to limit its foraging potential due to both increasing temperatures and declining seasonal rainfall (Chapter 2). Several spatially-explicit models have been produced for developing an assisted migration strategy for the swamp turtle (Mitchell *et al.* 2013; Dade *et al.* 2014, Bin Tarque 2016; Mitchell *et al.* 2016; Chapter 4), and all have facilitated progression towards the identification of climatically suitable recipient sites. However, all current models lack forecasts of life history responses such as growth rate, age at maturity, and reproductive output, which prevents them from being used to predict population success (e.g. Gotthard 2001). Because of this, many questions remain unresolved regarding the long term suitability of current habitats, the suitability of potential assisted migration sites, and the consequences of different thermoregulatory and foraging behaviours on the turtle's fitness under future climates. Here I present an energetically-based biophysical niche model for *P. umbrina*, and test its ability to simulate current and historic conditions in the natural habitat at Ellen Brook Nature Reserve. I then impose three climate scenarios to the simulations to assess the swamp turtle's capacity to persist under a hotter and drier climatic future. I specifically ask: 1) at what point does the current core habitat for *P. umbrina* (Ellen Brook Nature Reserve) become climatically unsuitable?; 2) how suitable are candidate assisted migration sites to the south of Ellen Brook Nature Reserve?; and 3) what thermoregulatory strategies best benefit survival, growth and reproduction at these locations?

5.2 METHODS

5.2.1 STUDY ANIMAL

The western swamp turtle is a highly threatened (Critically Endangered; TSSC 2004; IUCN 2015) semi-aquatic turtle endemic to Western Australia. It was formally described in 1901, not recorded again until 1953, and then existed at estimated abundance of <50 – 250 individuals until captive breeding became successful in the late 1980s (Kuchling & DeJose 1989; TSSC 2004). The turtle occupies ephemeral wetland swamps, where it spends the wet winter/spring season feeding, growing and mating, and the dry summer/autumn season aestivating under leaf litter or in natural tunnels formed in the ground (Burbidge 1981; Chapter 1). The bioregion it inhabits is expected to undergo a 40 % reduction in rainfall with up to a 5 °C increase in temperature by 2070 (Pearce *et al.* 2007; Cai *et al.* 2009; CSIRO 2009a; CSIRO 2009b).

5.2.2 ENVIRONMENTAL MODEL

The microclimate routine of the mechanistic niche model 'NicheMapR' (https://github.com/mrke/NicheMapR/releases) was used to predict the range of microclimates available to *P. umbrina*. These microclimates were in turn used to estimate the activity and body temperature of individual turtles, which when integrated with a Dynamic Energy Budget model (DEB, Kooijman 2010; Chapter 4 and 5.2.3) allowed a mechanistic prediction of growth, reproduction and survival under various climate scenarios. In brief, NicheMapR (Kearney & Porter 2017) is an R implementation of the biophysical models originally developed by Porter and colleagues (Porter *et al.* 1973) which generate predictions of heat, water, energy, and activity budgets of an organism, based on its behavioural, morphological and physiological constraints, and its surrounding environment (i.e. its microclimate; Porter & Mitchell 2006; Porter *et al.* 2010; Kearney *et al.* 2013).

The microclimate model was driven with data from a historical (1990-2009) continental-wide 0.05° grid (~5 km) of daily minimum and maximum temperature, vapour pressure, rainfall, and daily solar radiation, available through the Australian Water Availability Project (Raupach *et al.* 2009), and following Kearney *et al.* (2014). In addition, hourly wind speed was derived from a gridded dataset of daily mean wind speed (McVicar *et al.* 2008), assuming that the maximum wind speed was double, and that the minimum wind speed was half, the mean value respectively. Hourly microclimate predictions of air temperature (°C), relative humidity (%), wind speed (m/s), zenith angle of the sun (°), solar radiation (W/m^2), sky radiant temperature (°C), and day length (hours) were generated at a reference height of 1.2 m for the years 1972 to 2015, to cover the timespan for which historical *P. umbrina* data were available (Chapter 2; and where the reference height approximates the height of local weather stations; Kearney *et al.* 2014). For estimates of air temperature, wind speed, and humidity at the local (animal) level, I specified an animal height of 3 cm (Chapter 4), and a shade range of 0-90 %.

A wetland environment was then simulated by invoking NicheMapR's soil moisture model, which was calibrated to Ellen Brook Nature Reserve (the current core habitat of *P. umbrina*) using water depth data from 1972-2015 (Chapter 2). The soil moisture model simulated infiltration, transpiration, and evaporation after Campbell (1985), and allowed the depth of water pooling on the surface to be computed, which I used to approximate a natural wetland environment. Daily rainfall was set to be evenly distributed through the day, and was then multiplied by a factor (4.5) to create a catchment that matched observed historic hydroperiods. A maximum pooling depth of 750 mm (greater than is observed in the wild; Burbidge 1981) was necessary to adequately capture the boundaries of the wetland dynamics (values below this underestimated the hydroperiod duration). I assumed that the saturated soil temperatures would approximate water temperatures, and I compared this against water temperatures measured in the field (5.2.4). Substrate was set to a 10 % sand and 90 % clay mix ('heavy clay') to approximate the claypan underlying Ellen Brook Nature Reserve (Bin Tarque 2016), with soil bulk density set to 1.4 Mg/m^3. The hydraulic properties for this mixture of sand and clay were derived from the 'pedotransfer' function of Cosby *et al.* (1984). The solar absorptivity of the pond was set using Fresnel's reflection law (Gates 1980), and a dry substrate solar reflectivity of 20 % was specified following Mitchell *et al*. (2016) to approximate the albedo of wetted soils.

5.2.3 ANIMAL MODEL

I used the DEB coupled ectotherm model within NicheMapR to simulate the growth, maturation, reproduction, and survival of western swamp turtles at Ellen Brook Nature Reserve, and five candidate assisted migration sites. Parameters for this model are listed in Table 5.1. Most parameters were sourced from Chapter 4, but the behavioural routine originated from Mitchell *et al.* (2013), which in turn was based upon thermal preference data collected for *P. umbrina* in 1963 (Lucas, in Lucas 1963).

Following Mitchell *et al.* (2013), I explored three behavioural scenarios to understand how each scenario could shape growth and reproduction under different climates. In each behavioural routine, the simulated turtle selected a microhabitat that defended its preferred body temperature (T_p; the temperature around which the turtles would seek to regulate). When water was present, and in hourly time steps, simulated turtles would become active at their voluntary thermal minimum temperature (VT_{min}), and forage when their body temperature remained above this but below their VT_{max} (the latter being the temperature at which turtles would leave the water due to warm temperatures). If body temperature fell outside of this range they would become inactive. However, under two routines, simulated individuals could bask in terrestrial conditions to raise their body temperature and counter the low water temperatures experienced. The 'minimal basking' scenario allowed turtles to bask when water temperatures fell below the VT_{min}. Individuals in this scenario were preferentially set to forage, but were able to raise body temperatures when conditions were too cold to permit feeding. The 'maximal basking' scenario represented a situation where basking was preferentially selected over foraging (i.e. turtles would always seek out the warmest thermal environment above the VT_{min}, which would usually be out of the water). This situation assumed that only very short bouts of foraging in the water were necessary to fill the gut, after which the turtles would bask to maximise assimilation rates. For both basking scenarios, if there were no

Table 5.1- Parameters for the biophysical model of *P. umbrina*.

Ectotherm Model Parameters			Dynamic Energy Budget Model Parameters		
Proportion of surface area acting like a free water surface (%)	1	Default	z, zoom factor (-)	2.7	Chapter 4
Temperature difference between expired and inspired air (%)	0.1	Default	δ_M, shape correction factor (-)	0.2	Chapter 4
Configuration factor to substrate (%)	40	Default	v, energy conductance (cm day^{-1})	0.014	Chapter 4
Configuration factor to sky (%)	40	Default	κ,allocation fraction to soma (-)	0.7	Chapter 4
Proportion of body surface area in water while basking (%)	30	Mitchell *et al.* (2013)	$[p_M]$, somatic maintenance (J cm^{-3} day^{-1})	500.8	Chapter 4
Reflectance of animal (-)	1	Assumed	$[E_G]$, cost of structure (J cm^{-3})	7023	Chapter 4
Emissivity of animal (-)	1	Default value	E_H^b, maturity at birth (J)	2486	Chapter 4
Minimum and maximum solar absorptivity (%)	0.90	Mitchell *et al.* (2013)	E_H^p, maturity at puberty (J)	5.33E+05	Chapter 4
Density of flesh (kg/m3)	1000	Default value	κ_X, digestion efficiency (-)	0.80	Default
Specific heat of flesh (J kg-K)	4, 185	Default value	κ_R, reproduction efficiency (-)	0.95	Default
Thermal conductivity of flesh (W/mC)	0.5	Default value	$[E_s^m]$, maximum specific stomach energy (J cm^{-3})	372.06	Estimated
			X_K, half saturation constant (J ha^{-1})	365	Assumed

Behavioural Parameters					
VT_{min}, minimum foraging temperature (°C)	14	Lucas (1963)	d_V, density of structure (g cm^{-3})	0.3	Assumed
VT_{max}, maximum foraging temperature (°C)	28	Lucas (1963)	W_V, molecular weight of structure (g C-mol^{-1})	23.9	Default
T_p, preferred temperature (°C)	27	Lucas (1963)	μ_X, chemical potential of food (g J-mol^{-1})	525 000	Default
CT_{min}, critical thermal minimum (°C)	1	Assumed	μ_E, chemical potential of reserve (g J-mol^{-1})	585 000	Default
CT_{max}, critical thermal maximum (°C)	42.5	Burbidge (1967)	μ_V, chemical potential of structure (g J-mol^{-1})	500 000	Default
Activity phase	Diurnal	Burbidge (1981); Mitchell *et al.* (2013)	μ_p , chemical potential of faeces (g J-mol^{-1})	480 000	Default
Retreat underground	To depth of 1m	Kuchling unpublished data; Mitchell *et al.* (2013)	$\varkappa_{XP}$,fraction of food energy into faeces	0.1	Default
Shade availability (%)	0-90 %	King *et al. (*1998); Mitchell *et al.* (2013)	T_A, Arrhenius temperature (K)	19731	Chapter 4
			T_L, lower tolerance temperature (K)	278.15	Chapter 4
			T_H, upper tolerance temperature (K)	304.15	Chapter 4
			T_{AL}, lower bound for T_A (K)	50000	Chapter 4
			T_{AH}, upper bound for T_A (K)	90000	Chapter 4

suitable basking microclimates available (i.e. terrestrial microclimates were below VT_{max}) turtles would remain inactive in the water until the next hourly time-step, when they could re-surface to seek a basking microclimate again. The final basking scenario (‘no basking’) maximised the time turtles spent in the water by preventing individuals from basking at all (Figure 5.1).

Outside of the wet period and during aestivation, turtles were simulated to shelter in burrows where they could thermoregulate by seeking different depths up to a maximum of 1 m. For example, at low ambient temperatures the turtle would aestivate near to the surface, while at high ambient temperatures they could select an increased depth that buffered the warmer conditions. This reflects behavioural observations of *P. umbrina* aestivating in the wild (G. Kuchling, pers. comm.). I assumed a shade value of 90 % given that aestivation sites in the wild are often located under shrubs and small trees (Mitchell *et al.* 2013). Finally, an individual was simulated to die if the critical thermal minimum (CT_{min}) or maximum (CT_{max}) was exceeded (though note, these values actually represent the loss of righting response and not lethality; Lutterschmidt & Hutchinson 1997).

5.2.4 MODEL VALIDATION USING FIELD DATA

The statistical methods for testing model predictions against field data are outlined in 2.5.7 (data analysis) below. Microclimate predictions were compared to meteorological data collected by a remote weather station (Inmarsat 2022E; Unidata, Western Australia), logging at 15 minute intervals since February 2009. The weather station was situated at the longest standing pond within Ellen Brook Nature Reserve, where water temperatures were measured with a linear temperature probe positioned in the deepest part of the pond.

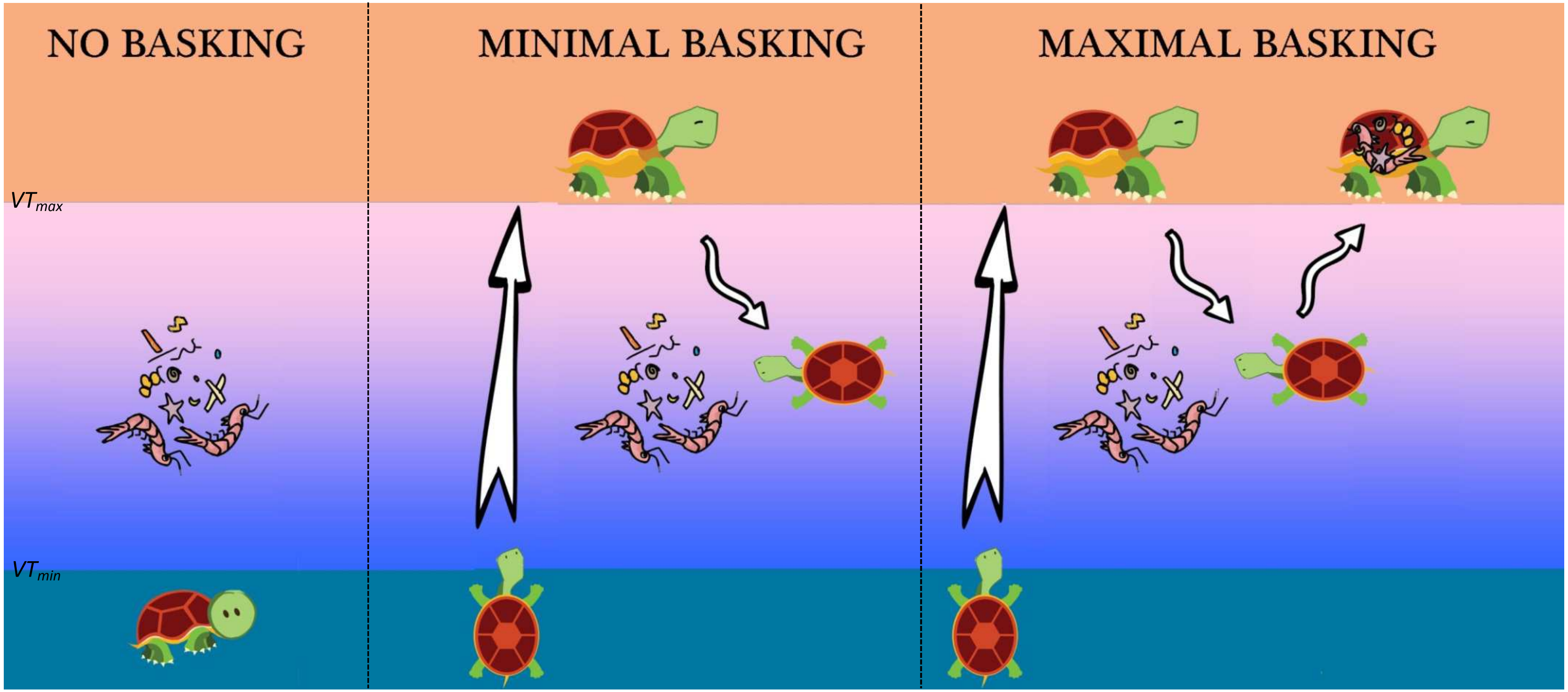


Figure 5.1 – Schematic representing the three user-defined basking options available to a simulated cold western swamp turtle when its body temperature is below VT_{min} (the minimum temperature required for foraging), and basking microclimates are available (above VT_{max}, the maximum temperature in which foraging occurs). In the no basking scenario, the turtle cannot bask to raise body temperatures to forage. In the ‘minimal basking’ scenario, the turtle is able to bask to raise body temperature when conditions do not permit feeding, but otherwise time is spent foraging. In the ‘maximal basking’ scenario, the turtle always seeks out the warmest available microclimate above VT_{max}. This situation assumes that only very short bouts of foraging in the water are necessary to fill the gut, after which the turtle will bask to maximise assimilation rates (illustrated).

Body temperature and growth predictions were validated for the sub-adult and adult life stages of *P. umbrina*. Predictions of body temperature were tested against published (King *et al.* 1998) and unpublished (G. Kuchling, unpublished data) temperature traces available for radio-tracked western swamp turtles at Ellen Brook Nature Reserve. King *et al.*'s temperatures were recorded from temperature-sensitive radio transmitters deployed during the spring of 1993. Kuchling's observations were continuous temperature traces recorded by iButtons (Thermochron DS1921G) secured to the carapace of individuals, logging at 15 minute intervals between the 1st of August and 30th of September, 2006.

Growth and reproduction data from the repeated recapture of individuals at Ellen Brook Nature Reserve were compiled for comparisons of observed and predicted body mass, length, and reproductive output (G. Kuchling, unpublished data). For growth data, I constrained analyses to those individuals who had been recaptured at least nine times since their initial discovery (n=12). Carapace lengths in all instances were measured to the nearest mm using Vernier callipers, while weights were obtained using a Persola spring balance for field measurements (±0.1 g). For reproduction data, I noted all instances that females were recorded as being gravid during routine monitoring and opportunistic capture between 2003 and 2013. Gravidity was assessed in the field using a portable ultrasound machine (M-Turbo, Fujifilm SonoSite Inc, United States).

5.2.5 'Virtual experiments' manipulating basking behaviour, shade, and climate scenario at Ellen Brook Nature Reserve

I examined how behaviour and shade availability constrained growth potential by running simulations across three behaviours ('no basking', 'minimal basking', and ‘maximal basking’) and three shading conditions (0 % minimal shade, 50 % minimal shade, and 90 % minimal shade), giving nine possible combinations of behaviour and shading type. I examined the outputs for body temperature, activity, wet mass, time to maturity, cumulative reproduction, and survival of turtles at Ellen Brook Nature Reserve, where I simulated all years for which there was historic environmental data (1972-2015).

Future climates were then considered by imposing the projected monthly changes in temperature, humidity, solar radiation, and wind speed for 2050 and 2070 upon the daily trends from 1972-2015 (see Briscoe *et al.* 2016 for full details). Future climate predictions were splined to daily resolution, based on the interpolated daily weather data obtained from McVicar *et al.* (2008) and AWAP (Raupach *et al.* 2009). I ran three global circulation models which were known to realistically capture the historic climate of Australia (Watterson *et al.* 2013): GDFL-CM3 (because of its highest impact on the hydroperiod), CanESM2 (because of its highest impact on air temperature) and HadGem2-CC (for consistency with Mitchell *et al.* 2016 which modelled the embryonic development of *P. umbrina*). These were downscaled to the resolution of the AWAP data, with the projected monthly changes for 2050 and 2070 given by SimClim (Yin *et al.* 2013; 1 km resolution).

5.2.6 ASSESSMENT OF POTENTIAL ASSISTED MIGRATION SITES

Climate predictions were generated as per 5.2.5 for five potential assisted migration sites (Figure 5.2). These sites (Ambergate, East Augusta, Donnelly River, Doggerup Creek, and D’Entrecasteux) have been the focus of previous investigations into the assisted migration of *P. umbrina* (Dade *et al.* 2014; Mitchell *et al.* 2016; refer Dade *et al.* 2014 for the rationale behind site selection). Trial translocations at two of these locations commenced in 2016. I examined potential growth and reproduction at each candidate assisted migration site, and compared them to those within the turtles' natural range at Ellen Brook Nature Reserve.

5.2.7 DATA ANALYSIS

Summary statistics were used to compare the observed and predicted values of microclimate, body temperature, and turtle growth across the years simulated, and I calculated the correlation coefficient (r^2) and root-mean-squared error (RMSE) of each comparison to assess the goodness of the fit. Summary statistics were calculated using the 'Metrics' (Hamner 2012) and 'plyr' (Zambrano-Bigiarini 2014) packages in R (version 3.3.2; R Core Team 2017). Lower RMSE values and higher r^2 values represented a better fit between the observed and predicted values.

For virtual experiments (5.2.5) I evenly grouped the years for which *P. umbrina* habitat data was available into four categories based on rankings given for observed hydroperiod length and projected water temperatures (N = 44; n = 11; Appendix E). 'Good years' were those that had the longest hydroperiods and the warmest projected water temperatures, while 'poor years' were those with the shortest hydroperiods and the coldest temperatures. Because of the hypothesised capacity for short hydroperiods to be offset by increased growth arising from warmer temperatures under climate change (Mitchell *et al.* 2012), the two remaining categories were defined as 'medium-poor' (those years with long hydroperiods but cool temperatures) and 'medium-good' (those years with short hydroperiods and warm temperatures). I compared differences between these groups using ANOVA assuming $P = 0.05$, with post-hoc Tukey tests (StatistiXL, ver. 1.8.).

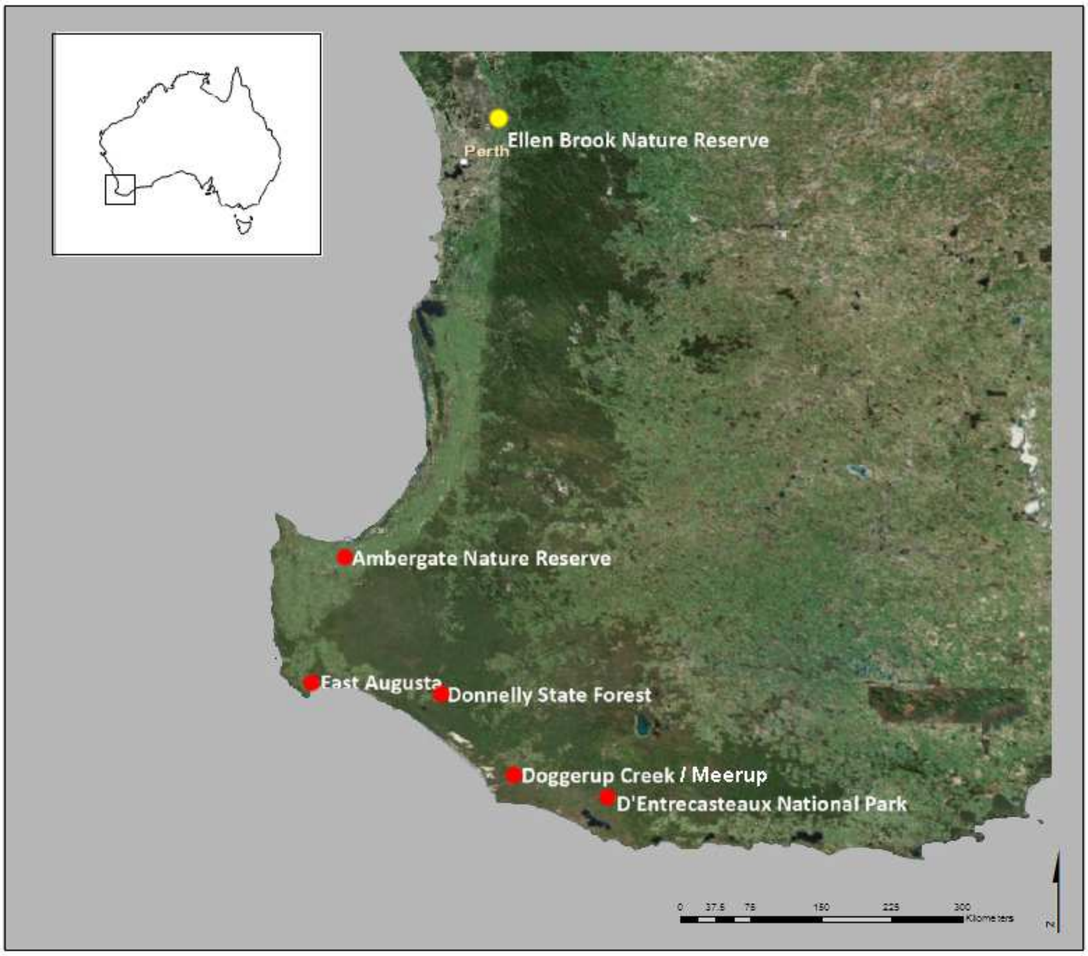


Figure 5.2 – Locations of five potential assisted migration sites (red; as identified in the multiple criteria analysis of Dade *et al.* 2014, and further refined by Mitchell *et al.* 2016), and the current core habitat of *P. umbrina* (yellow; at Ellen Brook Nature Reserve), as modified from Rodriguez (2015). Note Doggerup Creek is also known elsewhere as Meerup.

Because of a hypothesised requirement for swamp turtles to attain a mass of 18 g within their first year to survive aestivation (the ‘critical mass’; Chapter 2; Mitchell *et al.* 2016) I reported the survivorship outcomes at Ellen Brook and the candidate assisted migration sites in four ways: 1) ‘no survival’ where neither the critical mass or survivorship to 20 years was reached; 2) ‘assumed no survival’ where survival to 20 years was met but the critical mass was not attained; 3) ‘some survival’ where critical mass was attained but survival to 20 years was not met; and 4) ‘full survival’ where both the critical mass and survivorship to 20 years were reached. Growth and reproduction at Ellen Brook Nature Reserve and the candidate assisted migration sites were also examined using ANOVA assuming $P = 0.05$, with post-hoc Tukey tests (StatistiXL, ver. 1.8.).

5.3 RESULTS

5.3.1 PERFORMANCE OF THE MICROCLIMATE MODEL

The NicheMapR microclimate model (driven by the gridded AWAP weather data and as compared to the climate and wetland data collected *in-situ* at Ellen Brook Nature Reserve) reconstructed the hydroperiods at this reserve with reasonable accuracy (Figure 5.3; Appendix E). While water depth was overestimated (see 5.2.2), fits of air and water temperature were realistic ($r^2 = 0.83$; RMSE = 4.60 °C; air and water temperatures pooled), with water temperatures (as derived from saturated soil temperatures; $r^2 = 0.81$; RMSE = 2.92 °C) being more accurately predicted than air temperatures ($r^2 = 0.62$; RMSE = 5.28 °C).

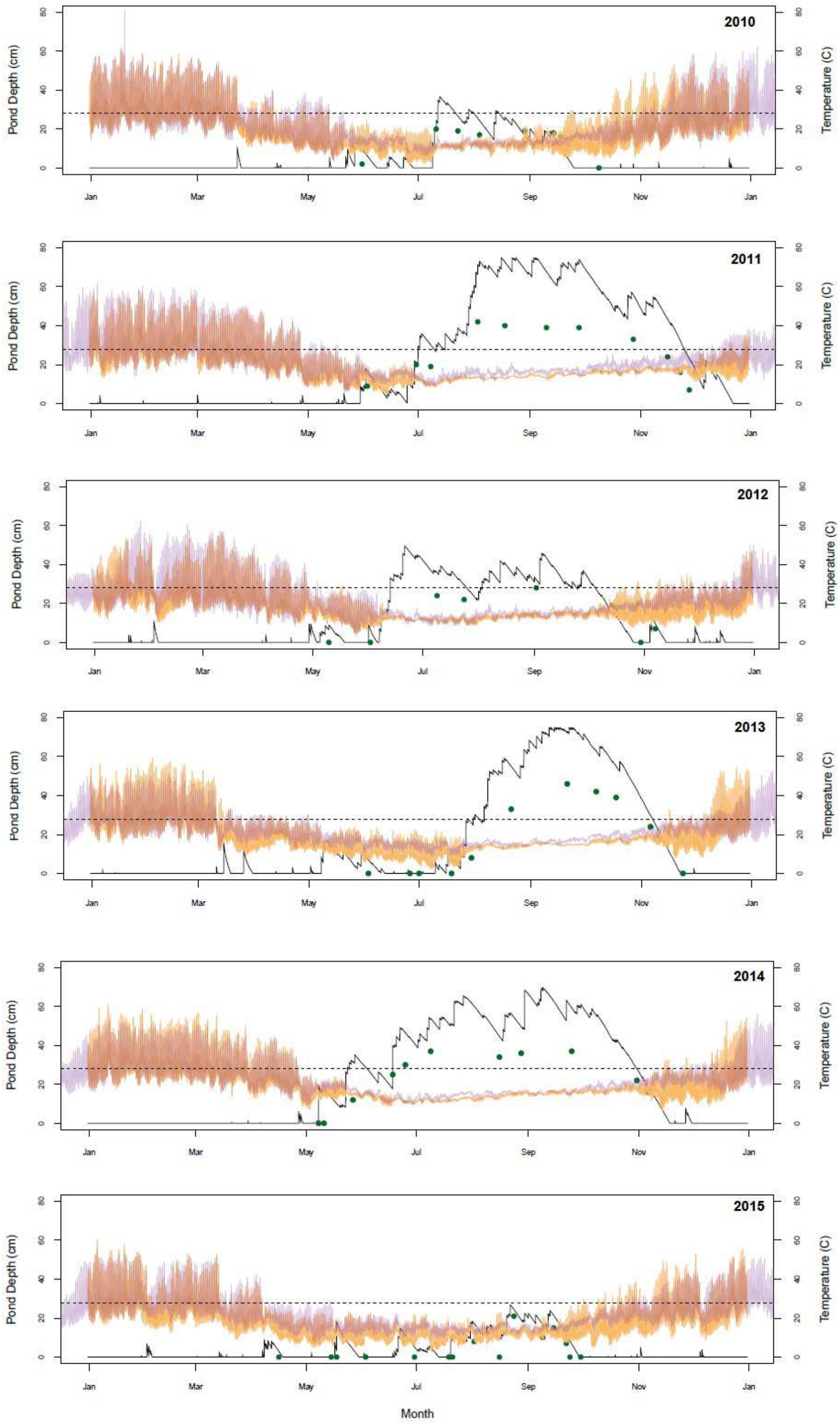


Figure 5.3 – Observed temperatures as recorded by an *in-situ* weather station (orange), and predicted temperatures as derived from NicheMapR's microclimate model (grey) at Ellen Brook Nature Reserve from 2010-2015. The corresponding predicted wetland depth is shown in black, with observed water depths shown as green points. The dashed line marks 28 °C which is the maximum foraging temperature for *P. umbrina* (Lucas 1963). Hydroperiod predictions for previous years are shown in Appendix E.

5.3.2 PERFORMANCE OF THE ANIMAL MODEL

Temperature and growth data from individuals at Ellen Brook Nature Reserve best matched the model predictions when using a ‘minimal’ or ‘maximal’ basking scenario and 0 % shade (Figure 5.4 and 5.5). These combinations are hereafter reported below, with the remainder of comparisons provided in Appendix E.

Using the ‘minimal basking’ and 0 % shade scenario, the model accurately captured the daily temperature profile of the individual recorded by King *et al.* (1998) (Figure 5.4a; r^2 = 0.95; RMSE = 1.11 °C) but tended to underestimate body temperatures of individuals monitored in 2006, particularly during the middle of the day (Figure 5.4b-d; r^2 = 0.71; RMSE = 3.98 °C, data pooled). A ‘maximal basking’ and 0 % shade combination provided the closest match between the observed and predicted values of these 2006 individuals (r^2 = 0.73; RMSE = 3.87 °C; data pooled).

The ‘minimal basking’ and 0 % shade combination best fitted the growth data, where fits to mass (Figure 5.5b; r^2 = 0.97; RMSE = 14.9 g) were slightly weaker than those to length (Figure 5.5a; r^2 = 0.99; RMSE = 2.3 cm) during early life stages (though note, the RMSE was in the same order of magnitude as the critical mass of 18 g, reducing certainty). Fits at maximal size were stronger and the same pattern held true, with predictions of length (Figure 5.5c; r^2 = 0.80; RMSE = 3.1 cm) outperforming predictions of mass (Figure 5.5d; r^2 = 0.72; RMSE = 18.6 g).

Between 2003 and 2013, gravid females were recorded at Ellen Brook Nature Reserve in every year except 2006 and 2011. Filtered by individual, the most fecund female (a

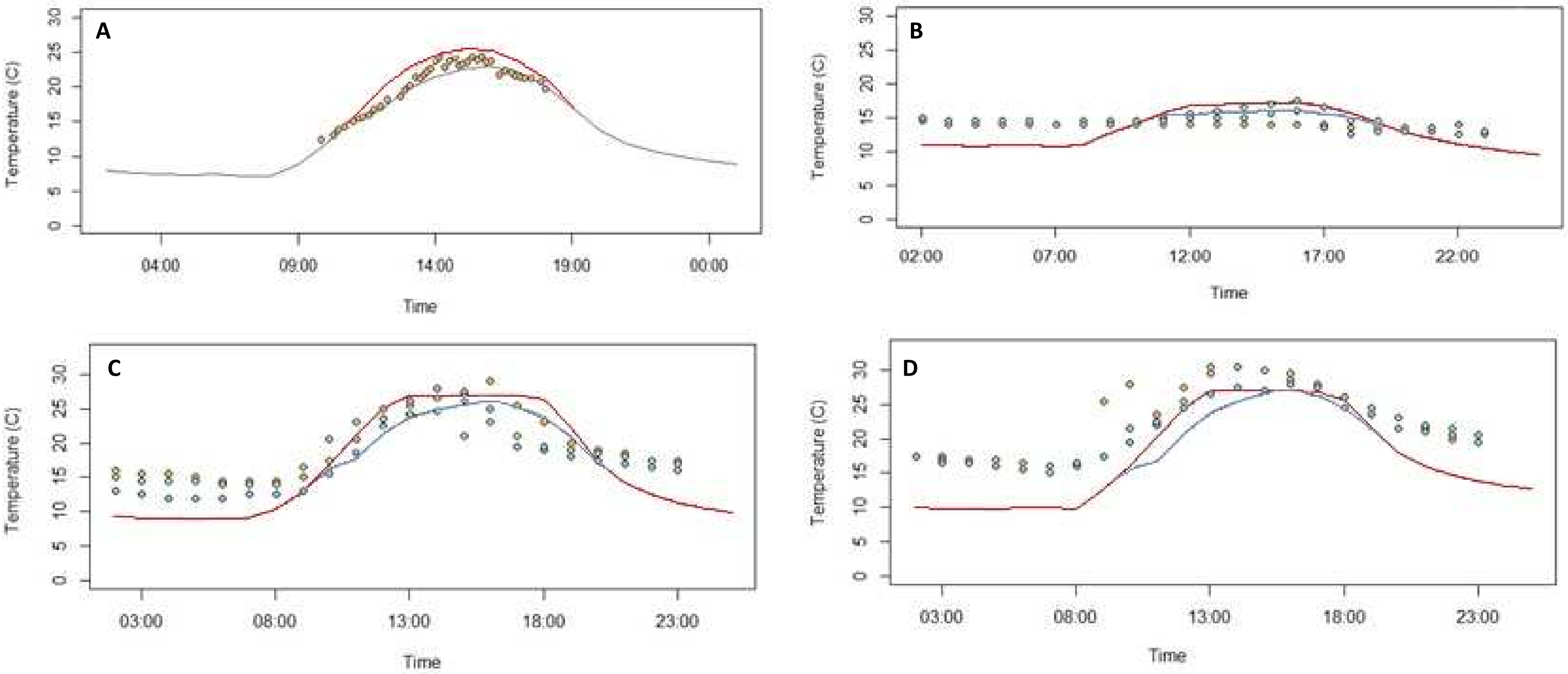


Figure 5.4a-d – Comparison of body temperature predictions generated by NicheMapR (solid lines), against data obtained for field individuals (yellow, blue, and green points) at Ellen Brook Nature Reserve during the same time periods, showing 0 % shade with ‘minimal basking’ (light blue line) and ‘maximal basking’ (dark red line) combinations: **(a)** shows the temperature of a single individual on the 9th of September, 1993 (from Figure 2, King *et al.* 1998); **(b-d)** show temperatures for three different individuals in each plot on the 15th of August, 15th of September, and 15th of October 2006, respectively (n = 9 unique individuals total).

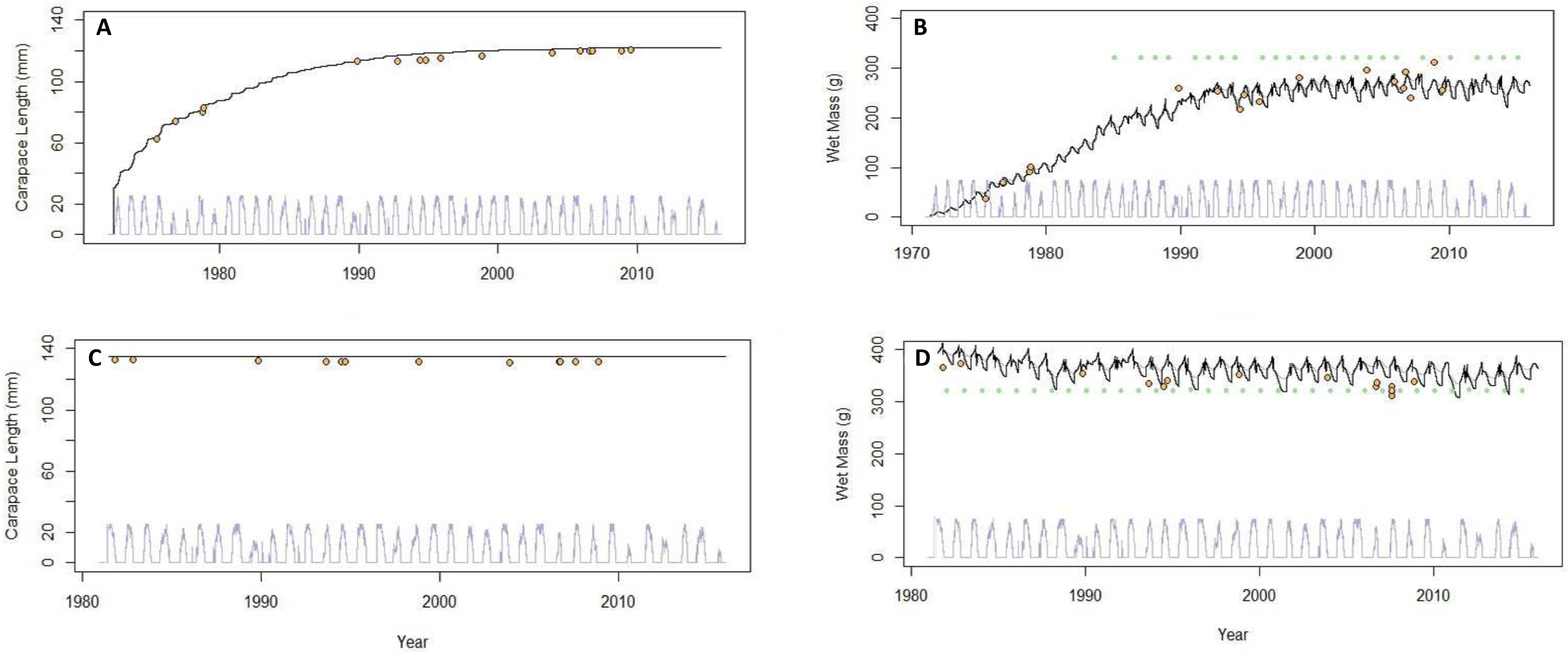


Figure 5.5a-d - Comparison of growth predictions generated by NicheMapR (black lines), against observed growth data from two individuals (yellow points) at Ellen Brook Nature Reserve: **(a)** shows predicted length for an individual born in 1972 (where starting carapace length at birth is 270 mm) and **(b)** gives the corresponding mass prediction (where mass at birth is 5.2 g; Chapter 4). Observed growth data for the corresponding time period is shown for an individual first captured as a juvenile in 1975 with a predicted birthdate of early 1970s. Plot **(c)** gives the predicted carapace length of an individual at reproductive size (> 107 mm; Chapter 4) and **(d)** gives the corresponding mass prediction. Observed growth data for the corresponding time period is shown for an individual who had a carapace length of over 120 mm when captured in 1980. Blue lines at the bottom of each plot show the predicted hydroperiods for each year, and the green points depict times when the reproductive buffer is predicted to be emptied in the form of gametes (refer Chapter 4).

mature female of unknown age collected in 1989; ID 182) was recorded as being gravid five times during this interval (but note she was not captured in 2008 and 2012). The model simulated gravidity in the corresponding years 60.0 % of the time at the population level, and 67.7 % of the time for Female 182 (Table 5.2).

5.3.3 VIRTUAL EXPERIMENTS UNDER CURRENT CONDITIONS AT ELLEN BROOK NATURE RESERVE: EFFECTS OF BEHAVIOUR, SHADING, AND YEAR CLASSIFICATION

A comparison of first-year growth under different year classifications is shown in Table 5.3. The year classification had a significant effect on the length ($F_{3,\ 43} = 3.27$, $P < 0.031$) and mass ($F_{3,\ 43} = 4.28$, $P < 0.010$) of individuals, where turtles that hatched in a ‘good’ year grew significantly larger (44.9 ± 1.5 mm; $P = < 0.047$) and heavier (13.7 ± 1.2 g; $P = < 0.030$) than individuals in other year types (under a ‘minimal basking’ 0 % shade combination; i.e. the combination most reflective of current length and mass observations in the wild; see 5.3.2). There was no significant difference between the sizes and masses of individuals born in the other year types ($P > 0.072$ and $P > 0.183$, in mass and length, respectively; data from Table 5.3a).

Regardless of year classification, an individual that hatched on the 15th of May would only reach the critical mass of 18 g if it basked ‘maximally’ in 0 % shade over the preceding wet period (Table 5.3b). However, during ‘good’ years, the critical mass was almost attained under the ‘minimal basking’ scenario (with shade level greatly affecting growth; Figure 5.6a-c). The typical mass lost across aestivation ranged from 3.8 % in a ‘medium-poor’ year, to 6.2 % in a ‘medium-good’ year. Basking ‘maximally’ approximately halved the time to maturity (e.g. from 10.4 years to 5.5 years in a

Table 5.2 – Predictions of gravidity as simulated by NicheMapR for an adult born prior to 1990 ('Model Prediction'), in comparison to gravidity recorded in females at Ellen Brook Nature Reserve ('All Females' and 'Female 182') obtained during routine monitoring and opportunistic recapture between 2003 and 2013. 'All females' refers to all years in which at least one located individual was found to be gravid, while the individual level is shown by the gravidity of the female most frequently scanned gravid during this time period (Female 182) who was captured annually with the exception of 2008 and 2012 (though note this individual was found with an eye missing in 2013 and may have been attacked by a raven, the stress of which might have influenced reproduction; G. Kuchling, pers. comm.).

Year	All Females	Female 182	Model Prediction
2003	Gravid	Gravid	Gravid
2004	Gravid	Gravid	Gravid
2005	Gravid	Gravid	Gravid
2006	Not Gravid Records	Not Gravid	Gravid
2007	Gravid	Not Gravid	Not Gravid
2008	Gravid	Not Captured	Not Gravid
2009	Gravid	Gravid	Not Gravid
2010	Gravid	Gravid	Gravid
2011	Not Gravid Records	Not Gravid	Not Gravid
2012	No Data	Not Captured	Gravid
2013	Gravid	Not Gravid	Gravid

Table 5.3a-b – Growth predictions for hypothetical turtles born on the 15th of May at Ellen Brook Nature Reserve during 'poor', 'medium-poor', 'medium-good' and 'good' years (refer 5.2.7 in main text for definitions, and Appendix E for the differences between these year groups): **(a)** shows the averages for the 11 individuals in each year type under a 'minimal basking' 0 % shade combination; and **(b)** demonstrates the effects of each year classification at the individual level, where a random representative year is shown for each group. Four basking and shading levels are given to encompass the breadth of conditions experienced: 90 % shade and 'no basking' demonstrating the coldest combination, 0 % shade and 'maximal basking' demonstrating the warmest combination, and 'minimal basking' at 50 % shade demonstrating an intermediate combination. 'Minimal basking' at 0 % is also provided for comparison. Numbers in parentheses represent the ratio of days spent active and in aestivation each year, and the critical mass refers to an 18 g threshold hypothesised to be the minimum size requirement for a hatchling to survive aestivation (Mitchell *et al.* 2013).

(A) All Year Classifications

Year Type	Poor	Medium-Poor	Medium-Good	Good
Mean Water Temperature (°C)	12.2 ± 0.2	12.7 ± 0.1	13.0 ± 0.2	13.2 ± 0.2
Mean Hydroperiod (days)	111.9 ± 10.6	155.1 ± 4.5	128.83 ± 7.9	175.4 ± 4.1
Mean Mass at End of 1st Wet Season (g)	9.5 ± 1.2	10.0 ± 0.8	9.0 ± 1.1	13.7 ± 0.9
Mean Length at End of 1st Wet Season (mm)	39.8 ±1.8	40.1 ± 1.4	38.3 ± 1.8	44.9 ± 1.5

(B) Individual Growth in a Representative Year

Year	1986				1981				2007				1996			
Year Type	Poor				Medium-Poor				Medium-Good				Good			
(Active: Aestivating)	(170:189)				(199:190)				(194:197)				(196:196)			
Basking Level	None	Minimal		Maximal	None	Minimal		Maximal	None	Minimal		Maximal	None	Minimal		Maximal
Shade Level	90 %	0 %	50 %	0 %	90 %	0 %	50 %	0 %	90 %	0 %	50 %	0 %	90 %	0 %	50 %	0 %
Mass at End of 1st Wet Season (g)	10.9	11.9	11.3	19.8	10.7	12.0	11.3	18.5	11.8	12.3	12.0	19.8	16.3	17.1	16.7	27.9
Mass at End of 1st Dry Season (g)	10.3	11.2	10.7	18.8	10.2	11.5	10.8	17.8	11.1	11.6	11.3	18.6	15.3	16.1	15.8	26.3
Mass Lost Over Aestivation (%)	5.6	5.1	5.5	5.0	4.1	3.8	3.9	3.8	6.1	6.0	6.0	6.2	5.8	5.6	5.7	5.7
Meets Critical Mass	No	No	No	Yes	No	No	No	Yes	No	No	No	Yes	No	No	No	Yes
Time to Maturity (Years)	9.5	9.4	9.5	5.4	10.4	10.4	10.4	5.5	NA	NA	NA	NA	9.5	9.4	9.4	5.4

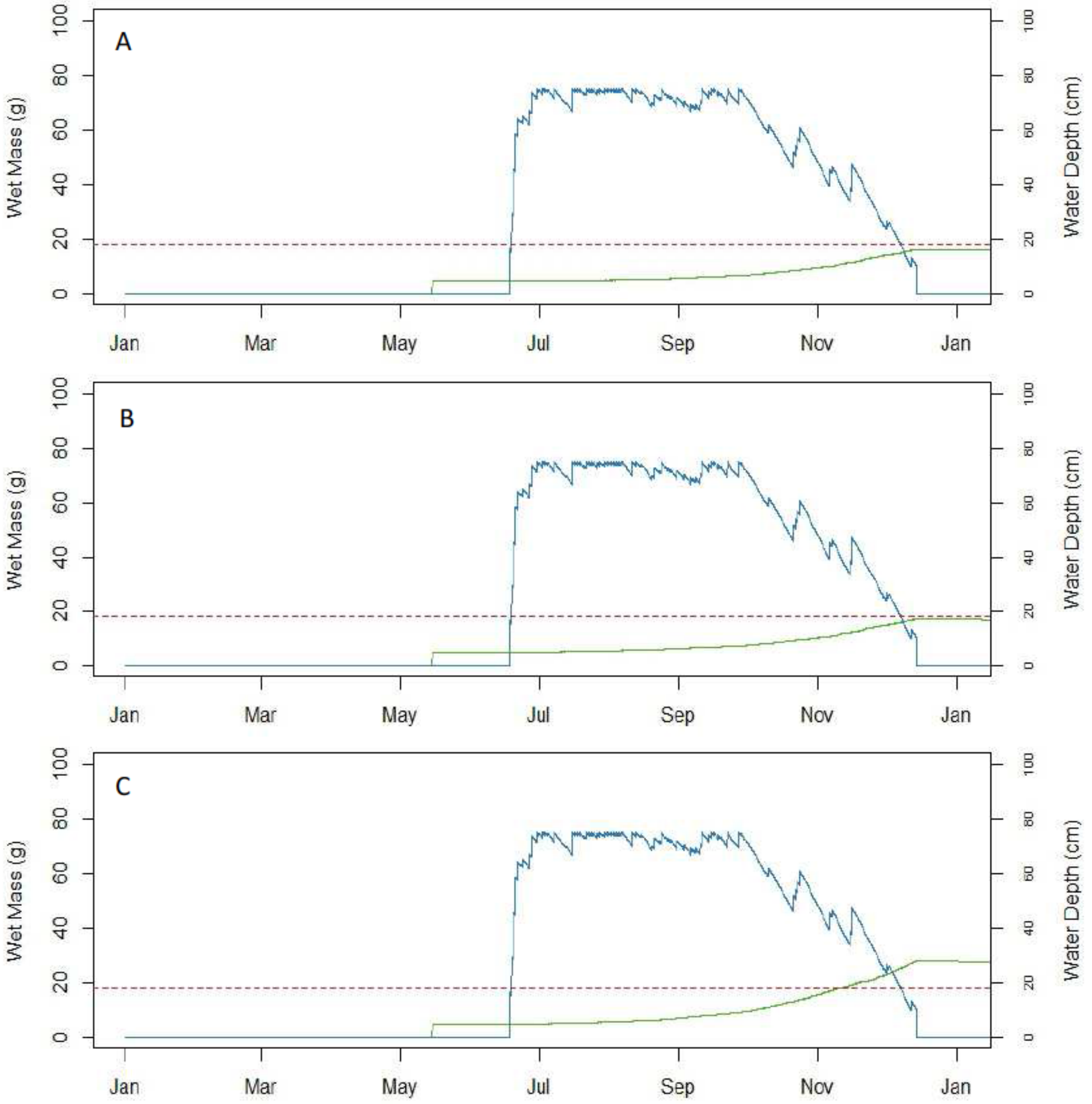


Figure 5.6a-c – Comparison of the effects of basking on wet mass (g, green line) in a single feeding season during a typical 'good' year (1996 shown), where the dotted line denotes the 'critical mass' of 18 g (refer 5.2.7 in main text for definitions). **(a)** shows 'no basking' during the wet season (all shade combinations); **(b)** shows 'minimal basking' with 0 % shade; and **(c)** shows 'maximal basking' with 0 % shade. The wet mass under the 'minimal basking' and 0 % shade combination almost reaches the critical mass (17.7 g at the end of the hydroperiod).

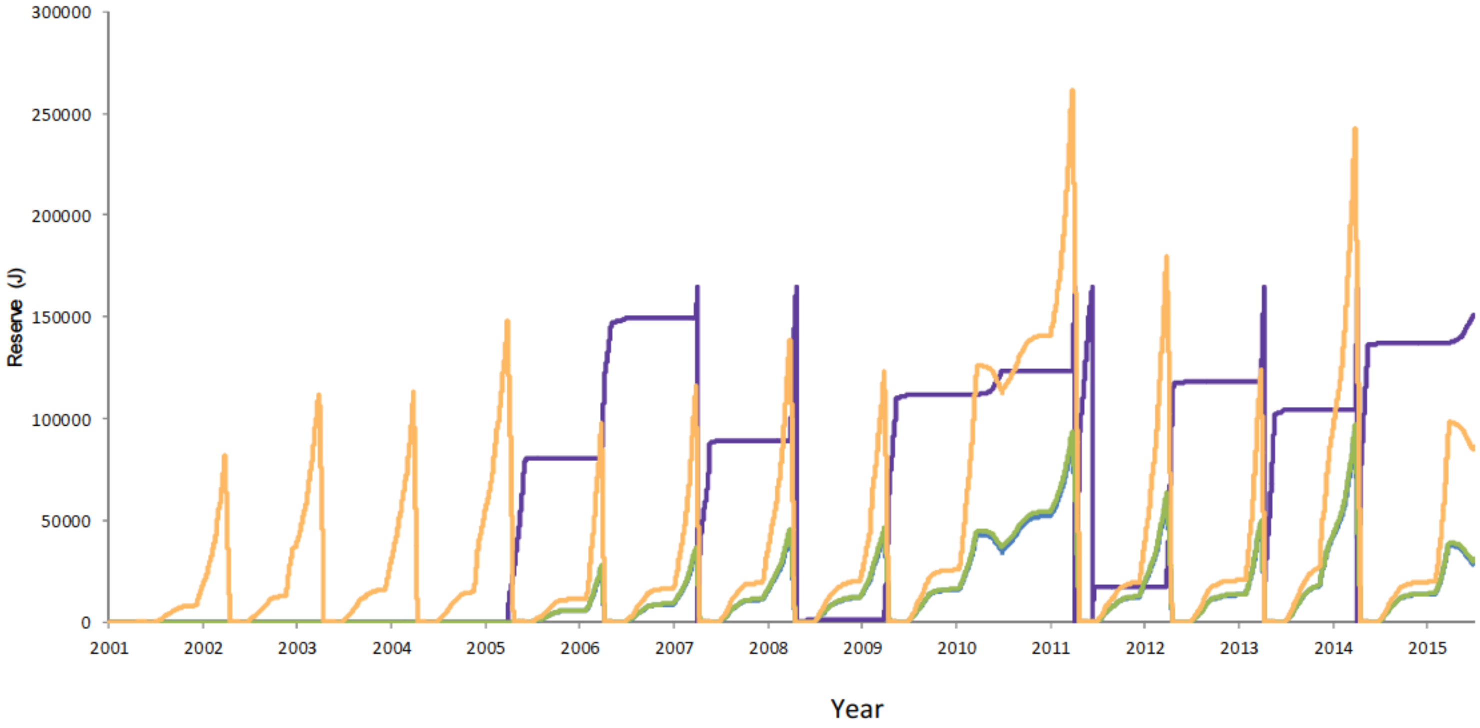


Figure 5.7 – Allocation of reserve into the reproductive buffer over time, as modelled for a turtle born on the 15th of May in 1996 (classed as a 'good' year). 'Maximal basking' (in 0 % shade; orange) allowed turtles to reach maturity faster than any other behavioural scenario ('minimal basking' in 0 % shade, purple; 'minimal basking' in 50 % shade, green; and 'no basking', grey; hidden by green line), with individuals producing clutches four years prior to the other scenarios. A drop in reserve to 0 J signifies the production of a clutch.

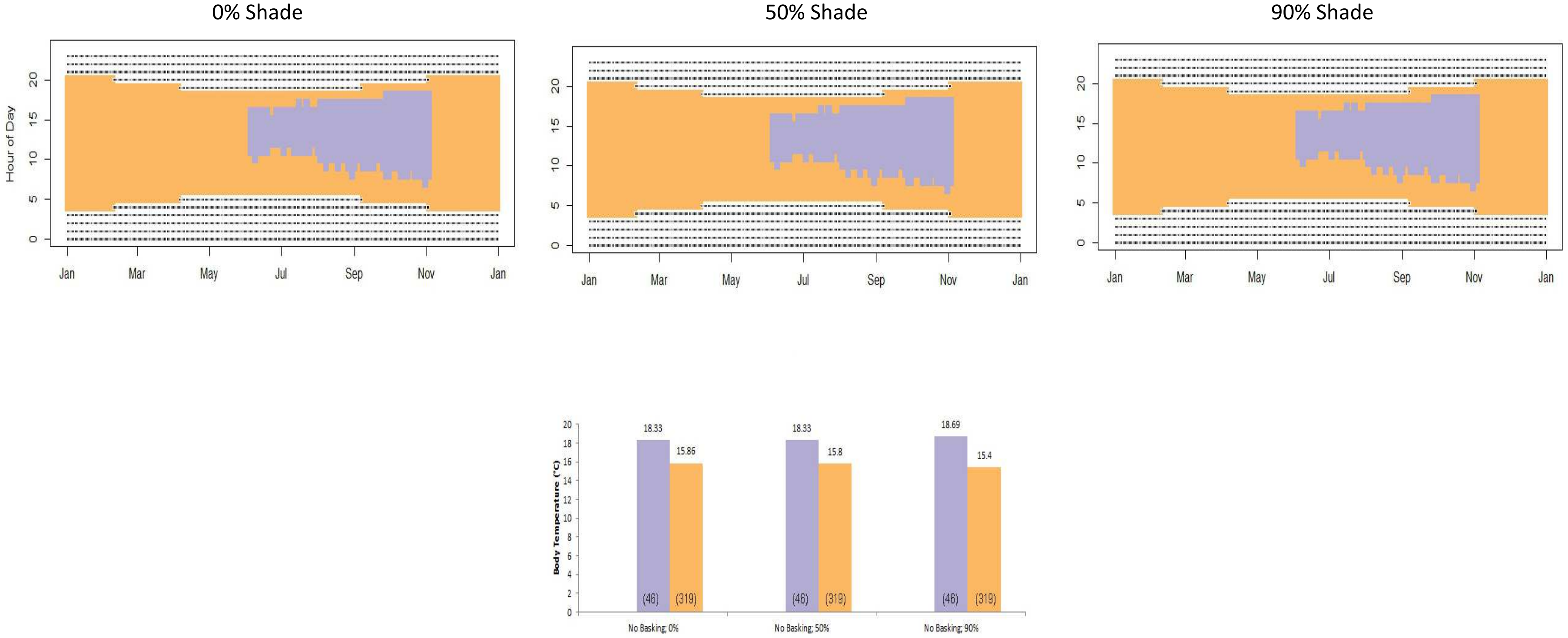
‘medium-poor’ year), and increased the cumulative reproduction of individuals (Figure 5.7). On a typical ‘good’ year, the proportion of time spent foraging each day increased from winter to spring, peaking in November prior to aestivation (Figure 5.8a-c). Under the ‘no basking’ scenario, activity windows remained the same across shading levels, but body temperatures decreased by approximately 0.5 °C with increasing shade (Figure 5.8a). The ‘minimal’ (Figure 5.8b) and ‘maximal’ (Figure 5.8c) basking scenarios yielded identical activity windows, with 46 days spent foraging in each.

The proportion of time spent inactive or basking was influence by shading level, where 0 % shade yielded 311 days of inactivity, and 90 % shade yielded 318 days (i.e. as shade level increased basking decreased, from 8 days to 1). Body temperatures were highest at 0 % shade when basking was maximised, generating up to a 2.4 °C difference in body temperature between the coldest (‘no basking’, 90 % shade) and warmest (‘maximal basking’, 0 % shade) combinations.

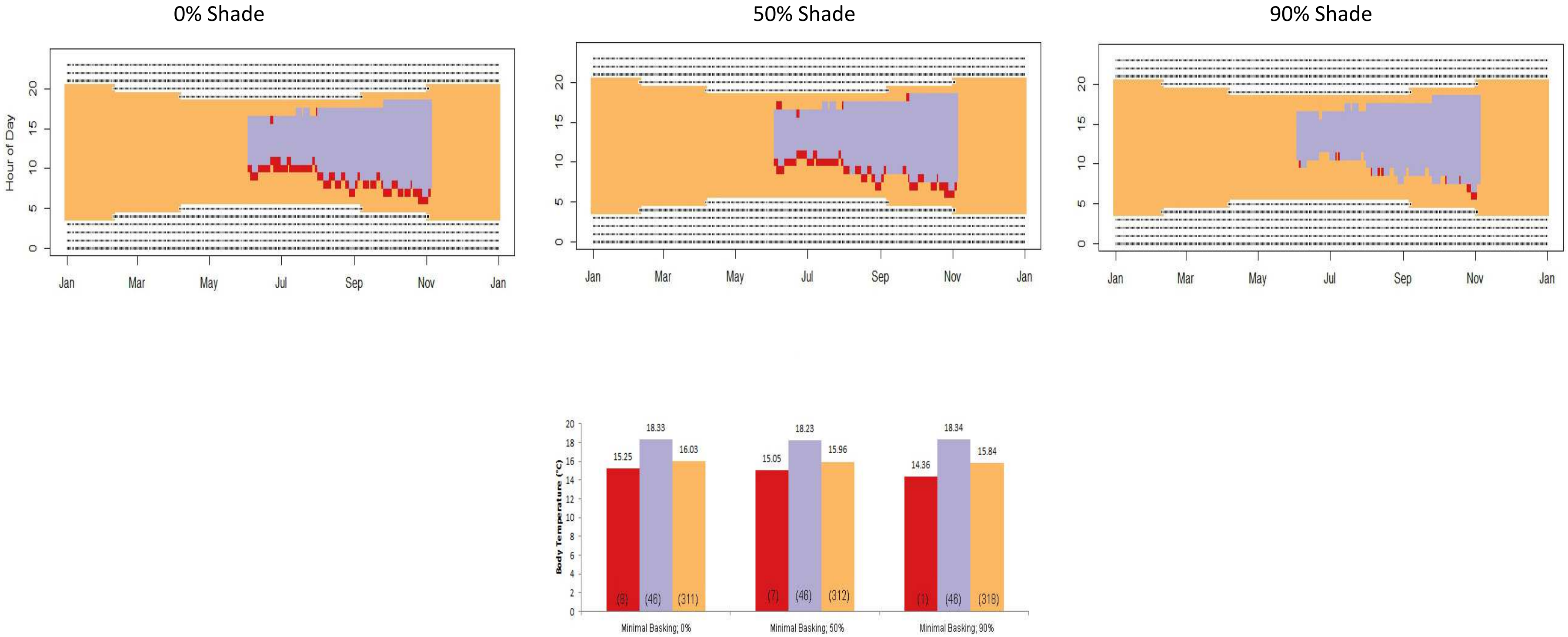
5.3.4 VIRTUAL EXPERIMENTS UNDER FUTURE CONDITIONS AT ELLEN BROOK NATURE RESERVE: CONSEQUENCES OF CLIMATE CHANGE

‘Full survival’ was achieved under all 2050 simulations with a ‘maximal basking’ 0 % shade combination (2050 HadGem2-CC, 2050 GDFL-CM3, and 2050 CanESM2 Global Climate Models). At 0 % shade and ‘maximal basking’, individuals simulated under CanESM2 2050 conditions grew largest and matured fastest, and those under GDFL-CM3 2050 had the slowest growth and times to maturity (Table 5.4). At the end of their first season, individuals under CanESM2 were 3.2 g heavier than those under GDFL-CM3, and at the end of 20 years this weight difference was 21.6 g. The

A


0% Shade
50% Shade
90% Shade
Hour of Day
0
5
10
15
20
Jan
Mar
May
Jul
Sep
Nov
Jan
Body Temperature (°C)
0
2
4
6
8
10
12
14
16
18
20
18.33
15.86
18.33
15.8
18.69
15.4
(46)
(319)
(46)
(319)
(46)
(319)
No Basking; 0%
No Basking; 50%
No Basking; 90%

B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Body Temperature (°C)
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12
14
16
18
20
15.25
18.33
16.03
(8)
(46)
(311)
15.05
18.23
15.96
(7)
(46)
(312)
14.36
18.34
15.84
(1)
(46)
(318)
Minimal Basking; 0%
Minimal Basking; 50%
Minimal Basking; 90%

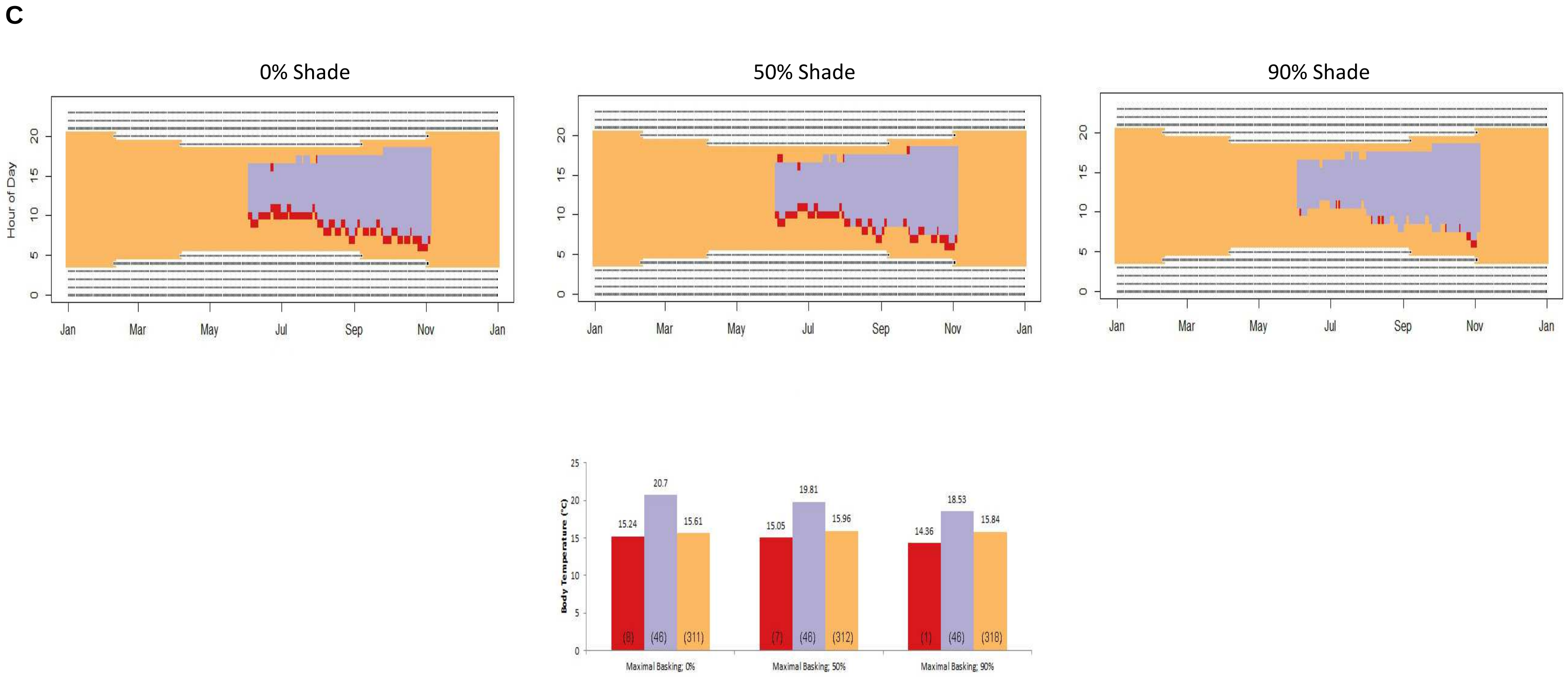

Figure 5.8a-c – Sensitivity of body temperature and activity to basking scenario and shade level, as demonstrated by an activity window for *P. umbrina* during 1974 (classed as a 'good' year). Black lines denote night time hours, while orange symbolises daylight hours in which the turtles were inactive. Foraging (purple) occurred during day time hours where water was present (mid-May to November in this example) and when body temperature was above 14 °C (the VT_{min}). Basking is shown in red. **(a)** gives the 'no basking' scenario with increasing shade levels; **(b)** gives the 'minimal basking' scenario; and **(c)** gives the 'maximal basking' scenario. The corresponding bar charts display the average yearly body temperature experienced for each state (inactive, foraging and basking), with the number of days spent in each state given in parentheses.

Table 5.4 – Predictions of growth, survivorship, and reproductive age under 2050 climate simulations at Ellen Brook Nature Reserve, showing all combinations of basking scenario and shading level. Cell colour indicates survival outcome, where red reflects 'no survival', orange reflects 'assumed no survival', and green reflects 'survival' (refer 2.5.7 main text for definitions). The maximum standard error for average body temperature was ± 0.034 °C.

Behavioural Routine	Climate Simulation	HadGem2			CanESM2			GDFL-CM3		
	Shading Level	**0 %**	**50 %**	**90 %**	**0 %**	**50 %**	**90 %**	**0 %**	**50 %**	**90 %**
No Basking	Size reached at 1st season: Mass (g)	15.4	15.4	15.4	15.5	15.5	15.5	13.4	13.4	13.4
	Size reached at 1st season: Length (mm)	47.4	47.4	47.4	47.2	47.2	47.2	45.4	45.4	45.4
	Size reached at 20th season (or death): Mass (g)	284.1	284.1	248.1	18.9	18.9	18.9	17.2	17.2	17.2
	Size reached at 20th season (or death): Length (mm)	118.6	118.6	118.6	50.4	50.4	50.4	48.9	48.9	48.9
	Mean body temperature (°C)	18.1	18.1	18.1	18.2	18.2	18.2	18.0	18.0	18.0
	Age at first reproduction (years)	14	14	14	NA	NA	NA	NA	NA	NA
	Survival probability <50 %	NA	NA	NA	Year 3; 20th May	Year 3; 20th May	Year 3; 20th May	Year 3; 16th May	Year 3; 16th May	Year 3; 16th May
Minimal Basking	Size reached at 1st season: Mass (g)	15.4	15.4	15.4	15.5	15.2	15.2	14.2	13.4	13.4
	Size reached at 1st season: Length (mm)	47.5	47.4	47.4	47.4	47.2	47.2	46.0	45.4	45.4
	Size reached at 20th season: Mass (g)	292.2	285.6	284.1	19.7	18.9	18.9	18.6	17.3	17.2
	Size reached at 20th season: Length (mm)	120.5	118.7	118.6	50.9	50.4	50.4	49.9	48.9	48.9
	Mean body temperature (°C)	17.8	18.0	18.1	17.8	18.1	18.2	17.6	17.9	18.0
	Age at first reproduction (years)	13	14	14	NA	NA	NA	NA	NA	NA
	Survival probability <50 %	NA	NA	NA	Year 3; 22nd May	Year 3; 20th May	Year 3; 20th May	Year 3; 20th May	Year 3; 16th May	Year 3; 16th May
Maximal Basking	Size reached at 1st season: Mass (g)	30.8	15.4	15.4	31.2	15.2	15.2	28.0	13.4	13.4
	Size reached at 1st season: Length (mm)	58.9	47.4	47.4	59.1	47.2	47.2	57.0	45.4	45.4
	Size reached at 20th season: Mass (g)	423.6	291.9	284.1	419.0	18.9	18.9	397.3	17.3	17.2
	Size reached at 20th season: Length (mm)	132.7	119.1	118.6	132.7	50.4	50.4	130.3	48.9	48.9
	Mean body temperature (°C)	21.0	18.1	18.1	21.2	21.2	18.2	20.9	17.9	17.9
	Age at first reproduction (years)	6	13	14	7	NA	NA	8	NA	NA
	Survival probability <50 %	NA	NA	NA	NA	Year 3; 20th May	Year 3; 20th May	NA	Year 3; 16th May	Year 3; 16th May

remainder of the 2050 HadGem2-CC simulations resulted in an ‘assumed no survival’ outcome, and all other 2050 GDFL-CM3 and CanESM2 behaviour and shading combinations resulted in a ‘no survival’ outcome. In 2070, ‘full survival’ was only attained under a ‘maximal basking’ 0 % shade HadGem2-CC climate prediction. Survivorship to eight years (‘some survival’) was achieved in the GDFL-CM3 simulation using the same behavioural and shading combination, and all other combinations resulted in either ‘assumed no survival’ or ‘no survival’ (Table 5.5).

In both 2050 and 2070, HadGem2-CC simulations resulted in the highest likelihood to reach 20-year survival. At the end of their first year, individuals born in 2070 under this climate model grew larger than individuals born in 2050, but this trend was reversed at the conclusion of the 20 years modelled. Time to maturity was fastest under the 2070 ‘maximal basking’ 0 % shade combination, where individuals commenced allocating to egg batches at six years of age (compared to a mean of 13.4 ± 0.4 years for all other HadGem2-CC combinations, and compared to a mean of 8.7 ± 0.6 years under current and historic conditions, i.e. Table 5.3).

5.3.5 CANDIDATE ASSISTED MIGRATION SITES

Under the ‘maximal basking’ and 0 % shade combination (i.e. the combination most likely to result in ‘full survival’ under climate change; see 5.3.4) three of five candidate assisted migration sites resulted in ‘full survival’ and positive reproduction under all climate models applied (Table 5.6). These were Doggerup Creek, Donnelly River, and D’Entrecasteaux National Park. The onset of reproduction was similar at all three sites

Table 5.5 – Predictions of growth, survivorship, and reproductive age under 2070 climate simulations at Ellen Brook Nature Reserve, showing all combinations of basking scenario and shading level. Cell colour indicates survival outcome, where red reflects 'no survival', orange reflects 'assumed no survival', blue reflects 'some survival', and green reflects 'survival' (refer 2.5.7 main text for definitions). Maximum standard error for average body temperature was ± 0.035 °C.

Behavioural Routine	Climate Simulation	HadGem2			CanESM2			GDFL-CM3		
	Shading Level	0 %	50 %	90 %	0 %	50 %	90 %	0 %	50 %	90 %
No Basking	Size reached at 1st season: Mass (g)	16.2	16.2	16.2	14.8	14.8	14.8	12.1	12.1	12.1
	Size reached at 1st season: Length (mm)	48.3	48.3	48.3	46.9	46.9	46.9	43.8	43.8	43.8
	Size reached at 20th season: Mass (g)	272.5	272.5	272.5	15.2	15.2	15.2	12.1	12.2	12.1
	Size reached at 20th season: Length (mm)	117.0	117.0	117.0	47.3	47.3	47.3	43.8	43.8	43.8
	Mean body temperature (°C)	18.2	18.2	18.2	18.2	18.6	18.6	18.0	18.0	18.0
	Age at first reproduction (years)	14	14	14	NA	NA	NA	NA	NA	NA
	Survival probability <50 %	NA	NA	NA	Year 3; Jan 25th	Year 3; Jan 25th	Year 3; Jan 25th	Year 2; Jun 13th	Year 2; Jun 13th	Year 2; Jun 13th
Minimal Basking	Size reached at 1st season: Mass (g)	16.4	16.2	16.2	15.0	14.8	14.8	12.7	12.1	12.1
	Size reached at 1st season: Length (mm)	48.4	48.3	48.3	47.1	46.9	46.9	44.3	43.8	43.8
	Size reached at 20th season: Mass (g)	281.2	272.5	272.5	15.6	15.2	15.2	12.7	12.1	12.1
	Size reached at 20th season: Length (mm)	118.5	117.1	117.0	47.6	47.3	47.3	44.3	43.8	43.8
	Mean body temperature (°C)	18.0	18.1	18.2	17.9	18.1	18.2	17.7	18.0	18.0
	Age at first reproduction (years)	13	14	14	NA	NA	NA	NA	NA	NA
	Survival probability <50 %	NA	NA	NA	Year 3; Jan 26th	Year 3; Jan 25th	Year 3; Jan 25th	Year 2; Jun 15th	Year 2; Jun 13th	Year 2; Jun 13th
Maximal Basking	Size reached at 1st season: Mass (g)	31.8	16.2	16.2	30.4	14.8	14.8	24.6	12.1	12.1
	Size reached at 1st season: Length (mm)	59.6	48.3	48.3	58.8	46.9	46.9	54.6	43.8	43.8
	Size reached at 20th season: Mass (g)	398.9	272.6	272.5	31.7	15.2	15.2	121.2	12.1	12.1
	Size reached at 20th season: Length (mm)	132.0	117.4	117.0	59.5	47.3	47.3	91.4	43.8	43.8
	Mean body temperature (°C)	21.3	18.2	18.2	21.0	18.1	18.2	20.9	18.0	18.0
	Age at first reproduction (years)	8	14	14	NA	NA	NA	NA	NA	NA
	Survival probability <50 %	NA	NA	NA	Year 3; Apr 4th	Year 3; Jan 25th	Year 3; Jan 25th	Year 8; Mar 6th	Year 2; Jun 13th	Year 2; Jun 13th

Table 5.6 – Predictions of growth, survivorship, and reproductive age under 2050 and 2070 climate simulations at Ellen Brook Nature Reserve and at five candidate assisted migration sites, using a 'maximal basking' and 0 % shade scenario. Cell colour indicates survival outcome, where red reflects 'no survival', orange reflects 'assumed no survival', blue reflects 'some survival', and green reflects 'survival' (refer 2.5.7 main text for definitions). Standard error for average body temperature, annual hydroperiod, and annual water temperature were within ± 0.030 °C, ± 1.024 days, and ± 0.019 °C, respectively.

Climate Model	**HadGem2**		**CanESM2**		**GDFL-CM3**		**HadGem2**		**CanESM2**		**GDFL-CM3**	
Year	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**	**2050**	**2070**
	Ambergate						East Augusta					
Size reached at 1st season: Mass (g)	22.6	23.8	23.3	24.7	23.6	23.4	16.2	16.2	18.4	18.9	16.6	16.9
Size reached at 1st season: Length (mm)	52.3	53.3	52.9	54.0	52.8	53.0	47.1	47.1	49.2	49.6	47.5	47.8
Size reached at 20th season: Mass (g)	408.6	396.0	414.5	414.1	174.7	165.9	406.3	395.1	415.6	412.8	400.5	392.2
Size reached at 20th season: Length (mm)	132.4	131.4	133.1	132.4	101.9	101.4	132.1	130.8	132.8	132.6	132.0	130.6
Mean body temperature (°C)	20.6	20.4	20.7	20.9	20.4	20.4	19.4	19.5	19.7	19.9	19.5	19.5
Mean annual water temperature (°C)	14.2	14.4	14.3	14.5	13.4	14.0	14.2	14.4	14.3	14.5	14.1	14.4
Mean annual hydroperiod (days)	124	123	124	123	121	123	128	127	128	127	127	125
Age at first reproduction (years)	8	10	7	7	NA	NA	9	9	8	8	9	10
Survival probability <50 %	NA	NA	NA	NA	Year 8; May 1st	Year 7; Apr 5th	NA	NA	NA	NA	NA	NA
	Doggerup Creek						D'Entrecasteux National Park					
Size reached at 1st season: Mass (g)	22.4	23.4	22.4	22.7	22.0	22.2	22.9	23.7	22.9	23.1	22.6	22.6
Size reached at 1st season: Length (mm)	52.3	53.0	52.3	52.6	51.9	52.1	52.6	53.3	52.7	53.0	52.4	52.5
Size reached at 20th season: Mass (g)	443.0	437.9	459.2	447.6	447.4	429.5	448.8	437.2	455.4	452.5	440.2	440.6
Size reached at 20th season: Length (mm)	134.4	134.3	134.5	134.5	134.4	134.3	134.4	133.7	134.5	134.4	134.4	134.3
Mean body temperature (°C)	20.1	20.2	20.3	20.5	20.1	20.2	20.2	20.3	20.4	20.6	20.2	20.3
Mean annual water temperature (°C)	14.4	14.4	14.3	14.2	13.9	13.9	14.3	14.4	14.2	14.3	14.0	14.0
Mean annual hydroperiod (days)	133	131	132	130	131	129	131	133	135	129	129	127
Age at first reproduction (years)	6	6	6	6	7	7	7	7	6	6	7	7
Survival probability <50 %	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

	HadGem2		CanESM2		GDFL-CM3		HadGem2		CanESM2		GDFL-CM3	
	2050	2070	2050	2070	2050	2070	2050	2070	2050	2070	2050	2070
	Donnelly River						Ellen Brook Nature Reserve					
Size reached at 1st season: Mass (g)	26.6	27.7	27.2	27.1	27.7	26.5	30.8	31.8	31.2	30.4	28.0	24.6
Size reached at 1st season: Length (mm)	55.5	56.2	55.9	56.0	55.5	55.4	58.9	59.6	59.1	58.8	57.0	54.6
Size reached at 20th season: Mass (g)	431.4	426.7	441.1	446.2	432.6	423.3	423.6	398.9	419.0	31.7	397.3	121.2
Size reached at 20th season: Length (mm)	134.4	134.2	134.5	134.5	134.3	133.9	132.7	132.0	132.7	59.5	130.3	91.4
Mean body temperature (°C)	20.4	20.5	20.6	20.8	20.4	20.4	21.0	21.3	21.2	21.0	20.9	20.9
Mean annual water temperature (°C)	14.7	14.8	14.5	14.5	14.3	14.1	15.1	15.4	15.4	15.17	14.6	15.1
Mean annual hydroperiod (days)	124	122	124	123	123	121	118	118	117	117	117	117
Age at first reproduction (years)	6	6	6	6	7	7	6	8	7	NA	8	NA
Survival probability <50 %	NA	NA	NA	NA	NA	NA	NA	NA	NA	Year 3; Apr 4th	NA	Year 8; Mar 6th

(range six to seven years). However, individuals hatched at Donnelly River were largest in mass and length in their first year ($F_{2, 15} = 3.68$, $P < 0.0001$; post-hoc Tukey tests $P < 0.0001$; mass at first year reported), and also had the greatest cumulative reproduction ($F_{2, 15} = 3.68$, $P < 0.049$; post-hoc Tukey tests $P < 0.030$-0.035).

Simulations at Ambergate and East Augusta both predicted slower rates of *P. umbrina* growth and reproduction, and lower survivorship. At East Augusta, hatchlings failed to reach the critical mass ('presumed no survival') under four of six climate scenarios, with those under CanESM2 only just meeting the criteria to within less than 1 g. At Ambergate, individuals modelled under GDFL-CM3 2050 and GDFL-CM3 2070 survived to eight and seven years respectively. Average body temperatures at East Augusta (19.59 ± 0.03) were significantly lower than at any of the other candidate assisted migration sites ($F_{4, 25} = 2.76$, $P < 0.0001$; post-hoc Tukey tests $P < 0.0001$). While some simulations at Ambergate (HadGem2-CC 2050, HadGem2-CC 2070, CanESM2 2050, and CanESM2 2070) predicted suitable first-season growth, overall survivorship, and reproduction, the predicted ages at reproduction were equal to or greater than that of other candidate assisted migration sites. Individuals also grew to smaller adult sizes than those at the other candidate assisted migration sites (i.e. Doggerup Creek, Donnelly River and D'Entrecasteux National Park; $F_{3, 20} = 3.10$, $P < 0.0099$; post-hoc Tukey tests $P < 0.004$-0.008; mass at 20 years reported).

Simulations run under the 'minimal basking' 0 % shade combination (i.e. the combination that was best able to predict current length and mass observations in the wild; see 5.3.2) had poor survival outcomes, with no hatchlings reaching the critical mass of 18 g under any climate change scenario. However, survivorship to 20 years was predicted in 80 % of the assisted migration scenarios (resulting in an ‘assumed no survival’ category). East Augusta and Ambergate had the lowest total survival likelihoods, with full mortality predicted under the GDFL-CM3 2050 and 2070, and HadGem2 2070 climate models (Table 5.7). In all simulations, Ellen Brook Nature Reserve had higher average water temperatures (15.13 ± 0.09 °C; $F_{4, 25} = 2.76$, $P < 0.0001$; post-hoc Tukey tests $P < 0.0001$), and shorter hydroperiods (117 ± 0.23 days; $F_{4, 25} = 2.76$, $P < 0.0001$) than any of the candidate assisted migration locations (range 14.18 - 14.48 °C and 122 - 131 days, respectively).

5.4 DISCUSSION

Altering thermoregulatory behaviour is one form of plasticity that can buffer the effects of climate change in the short term by allowing individuals to maintain body temperatures within the bounds of their critical thermal limits (Kearney *et al* 2009; Clusella-Trullas *et al.* 2011; Huey *et al.* 2012) or, as I have shown mechanistically, by boosting growth potential under novel climates. Assuming that suitable microclimates are not limiting, thermoregulatory behaviours such as basking can allow individuals to attain optimal body temperatures for their physiological processes (Hutchinson 1979). In species that use solar radiation as their primary method of heating (i.e. heliothermic species), basking can increase metabolic and digestive rates (Jackson 1971; Bennett & Dawson 1976; Parmenter 1980), activity rates (Gatten 1974), rates of follicular development (Ganzhorn & Licht 1983), and enhance the development of oviductal eggs (Moore & Seigel 2006). When western swamp turtles were simulated to maximise their basking behaviour under current and historic conditions, the age to first reproduction

Table 5.7 – Predictions of mass and survival outcomes for individuals simulated at candidate assisted migration sites under a 'minimal basking' 0 % shade combination. Ellen Brook Nature Reserve is provided for comparison. 'No survival' (red) is where neither the critical mass or survivorship to 20 years were reached. 'Assumed no survival' (orange) is where survival to 20 years was met but the critical mass was not attained. Other outcomes ('some survival' where the critical mass was attained but survival to 20 years was not met, and 'full survival' where both the critical mass and survivorship to 20 years were reached) were not met.

Site	Climate Simulation					
	HadGem2 2050	HadGem2 2070	CanESM2 2050	CanESM2 2070	GDFL-CM3 2050	GDFL-CM3 2070
Mass at End of 1st Season (g)						
Ambergate	10.3	10.6	10.4	10.6	10.2	10.1
East Augusta	8.0	8.1	8.6	8.7	8.0	8.0
Doggerup Creek	10.4	10.7	10.4	10.6	10.2	10.2
D'Entrecasteux	10.8	10.9	10.8	10.9	10.6	10.6
Donnelly River	11.9	12.3	12.1	12.2	11.8	11.7
Ellen Brook Nature Reserve	15.4	16.2	15.2	14.8	13.4	12.1
Survival to 20 years						
Ambergate	True	False	True	True	False	False
East Augusta	False	False	True	True	False	False
Doggerup Creek	True	True	True	True	True	True
D'Entrecasteux	True	True	True	True	True	True
Donnelly River	True	True	True	True	True	True
Ellen Brook Nature Reserve	True	True	False	False	False	False
Survival Outcome						
Ambergate	Assumed No Survival	No Survival	Assumed No Survival	Assumed No Survival	No Survival	No Survival
East Augusta	No Survival	No Survival	Assumed No Survival	Assumed No Survival	No Survival	No Survival
Doggerup Creek	Assumed No Survival	Assumed No Survival	Assumed No Survival	Assumed No Survival	Assumed No Survival	Assumed No Survival
D'Entrecasteux	Assumed No Survival	Assumed No Survival	Assumed No Survival	Assumed No Survival	Assumed No Survival	Assumed No Survival
Donnelly River	Assumed No Survival	Assumed No Survival	Assumed No Survival	Assumed No Survival	Assumed No Survival	Assumed No Survival
Ellen Brook Nature Reserve	Assumed No Survival	Assumed No Survival	No survival	No Survival	No Survival	No Survival

was shortened, reproductive output was maximised, and survival probabilities increased. However, when the mass, length, and temperature predictions generated from these simulations were compared to data from individuals inhabiting Ellen Brook Nature Reserve, the model predictions of these parameters were greater than the field observations. This suggests that *P. umbrina* tend to underutilise the warm microclimates available to them, thereby lessening rates of growth and reproduction.

Basking western swamp turtles are quick to retreat to the water when disturbed from a distance (S. Arnall, pers. obs.) and the species has also been variously described as "shy and retreating[1]", "easily disturbed" (Kuchling 1993), and having "extreme shyness" and a "secretive nature" (Burbidge 1967). These behaviours are indicative of predator avoidance (Ydenberg & Dill 1986), which could explain the disparity between the potential and realised growth in *P. umbrina*. Some animals lower or alter their foraging strategy in response to perceived increases in predation risk, which in turn lowers their growth rates (Lima & Dill 1990; Abrams & Rowe 1996). Likewise, there is evidence that high levels of activity (associated with high growth rates) increases the risk of predation (Bernays 1997; Anholt & Werner 1998; Gotthard 2000; Biro *et al.* 2006). Therefore, it is possible that swamp turtles do not achieve their growth potential because of a fundamental trade-off between growth rate and predation risk (Lima & Dill 1990; Werner & Anholt 1993).

How the swamp turtle has continued to persist at low abundances over a long time might also be related to this trade-off. In the notion of 'life or lunch' (*sensu* Abrams 2000a), the long-term risk of failing to accumulate body mass is overshadowed by the immediate (potential) risk of death. Given the major effects of predation on fitness,

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[1] http://www.abc.net.au/7.30/content/2013/s3729273.htm

traits that affect the ability to avoid predation should be under strong positive selection (Abrams 2000b). Escaping to a safe microhabitat might reduce immediate predation risk, but it also imposes fitness costs associated with the occupancy of a sub-optimal environment within which to forage (Maynard Smith 1982; Lima & Dill 1990; Downes 2001). *P. umbrina* is the sole surviving member of a genus that dates back 15-20 million years (Gaffney 1977; Zhang *et al.* 2017), and is both slow-growing and long-lived (Burbidge 1981; Chapter 4), which suggests that selection has favoured reduced growth rates and high levels of defence within their natural environment over time.

This hypothesised strategy (i.e. that *P. umbrina* avoid maximal basking and foraging in favour of safety from predation) has important implications for the movement of this species under climate change. Here I have predicted that without remedial action, Ellen Brook Nature Reserve (the species' core habitat) becomes unsuitable for supporting *P. umbrina* beyond 2050 under the majority of climate simulations, due to shorter hydroperiods and warmer temperatures. However, I have also shown that if individuals employed behavioural flexibility in their capacity to bask (i.e. if they switched to a maximal basking strategy in full sun), death could be delayed or avoided. Similarly, for hatchlings to attain the critical mass in any of the sites evaluated for assisted migration, my model predicts they must also employ a maximal basking strategy. Developmental and behavioural plasticity has been widely hypothesised to mitigate the negative effects of climate change, and this has been explored in several ectothermic species (e.g. Kearney *et al.* 2009; Aubret & Shine 2010; Refsnider & Janzen 2012). Options for behavioural adjustments include changes to nesting site choice, depth and time (Doody 2009), alterations to thermal basking and retreat patterns (Refsnider & Janzen 2012), and changes to site selection for aestivation (Roe & Georges 2008; Roe *et al.* 2008).

The scope for behavioural plasticity in *P. umbrina* is unknown, but anecdotal evidence from captive conditions suggests that the species may be moderately adaptable to environments that deviate from natural conditions (Dade *et al.* 2014). In light of these results, the degree of behavioural flexibility in *P. umbrina* should be quantified, particularly when evaluating assisted migration.

Assuming a necessity to reach the critical mass of 18 g, virtual experiments performed at all five candidate assisted migration sites indicated no survival if *P. umbrina* basked only when temperatures were too cold to forage. However, altering this assumption resulted in a very different outcome, where the model predicted good long term (20-year) survival in almost all assisted migration scenarios, despite 18 g not being met in the first year of life (refer Table 5.7 main text). The precautionary principal (O'Riordan 1994) is therefore likely to play a large role in the selection of assisted migration sites for this species (McLachlan *et al.* 2007; Vitt *et al.* 2009; Ste-Marie *et al.* 2011; but see also Schwartz *et al.* 2009), whereby choosing to apply this principal to the 'critical mass' assumption (i.e. assuming that only those sites where the critical mass is met will be suitable under climate change, rather than selecting sites where the critical mass is not met but the model nevertheless predicts good long term survival) greatly influences the appropriateness of the candidate assisted migration locations.

The critical mass of 18 g is derived from the smallest hatchling known to survive aestivation in the wild (Burbidge *et al.* 2010; Chapter 2), and suggests that a failure to reach 18 g prior to aestivation results in death, either from starvation or dehydration. Water balance was not examined here, though this can also underlie the behaviour and activity budgets of individuals and therefore constrain growth, survival, and reproductive potential (Sinervo *et al.* 2010). In turtles, lethal dehydration occurs at a loss of approximately 30-35 % of body water (Seidel 1978; Mautz 1982; Peterson & Stone 2000; Ligon & Peterson 2002; Roe *et al.* 2008), with rates of water loss influenced by initial body size, body position, and the characteristics of the surrounding environment (e.g. wind speed, air and substrate temperature, humidity, and vapour potential; Bentley & Schmidt-Nielsen 1966; Shoemaker & Nagy 1977; Foley & Spotila 1978; Nagy & Peterson 1988; Zimmerman *et al.* 1994; Cloudsley-Thompson 1999; Bulova 2002). Hence, a small western swamp turtle aestivating in a comparatively exposed environment (such as in a shallow depression covered by leaf litter) is likely to be at greater risk of dehydration over aestivation than a larger individual buried deeper in wet clay tunnel. This is similar to the egg stage, where embryonic survival is influence by factors such as the size of the egg, the physical characteristics of the shell, the water potential of the surrounding substrate, and the proportion of the egg contacting the substrate (Packard 1991). For example, in the painted turtle (*Chrysemys picta*), embryos exposed to wet substrates consume yolk more rapidly, grow faster, and incubate longer than embryos exposed to dry substrates and as a result, hatchlings emerging in wet environments are larger and contain less residual yolk than hatchlings emerging in dry environments (Packard and Packard 1986). However, some turtle eggs (e.g. those of softshell turtles) may also contain sufficient water at oviposition to allow embryos to fully exploit their energy reserves in growth, without being influenced by outside water (Packard *et al.* 1981). Exploration of the relationship between body size, reserve dynamics, and water balance in *P. umbrina* is a logical next step, and my model should be explored to determine how dehydration and desiccation risk interact with starvation risk during critical life stages (such as nesting, embryonic development, post-hatchling growth, and aestivation) to determine the key constraining factors for survival under future climates. In a drying climate where rainfall events become less frequent, it may be dehydration rather than starvation that primarily influences survival probabilities during aestivation (*sensu* Roe *et al.* 2008).

The virtual experiments presented here have raised numerous questions about the basking requirements of *P. umbrina*, though have not considered the potential for basking strategies to differ between sexes, or to change across life stages (e.g. Lefevre & Brooks 1995). Similarly, the assessments of assisted migration sites should be interpreted with caution because of the magnitude of error associated with size and mass predictions during early life stages, and because of the limited scope to predict wetland characteristics at the candidate assisted migration sites. My wetland model was calibrated to Ellen Brook Nature Reserve (e.g. the soil characteristics and rainfall multiplier matched the local wetland conditions at Ellen Brook), and as such, predictions are limited to evaluating how turtles would respond to a wetland environment reflective of Ellen Brook Nature Reserve being transferred to the more southerly locations of the five candidate assisted migration sites. While still meeting the expected habitat requirements for *P. umbrina*, the candidate assisted migration locations differ from Ellen Brook Nature Reserve in terms of soil and vegetation characteristics (Dade *et al.* 2014; Mitchell *et al.* 2016), which both influence how wetlands pool water and absorb heat in response to local conditions (Coletti *et al.* 2012). Wetland models that specifically capture the local conditions at the candidate assisted migration sites are required to establish certainty in the preliminary model predictions generated here. Relatedly, the simplification of the model creates some uncertainties about water balance under climate change (Chapter 6), and does not capture external processes such as predation or anthropogenic change (e.g. groundwater abstraction) which may also influence the future success of *P. umbrina* at the individual and population levels. Thus my models should be considered as just one aspect within a range of considerations required when evaluating current and potential future wetland habitats.

An ability to predict fitness outcomes under novel conditions is particularly relevant in the context of threatened species management under climate change where strategies such as assisted migration are likely to progress (Javeline *et al.* 2015; Chapter 2). This chapter illustrates the value of ‘virtual experiments’ for predicting a species’ biophysical and behavioural capacity towards withstanding climate change: my model generated logical, mechanistically-based hypotheses of what might be expected in the wild, which can then be experimentally tested in the laboratory or field. The generation of hypotheses from modelling outputs is likely to become increasingly valuable for guiding conservation and research under novel futures (Tomlinson *et al.* 2014), and for assisted migration, I recommend the inclusion of the ‘virtual experiment’ approach when assessing a species’ vulnerability to climate change, and subsequently, determining whether assisted migration is necessary (e.g. Chapter 2).

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CHAPTER SIX

6. DISCUSSION

This study aimed to examine the suitability of the western swamp turtle as an assisted migration candidate, and to apply both an energetics model and a biophysical niche model to facilitate the evaluation of its current habitat, and potential assisted migration sites under future climates. In short, I have argued that:

1) The western swamp turtle is a good candidate for assisted migration, because on balance, the benefits of assisted migration outweigh the potential costs and risks, and it meets the majority of the qualitative selection criteria available for assessing a species' suitability towards assisted migration.
2) Metabolically, the performance of *P. umbrina* declines beyond 30 °C, and physiological performance is optimal between 25 °C and 30 °C.
3) Energetically, the western swamp turtle has high somatic maintenance costs which suggests it is suited to surviving periods of low resource availability following the "waste-to-hurry" hypothesis of Kooijman (2013). However, a high Arrhenius temperature is associated with its physiological rates, which indicates a high sensitivity to temperature.
4) The current core location for *P. umbrina* (Ellen Brook Nature Reserve) is unlikely to be suitable by 2050 without mitigation measures. However, this assessment is dependent on behavioural strategy, and if turtles basked maximally in full sunlight across their entire lifecycle, survival probabilities, growth rates, and reproductive outputs are greatly improved.
5) Three of five prospective assisted migration locations are likely to have positive survival and reproduction if a maximal basking strategy is used. However, these predictions are based on wetland characteristics that are identical to those at Ellen Brook Nature Reserve presently, and refinement is required to simulate their microclimates more realistically. Employing the 'precautionary principal'

(O’Riordan 1994), early indicators are that all candidate assisted migration locations will be unsuitable in 2050 and 2070 if swamp turtles are inflexible in their basking behaviours.

Basking behaviour makes all the difference to P. umbrina *performance under climate change*

Here I have provided further indication that climate change will almost certainly have negative impacts within *P. umbrina*’s current range: principally by reducing growth, survival, and reproduction (Chapter 5). Untangling the reasons behind the swamp turtles’ vulnerability to climate change is complex. Whilst certain biological traits (e.g. long generation times, slow maturation, and low reproductive outputs; Chapter 2; Chapter 4), suggest they are not well suited to adapting rapidly in a changing climate, the energetically-based biophysical model produced in this thesis reveals that their vulnerability is also dependent upon the interrelation between environmental constraints (temperature and hydroperiod) and behaviour. For example, vulnerability to climate change appears to be highest when turtles either do not bask, or bask only when temperatures are too cold to forage (Chapter 5). Conversely, under simulations of a ‘maximal basking’ strategy (whereby the warmest microclimates are always sought out) turtles increase growth rates, improve reproductive outputs, and improve survival in simulations that would otherwise result in climate-related mortality. This suggests that from an energetics perspective, thermoregulatory strategy has the potential to ‘make or break’ the western swamp turtle under climate change, and this applies both within their current core range and at potential assisted migration locations.

The capacity for plasticity in thermoregulatory strategy is yet to be quantified for *P. umbrina*, but flexibility in basking behaviour is well described in other turtles. For example, in the painted turtle (*Chrysemys picta*), juveniles bask for shorter periods than adults (Lefevre & Brooks 1995), and gravid females bask more frequently than non-gravid individuals, especially around oviposition (Krawchuk & Brooks 1998). In the slider turtle (*Pseudemys scripta*), females typically bask much longer than males (but season can have an effect; Hammond *et al.* 1988), and in the Spanish pond turtle (*Mauremys leprosa*), the temperature at which basking ceases is higher in fed individuals than in fasted ones (Polo-Cavia *et al.* 2011). Relatedly, thermal preferences may also change in response to feeding: Gatten (1974) found a 4.5 °C difference in thermal preference between fed and fasted slider turtles, a pattern also reported by Dubois *et al.* (2008) in wood turtles (*Glyptemys insculpta*). Clearly, thermoregulatory strategy can reflect several factors including size, season, sex, and state (i.e. nutritional and reproductive condition), the majority of which will not remain static across time.

A major limitation of the model produced at Chapter 5 was assumptions regarding *P. umbrina* basking behaviour, such that 1) the basking strategy remained constant over an individual's lifetime, 2) the basking strategy was generalised for all life stages and sexes, and 3) only aerial basking was considered. A better understanding of basking behaviour in the western swamp turtle would improve confidence in the model, and importantly, could improve future modelling. Whilst it might be impractical to include all behavioural variants, it would be possible to modify the routines in the biophysical model such that one behavioural strategy is applied to one life stage (e.g. juveniles) until a threshold is reached, after which a second behavioural strategy could be substituted. This may be particularly relevant for modelling the hatchling life stage which may preferentially bask aquatically rather than in terrestrial locations due to a small body size (Janzen *et al.* 1992). Freshwater turtle species (such as the similarly sized *Chrysemys picta bellii;* Beckmann *et al.* 2015) exploit aquatic thermoclines (a distinct layer in a body of water in which there is a large change in temperature over depth). Both aquatic and terrestrial basking have been recorded in hatchling *P. umbrina* (Mitchell *et al.* 2012), and more fine-scale information is required to assess the presence and potential use of thermoclines in the wild, especially as these can minimise exposure to predators when compared to terrestrial basking (Refsnider & Janzen 2012).

The suitability of candidate assisted migration sites are (mostly) well-aligned with existing predictions

This study complements the four pre-existing spatially-explicit models created to inform future translocations of *P. umbrina* (these being Mitchell *et al.* 2013, Dade *et al.* 2014, Bin Tarque 2016, and Mitchell *et al.* 2016). Whilst the spatial extent and methodology of these models are not identical, there is sufficient congruence to make some comparisons, particularly with Dade *et al.* (2014) and Mitchell *et al.* (2016) who examined the same wetland localities as covered by this thesis (Table 6.1).

All models that have been explored under climate change scenarios thus far are in agreement that current *P. umbrina* locations are likely to become increasingly unsuitable under forward climates without remedial management. At Ellen Brook Nature Reserve, poor survival, growth and reproduction thresholds were predicted in approximately 90% of the 2050 climate, shading, and behavioural combinations modelled in this thesis. This is consistent with Mitchell *et al.* (2013) who predicted a decline in swamp turtle activity potential as soon as 2030, and Mitchell *et al.* (2016)

Table 6.1 – Comparisons between the four spatially-explicit models generated to inform translocation and assisted migration decision making for *P. umbrina*. Ellen Brook Nature Reserve, Twin Swamp Nature Reserve, Mogumber and Moore River are current populations.

	Study				
	Mitchell *et al.* 2013	Dade *et al.* 2014	Bin Tarque 2016	Mitchell *et al.* 2016	This study
Focus	Integration of a mechanistic biophysical niche model and a wetland model to predict foraging potential	Ranking of wetlands by habitat factors (e.g. size, proximity to roads, soil type, predators) as weighted by expert elicitation	Comparison of clay-based wetlands and groundwater-fed wetlands, incorporating a suitability index based on a thermal response curve for *P. umbrina*	Examination of the embryonic niche by modelling soil temperatures, embryonic development, and the survival probabilities of embryos	Extension of Mitchell *et al.* 2013 to identify thresholds of survival, maturity and reproduction, for the extended post-hatchling life stage
Global Climate Model(s) Applied	"Wet future" (0.7 °C air temperature increase, 1 % rainfall decrease); "Median future" (1 °C air temperature increase, 7 % rainfall decrease); "Dry future" (1.3 °C air temperature increase, 14 % rainfall decrease)	Nil	"Wet future" (0.7 °C air temperature increase, 1 % rainfall decrease); "Median future" (1 °C air temperature increase, 7 % rainfall decrease); "Dry future" (1.3 °C air temperature increase, 14 % rainfall decrease)	HadGem2-CC	GDFL-CM3; CanESM2; HadGem2-CC
Years Applied	Current, 2030	NA	Current, 2030	Current, 2050, 2070	Current, 2050, 2070

	Mitchell *et al.* 2013	Dade *et al.* 2014	Bin Tarque 2016	Mitchell *et al.* 2016	This study
Ellen Brook Nature Reserve	Decline in activity potential	Three of the four current locations rated as 5 out of 5 for habitat suitability	Highest suitability index	2050 females need to deposit eggs deeper and in shadier sites to avoid mortality. 1/3rd of nest types experience lethal temperatures in a 2070 climate	Unsuitable by 2050 under 24/27 scenarios (mortality or critical mass not met)
Twin Swamps Nature Reserve	Areas to the north and inland of the current range unsuitable. No change or an improved activity potential for sites near the south-west coast. Sites around Bunbury, the Scott Coastal Plain (east of Augusta), and the Nuyts Wilderness (northwest of Walpole) were the best locations in terms of activity potential.		Translocation sites to the north of Ellen Brook Nature Reserve less suitable under future climates		
Mogumber					Not examined
Moore River					Not examined
Ambergate Nature Reserve		Poorly ranked (11/12)	Claypan wetlands: Narrow strip from the south of Geraldton to Mandurah suitable. Groundwater wetlands: Eastwards from Augusta suitable. Sites on the Swan Coastal Plain as far south as Bunbury will likely remain acceptable. Groundwater-type wetlands have longer hydroperiods than claypan-type wetlands across the domain.	Most thermally suitable candidate site for embryos	Ranked poorly (4/5)
East Augusta		NA		Ranked highest	Ranked worst (5/5)
Donnelly River		Intermediate suitability (7/12)		Ranked poorly	Ranked highest: fastest growth rates, largest cumulative reproduction
Doggerup Creek		Intermediate suitability (8/12)		Low: no nests in 75 % or 90 % shade reached maturity within 205 days. Cold and unsuitable.	Intermediate suitability
D'Entrecasteaux National Park		Ranked 1/12			Intermediate suitability

who suggested that by 2050, female turtles would likely need to deposit eggs deeper and in locations with higher shade levels to avoid mortality. The population of *P. umbrina* at Ellen Brook Nature Reserve is currently considered to be more robust than those at other locations (Chapter 2), but indications from these models suggest that “halfway technologies” (Frazer 1992; such as the pumping of bore water to extend hydroperiods) will be increasingly required to sustain this population *in-situ* over the long term.

The relative suitability of potential assisted migration sites is less clear. In 2013, Mitchell *et al.* produced a spatial model that introduced the coupling of an eco-hydrological (wetland) model and a biophysical niche model to predict the relative suitability of regions for *P. umbrina* with respect to foraging potential (that is, how the combination of the hydroperiod and water temperatures would permit foraging activity at suitable body temperatures). Sites near the south-west coast of Western Australia showed either no change or an improved activity potential by 2030, and in particular, sites around Bunbury, the Scott Coastal Plain (east of Augusta), and the Nuyts Wilderness (northwest of Walpole) were identified as the best locations in terms of activity potential. In a similar vein, Bin Tarque (2016) also concluded the suitability of the Augusta region was comparatively high, particularly for groundwater-fed type wetlands. Suitability in this instance was examined from the species perspective by creating an index that gave higher values to those locations with longer hydroperiods and which had water temperatures falling within the turtles’ active range.

Whilst the locations examined by Mitchell *et al.* (2013) and Bin Tareque (2016) were not identical to those examined in Chapter 5, their regional findings did contrast my own, in which East Augusta in particular was predicted to be one of the worst candidate assisted migration locations. This difference in suitability may be attributable to a major limitation in both Mitchell *et al.* (2013) and Bin Tarque (2016), this being that the terrestrial phase of *P. umbrina*'s biology was excluded (i.e. the suitability of the sites for annual aestivation was not considered). The importance of including the aestivation environment can be demonstrated by comparing the Chapter 5 predictions from one of the worst sites (East Augusta) against one of the best sites (Donnelly River). Individuals at Donnelly River were predicted to grow larger at the end of their first season (26-27 g) and mature faster (6-7 years) than individuals at East Augusta (16-19 g; 8-10 years). However, the aquatic conditions at these locations were practically identical in mean water temperature and hydroperiod (to within 0.4 °C, and 4 days, respectively). This suggests terrestrial conditions have a large influence on the thresholds of survival, growth, and reproduction.

Because the relative measures of suitability in both Mitchell *et al.* (2013) and Bin Tarque (2016) were driven by the aquatic stage of *P. umbrina*'s environment, these models did not have the capacity to capture the related biophysical constraints experienced by turtles during the aestivation period. This was addressed in this thesis through the incorporation of a dynamic energy budget routine into the biophysical niche model, and as such, the predictions of suitability generated in Chapter 5 are likely to be more refined and better resolved than those of previous models (from a species assessment perspective). The inclusion of a water budget routine would further highlight the mechanisms by which the aestivation environment drives survival and reproductive potential in *P. umbrina*, and would further improve the existing models.

The lack of a terrestrial component in the spatial models cannot account for the differences between Mitchell *et al.* (2016), who explicitly modelled the terrestrial nesting habitats of *P. umbrina* and subsequent embryonic development, and the predictions of this thesis. Based on the thresholds of survival, growth, and reproduction from Chapter 5, the candidate locations of Doggerup Creek, D'Entrecasteaux National Park, and Donnelly River were predicted to be comparatively better locations for the assisted migration of *P. umbrina* than East Augusta and Ambergate. This is virtually opposite to the findings of Mitchell *et al.* (2016) who predicted that Ambergate and East Augusta were the most thermally suitable candidate sites for embryos. Further, two of the sites predicted to be the best for post-hatching *P. umbrina* in this thesis (Doggerup Creek and D'Entrecasteaux National Park) were among the worst in Mitchell *et al.* (2016), where these locations were predicted to be too cold for embryonic development under most scenarios examined. It would be useful to repeat the models of Mitchell *et al.* (2016; which were modelled under the 'HadGem2' climate model) with the 'CanESM2' global climate model (as per Chapter 5) which has a comparatively high impact on air temperatures, to determine if these differences are preserved under alternate climate models. The HadGem2 simulations in this thesis produced the mildest impacts on growth, survival and reproduction across all locations examined. Whilst it is current practise to translocate captive-bred juveniles (Burbidge *et al*. 2010), the suitability of sites for nesting by mature females will be paramount to the establishment of self-sustaining populations at any translocation site. Therefore, these contrasting results require substantial consideration when planning an assisted migration strategy for this species.

Finally, in a multiple criteria analysis, Dade *et al.* (2014) examined habitat components such as wetland type, land use change, site size, predator control, and distance from main roads (weighted by importance by *P. umbrina* experts) to rank prospective assisted migration locations. Consistent with my findings, the region of D'Entrecasteaux

National Park was ranked highest in suitability (ranked 1/12; referred to as Chesapeake Road within Dade *et al.*), with Doggerup creek (8/12) and Donnelly River (7/12) ranking intermediately. Likewise, Ambergate was one of the least favourable locations (ranked 11/12). Dade *et al.*'s approach is particularly valuable for the post-hoc evaluation of sites, where locations identified as being climatically suitable via mechanistic modelling can be evaluated for site-specific factors which may otherwise influence their suitability. For example, D'Entrecasteaux National Park has some of the most suitable soil types, vegetation compositions, and salinity levels, and has a large land area relatively isolated from main roads, further broadening its appeal as a site to attempt assisted migration.

Notwithstanding the comments above, it should be noted that confidence in the microclimate predictions generated in this thesis is reasonably low when considering assisted migration sites. My findings should be taken as relative comparisons, rather than absolute predictions of survivorship, growth, and reproduction at these locations. Of emphasis again, is that the wetland parameters were based on Ellen Brook Nature Reserve, and not on the local wetland characteristics at the candidate sites. Therefore, the hydroperiod lengths and water temperature predictions may be inaccurate, consequently skewing the projections of the growth of *P. umbrina* at these sites. By contrast, projections for Ellen Brook Nature Reserve have a much higher confidence level, given the wetland model was calibrated at this location. It is recommended that the biophysical model of Chapter 5 be re-applied for each candidate assisted migration location once the local wetland conditions have been quantified and the wetland model has been recalibrated accordingly. This work will be critical before any major commitments are made to translocate turtles to these wetlands.

Questions regarding biological unknowns should be resolved to improve the prospects of assisted migration

Chapter 2 identified three key knowledge gaps regarding *P. umbrina* biology that currently remain unresolved, and these should be addressed to improve the likelihood that assisted migration will be successful. These factors were 1) a need for population-level modelling, 2) the lack of knowledge of the species' genetic diversity and evolutionary potential, and 3) a requirement for an improved understanding of home range and homing behaviours. A resolution of the first two unknowns will help guide how to best establish an assisted migration population, whilst the latter will be important for evaluating reserve size requirements, invasion potential, and potential impacts of the western swamp turtle on wetland ecosystems.

It is expected that experimental introductions at candidate assisted migration locations will follow existing translocation protocols (i.e. releases will comprise of captive-bred juvenile individuals of unknown sexes from different incubation regimes and lineages, because this is the established method that has been successfully implemented in the past, and trial introductions to two candidate assisted migration sites have already commenced using these protocols; A. Bouma, pers. comm.). However, the size, age composition, sex ratio, and genetic composition of the founding population is likely to influence the long term success of assisted migration initiatives (Seddon *et al.* 2007; e.g. Miller *et al.* 2009). Releasing juveniles with similar characteristics (e.g. age and size) allows for comparisons of growth and survival at different locations, and this may be the best approach for initial experimental releases. However, once a site is deemed suitable for assisted migration, individuals of the founder population should be carefully selected following the principals of conservation genetics (Frankham *et al.* 2002;

Allendorf & Luikart 2009), reintroduction biology (Armstrong & Seddon 2008; Jamieson & Lacy 2012), and use population viability modelling (e.g. Boyce 1992) to maximise success. Because assisted migration populations will be isolated from existing populations (e.g. the Ellen Brook Nature Reserve population), they will need to be established and managed similarly to closed island populations which have no natural immigration or gene flow. Unless individuals are moved between sites, the mean level of inbreeding could increase over time, leading to a loss of genetic diversity and reduced population fitness due to a lack of gene flow (Frankham *et al.* 2002). Environmental, ecological, and genetic stochasticity can expose small founder populations to extinction, especially during early stages (Ahlroth *et al.* 2003 and references therein), and so population modelling will help determine the minimum number of individuals to release initially to maximise establishment success. Given it will take several decades to determine recruitment success at assisted migration locations (due to the low fecundity of *P. umbrina*), knowledge of the genetic diversity of *P. umbrina* (and associated population modelling) will improve the likelihood of a self-sustaining population becoming established, and will likely yield a better return for investment in the long term.

Strengths, weaknesses, opportunities, and threats: reflections on the approach adopted

My thesis has demonstrated the practicality of an energetically-driven biophysical niche model for evaluating the susceptibility of the western swamp tortoise to climatic change, and for evaluating the potential merit of assisted migration as a mitigating strategy at some key locations. The ability to integrate an energy budget has allowed me to quantify the consequences of different hydroperiods and environmental temperatures on the growth and reproduction potential of *P. umbrina*, under both current and future climates, and particularly in relation to the potential for growth in the hatchlings' first season (and its influence on survival through their first summer). These findings can then contribute to decision making relating to the assisted migration of this species.

There are several strengths (S), weaknesses (W), opportunities (O) and threats (T) to the modelling approach adopted here, and a brief SWOT analysis is provided in Table 6.2. In short, the approach adopted in this thesis has facilitated a critical evaluation of the suitability of assisted migration for *P. umbrina* in context of other management strategies (such as the restoration of habitat corridors along climatic gradients; Chapter 2), and has improved knowledge of the species' physiology and energy balance (Chapters 3 and 4). The models have also contributed another layer of detail to the spatial models already in existence for evaluating translocation strategies for *P. umbrina*, but there are numerous avenues for exploration and improvements, particularly regarding the sensitivity and accuracy of the reproductive predictions (which were relatively coarse and had more error in comparison to the other life history traits modelled), and the effects of variable aestivation seasons (during which water balance is likely to be highly influential). It is likely the approach adopted in this thesis could be applied to other threatened species for which a lack of distribution data points prohibit the development of correlative species distribution models (e.g. the noisy scrub bird, *Atrichornis clamosus*, and the western ground parrot, *Pezoporus flaviventris*, which are both geographically restricted and thought to be negatively influenced by climate change; Garnett & Franklin 2014). However, the mechanistic approach I adopted is demanding in terms of the knowledge required for the parametrisation of the models, and this may limit the ability for implementation in other species where budgetary and/or time constraints apply.

Table 6.2 – SWOT (strengths, weaknesses, opportunities and threats) analysis of the modelling methodology used in this thesis which aimed to apply an energetically-informed biophysical niche model to evaluate species distribution at key sites under current and future climates.

Strengths

- Improved species knowledge through modelling process
- Species Distribution Model (SDM) based on high-resolution climate data
- Validation based on substantial historic data
- Operates independently of (limited) distribution data points
- Gives ability to test 'what if' scenarios (through virtual experiments)
- Performs well against observed data
- Input data robust (derived from captive conditions and through knowledgable stakeholders)

Weaknesses

- Low reproduction accuracy
- Assumes no limitation in prey/food availability
- Basking behaviours generalised and assumed to remain constant over time
- No water budget model integrated
- Assumes *P. umbrina* aestivate (not experimentally confirmed)
- Assumes no change in thermal preferences or performance over time
- Wetland model only calibrated for Ellen Brook Nature Reserve
- Does not consider biotic influencing processes (e.g. predation, competition)

Opportunities

- Modify husbandry protocols to increase reproduction sampling frequency
- Parameterise dynamic energy budget model by sex
- Quantify basking behaviours, including changes with life stage and time, and thermoclines
- Parametrise wetland models for specific sites
- Broaden spatial extent of model to screen the entire south-west WA bioregion and/or Australia
- Reassess logistical, ethical, and risk constraints once candidate assisted migration site selected
- Complete population viability modelling (can be informed by dynamic energy budget model in this thesis)
- Integrate a water balance model to examine desiccation risk
- Conduct a summer sensitivity analysis under current and future climates
- Quantify of how biotic interactions might shape current and future habitat occupancy and distribution

Threats

- Computationally intensive
- Resource (cost/time) intensive
- Requires large volume of specific data (e.g. thermal response curve, zero- and uni-variate data)
- Does not give absolute predictions (i.e. generally useful for relative comparisons only)
- Requires on ground validation (hypothesis testing)
- Rarity of species limits experimental scope

The logical next step for the assisted migration of *P. umbrina* is to resolve the wetland models for the candidate assisted migration locations, and then layer the key models (i.e. embryos, Mitchell *et al* 2016; hatchlings and adults, this study; and intrinsic factors, Dade *et al.* 2014), to identify the locations that best capture the collective positive outcomes. It may also be possible to extend the spatial resolution of the biophysical model produced in Chapter 5 to screen the wider south-west Western Australia bioregion for other potential suitable wetlands. It is important to emphasise that models are simply hypotheses, and it will now be pertinent to ground-truth the predictions made in this thesis, and modify the biophysical niche model in line with further empirical data that may be collected in the future. Further, this work represents the foundational 'fundamental niche' layer of *P. umbrina* distribution, and as such, forms the platform upon which to next introduce additional factors that might shape the turtles' realised niche, such as both prey and predator biotic interactions. The results of this thesis should also be incorporated into any future discussions regarding the ethics and values of adopting an assisted migration strategy for *P. umbrina*. For example, arguments for the assisted migration of species for their functional role, rather than a single-species rescue approach (e.g. Lunt *et al.* 2011), will be important to consider when deciding the extent of resources to be allocated to safeguarding wild populations of *P. umbrina*.

Concluding remark

The current persistence of the western swamp turtle is attributable to the investments of this species' "champions" – the recovery team, community members, research organisations, managers and scientists who have impelled a conservation agenda for this iconic and unique threatened species (Martin *et al.* 2012). It is hoped that in a similar fashion, the outcomes and questions raised in this thesis will further contribute to the long term persistence of the western swamp ‘tortoise’ in the wild. By establishing a general (eco-energetics based) methodology suitable for assessing a species’ distribution and habitat quality, it is hoped that this work will serve as a template for the evaluation of assisted migration strategies for other fauna whose habitat is likely to be marginalised by climate change.

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APPENDIX A

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Article

Linking Eco-Energetics and Eco-Hydrology to Select Sites for the Assisted Colonization of Australia's Rarest Reptile

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Abstract: Assisted colonization the deliberate translocation of species from unsuitable to suitable regions is a controversial management tool that aims to prevent the extinction of populations that are unable to migrate in response to climate change or to survive *in situ*. The identification of suitable translocation sites is therefore a pressing issue. Correlative species distribution models, which are based on occurrence data, are of limited use for site selection for species with historically restricted distributions. In contrast, mechanistic species distribution models hold considerable promise in selecting translocation sites. Here we integrate ecoenergetic and hydrological models to assess the longer-term suitability of the current habitat of one of the world's rarest chelonians, the Critically Endangered Western Swamp Tortoise (*Psuedemydura umbrina*). Our coupled model allows us to understand the interaction between thermal and hydric constraints on the foraging window of tortoises, based on hydrological projections of its current habitat. The process can then be repeated across a range of future climates to identify regions that would fall within the tortoise's thermodynamic niche. The predictions indicate that climate change will result in reduced hydroperiods for the tortoises. However, under some climate change scenarios, habitat suitability may remain stable or even improve due to increases in the heat budget. We discuss how our predictions can be integrated with energy budget models that can capture the consequences of these biophysical constraints on growth, reproduction and body condition.

Keywords: assisted colonization; climate change; rainfall decline; hydroperiod; thermodynamic niche; tortoise; *Pseudemydura umbrina*

1. Introduction

Climate change is occurring at a pace that may prohibit an evolutionary response in some species [1], and species threatened with extinction may need to be translocated to climatically favorable habitats capable of supporting them in the long-term. This process, known variously as assisted colonization, assisted migration or managed relocation [2], has generated much controversy [3,4] but may be the only means of maintaining some species in the wild under future climates or hydrological change [5,6].

A clear candidate for assisted colonization in Australia is the Critically Endangered Western Swamp Tortoise, *Pseudemydura umbrina,* of which less than 50 adults survive in the wild. The species is restricted to two ephemeral swamps on the fringe of Perth, Australia's fastest growing city [7], where the regional climate has demonstrated a notable shift to drier conditions over the past three decades [8,9] which has reduced the quality of the tortoise's habitat [10,11]. In particular, the reduction in rainfall and increasing abstraction of groundwater for domestic and agricultural use [12] is shortening the hydroperiod of the swamp habitat, and reducing the recruitment of juveniles into the population [10]. Moreover, long generation times, slow rates of reproduction and low genetic diversity [11] all mean that the tortoise is unlikely to mount an evolutionary response to a changing climate. Human intervention will be necessary to prevent the extinction of this species in the wild a fact recognized more than 40 years ago and that provided the impetus for a captive breeding program at the Perth Zoo [13] which has now produced more than 500 individuals for release. Translocation protocols are well developed and have demonstrated that captive-bred *P. umbrina* can be successfully introduced into novel habitats, but translocation sites that can offer good habitat under future climates are needed to ensure the persistence of populations in the wild [11]. Given that declining rainfall in southwestern Australia is expected to continue [14], future translocations sites are likely to fall well outside the historical range of *P. umbrina* and as such will be defined as assisted colonizations [2].

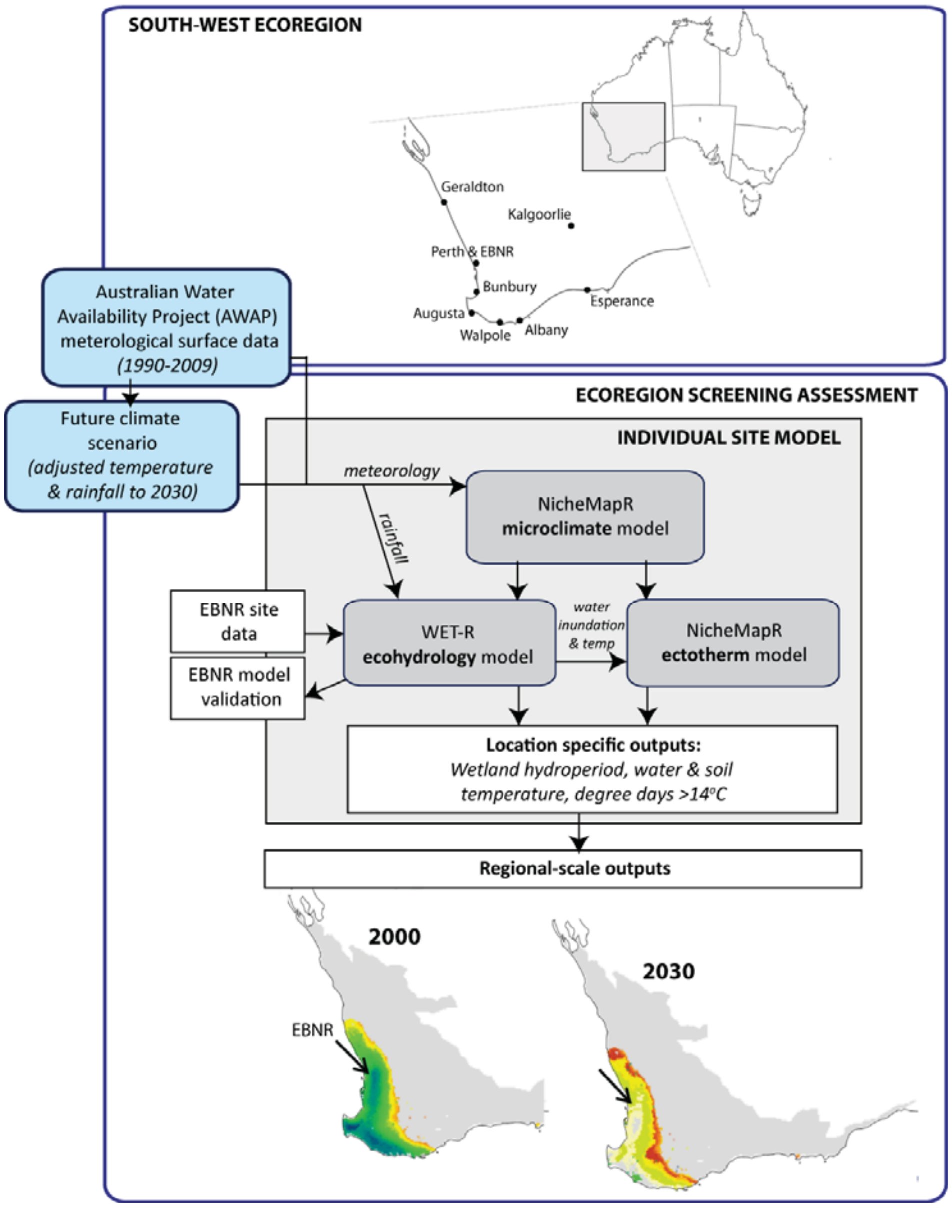
A challenge facing conservation managers is how to identify translocation sites where species could survive under future climates. Correlative or "climate-envelope" species distribution models (SDMs) are widely used to predict the future range of species and have been applied in the selection of sites for assisted colonizations [15]. These statistical approaches capture processes implicitly; they rely on strong (often indirect or nonlinear) empirical links between species distribution records and environmental variables to make predictions, and are consequently unsuitable for species with limited occurrence data [16,17]. Notably the many rare and/or endangered species that could be candidates for assisted colonizations will often (like *P. umbrina*) have naturally restricted distributions. A further limitation is that distribution models based on correlations can produce misleading predictions in novel or non-equilibrium situations such as climate change [18 20]. Predicting suitable translocation sites for rare species under uncertain future climates is therefore especially challenging, but it is critical that we develop these skills expeditiously because assisted colonizations that are technically and economically feasible will be prioritized by conservation agencies if the risk of *in situ* extinction is high [5,21].

Mechanistic SDMs are a compelling alternative to the many correlative methods for predicting future habitats. Mechanistic SDMs connect ecophysiological knowledge of climatic tolerances with spatial environmental data through the application of microclimate and heat/energy budget models and can be used to define and map species' fundamental or "thermodynamic" niche [22,23]. A major limitation of these models is the requirement for data on physiological tolerance limits and other environmentally determined thresholds, but such data is often well resolved for high profile threatened or invasive species [24,25]. Moreover, mechanistic SDMs can also simulate key components of the habitat, as in cases where temperatures of water bodies modeled as a "bucket" were used to drive thermal responses of amphibians [25,26].

In this paper we outline a mechanistic (*i.e.*, "process explicit") framework that numerically simulates the thermal and eco-hydrological processes of a wetland and its interactions and feedbacks with the hydrothermal processes of *P. umbrina*. This complexity is necessary because the projection of the hydroperiod drives critical components of the tortoise's heat and energy budget that in turn influence processes such as growth and reproductive provisioning. Hatchlings in particular must have a sufficiently long growing season in water to reach a critical mass before their first summer aestivation [10], and females will reabsorb their eggs after mating, or produce fewer or no eggs if their feeding opportunities are limited [27]. Hence wetland hydroperiods and water temperatures that suit the species' requirements should be a crucial consideration when selecting translocation sites, but accounting for the complex and non-linear eco-hydrological feedbacks that occur in wetland systems experiencing a non-stationary climate regime is particularly challenging [28].

To provide this information we employ an eco-hydrological model that is able to simulate the long-term response of a wetland's water balance and vegetation assemblage to shifts in climate forcing and couple it to a biophysical model that simulates the heat budget of the tortoise (Figure 1). This coupling provides a sophisticated connection between the tortoise's thermodynamic niche and the wetland water balance, as governed by climate, geomorphological and vegetation controls. We further examine three conceptual models of how tortoises regulate their body temperature during the hydroperiod to assess the activity potential of *P. umbrina* across more than 13,000 screening locations in the Southwest Australia Ecoregion. We drive our coupled models with 20 years of historical daily climate data centered on the year 2000, as well as with climate projections to 2030 to identify the parts of the ecoregion where tortoises could operate within their preferred temperature range within a suitable hydroperiod. While our model outputs are specific to *P. umbrina* and are discussed in the context of assisted colonization, the construct and approach we outline here can be generalized to any species dependent on wetland habitats. We also articulate the open questions and new understandings (both climatic, eco-hydrological and physiological) that will be required before such translocations could occur with confidence.

Figure 1. Framework coupling the eco-hydrological model WET-R to NicheMapR, where the former was validated by comparing actual hydroperiods and water temperatures at Ellen Brook Nature Reserve (EBNR) to those generated by the model. Final screening models of the Southwest Australia Ecoregion indicate relative site suitability for *P. umbrina* and are integrated using a GIS and supercomputing framework and driven using 20 years of daily climate surfaces (1990 2009) generated through the Australian Water Availability Project (AWAP [29]). Hydroperiod and water temperature outputs can be adjusted in accordance with projections of future changes in temperature and rainfall, while predictions of degree days >14 °C depend upon the behavioral routine coded in to the ectotherm model of NicheMapR.



2. Results and Discussion

2.1. Model Performance and Assessment of Current Habitat

The first step in developing our framework was to test the ability of the eco-hydrological model (WET-R see Experimental Section) to predict hydroperiods, water depths, and water temperatures of the current habitat of *P. umbrina*. The wild population occupies two ephemeral swamps in the 80 ha Ellen Brook Nature Reserve (EBNR) and 155 ha Twin Swamps Nature Reserve (TSNR) on the Swan Coastal Plain of Western Australia [11]. We developed an eco-hydrological model for EBNR because this site currently provides the best natural habitat for *P. umbrina* [11]. The calibrated model had an Root Mean Squared Error (RMSE) of 69.9 mm between the observed and predicted hydroperiod values over the ten-year period for which we had relevant data from surface water gauging stations (1999 2009: Figure 2a c). The frequency distribution of hydroperiod length over this period was also captured well (Figure 2d), with a peak frequency of approximately 6 months indicating the model captured the amount of inter-annual and intra-annual variability. We were only able to assess the thermal predictions of the model in 2009 (where we had continuous measures of water temperatures in the deepest part of the wetland), but seasonal trends in water temperatures and the magnitude of diel temperature fluctuations were comparable (Figure 2e), especially considering the model prediction represents a swamp average condition rather than the specific point where the sensor was recording. The ability of the model to hindcast, and therefore potentially forecast, the key microhabitat parameters at this site are clearly demonstrated.

The projected hydroperiods over the time frame of the AWAP historical daily climate database (1990 2009) ranged from 7.8 months in 1992 to only 3.0 months in 2006 (Table 1). The consequence of the very short hydroperiod in 2006 (a year of record low winter rainfall in southern Australia [30]) for the activity potential of tortoises becomes evident when the eco-hydrological model is coupled with the biophysical model. Figure 3 demonstrates for the year 2006 how variation between three behavioral subroutines within the ectotherm model in NicheMapR (Figure 1) drove our predictions of a tortoises' body temperature and "activity potential" the degree days >14 °C (expressed as the number of days above the threshold temperature of 14 °C, multiplied by the number of degrees above that threshold during the hydroperiod). The body temperature of the tortoise tracks an identical pattern during the terrestrial phase of the annual lifecycle (October July) but varied during the hydroperiod because we made different assumptions about the basking behavior of *P. umbrina* (Figure 3). The activity potential is substantially greater if the tortoise prioritizes basking over swimming and foraging (scenario **c**), whereas there was only a slight difference in scenario **a** and **b**, indicating that the option to bask in this particular year would have done little to increase the potential for activity. Notably, 2006 was also marked by an especially cold winter in South Western Australia [29].

When comparing activity potential across the 20 years with historical daily climate data, the anomalous year of 2006 is particularly apparent (Figure 4). In 2006, the activity potential was 41% 49% less than in the much wetter preceding year of 2005 (values depending on the behavioral scenario used) where the hydroperiod was 6.75 months (Figure 4, Table 1). Limited activity is manifest in reduced opportunities for feeding and assimilation, which can be assessed by measuring growth. For example, a study of *P. umbrina* in the mid-1960s revealed that hatchling tortoises grew to only 17.1 g in a three month hydroperiod in 1966, whereas hatchlings were able to attain masses of 60 g after a 6.5 7.0 month hydroperiod in 1964 [31]. Although we have no direct evidence that tortoises' activity or growth was limited in 2006, once of us (GK) found an exceptionally large number of *P. umbrina* carcasses at EBNR over the 2006/2007 dry season (four females, two males and four juveniles, only two of which were clearly predated). Such large numbers of carcasses have not been found either before or after 2006, over more than 15 years of monitoring. Potentially some animals were in energy deficit over the long 2006 2007 dry period, and may have died of starvation.

Figure 2. Time series of modeled (solid black line) and actual (red dotted line) hydroperiods and water temperatures at Ellen Brook Nature Reserve (EBNR). (**a**) water levels and hydroperiods of EBNR from the WET-R simulation from 1999 to 2009; (**b**) and (**c**) magnified views of water levels and hydroperiods for a wet (2005 2006) and dry (2006 2007) year; (**d**) normalized frequency of actual and simulated hydro periods (months) over 1999 2009; (**e**) actual and simulated water temperature during the 2009 hydroperiod (days 175 326).

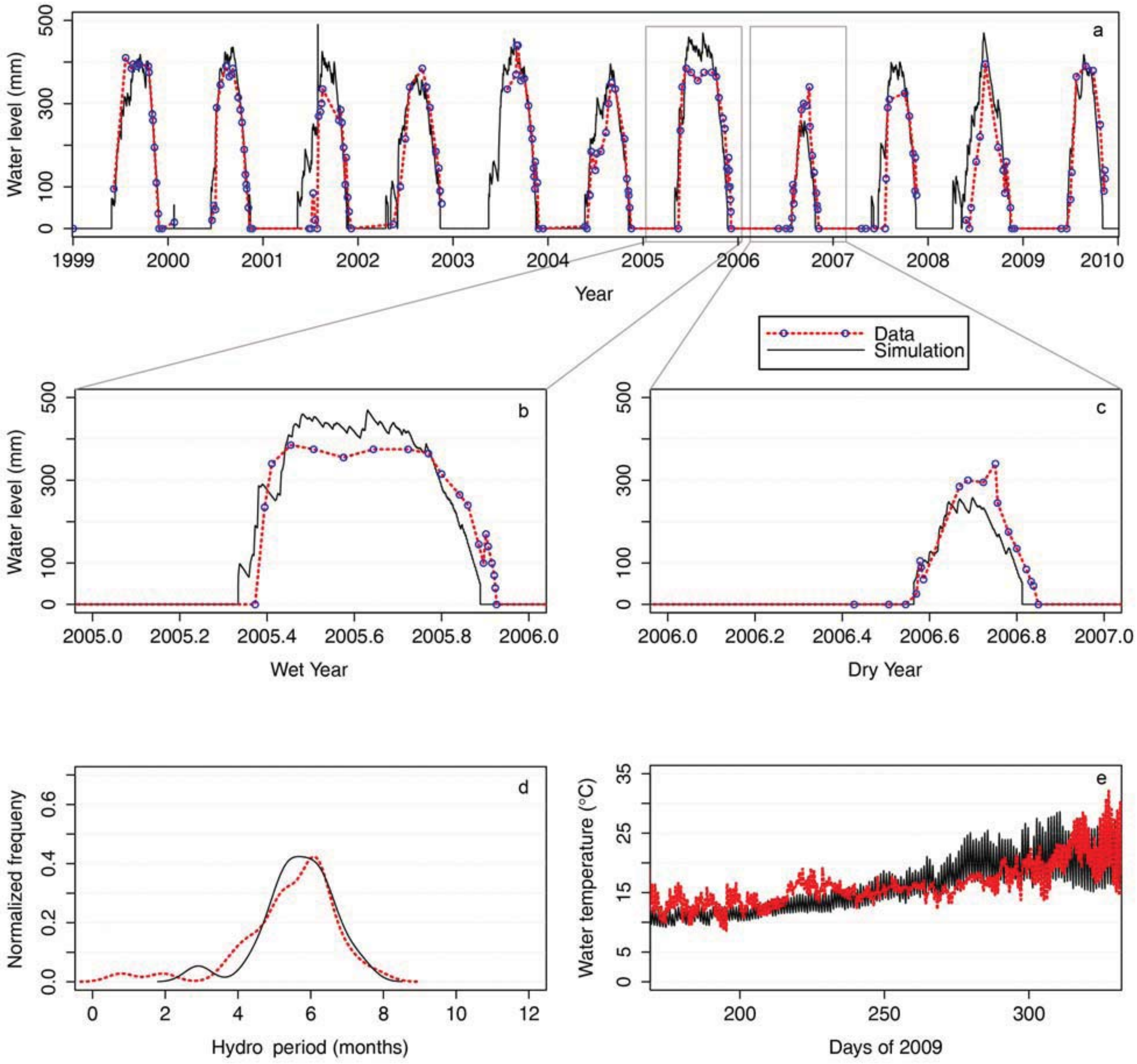


Table 1. Summary of the hydroperiod and water temperatures predicted by WET-R for the years 1990 2009 at Ellen Brook Nature Reserve.

Year	Hydroperiod (mo.)	Average water temperature °C
1990	6.45	15.43
1991	6.08	15.17
1992	7.77	15.78
1993	5.36	14.48
1994	5.51	14.48
1995	6.74	15.17
1996	5.82	15.85
1997	5.38	14.65
1998	5.61	15.14
1999	6.03	15.08
2000	5.06	14.99
2001	6.51	14.93
2002	6.57	14.63
2003	6.17	14.80
2004	5.67	14.53
2005	6.75	14.80
2006	3.02	15.36
2007	5.09	15.10
2008	7.26	14.72
2009	4.49	14.75
Mean	**5.87**	**14.99**

While the values in Figure 4 are based on our coupled model rather than empirical data, they suggest that there has been a decline in the activity potential during the 20-year period 1990 2009. We tested for significance of the relationship between time (year) and the degree day metric for each of the three behavioral routines, and confirmed that a linear decline was apparent for the basking-only routine scenario C (R^2 0.35, n 20, p 0.005). This result was also robust to the exclusion of the extremely low value in 2006 (R^2 0.32, n 19, p 0.01). The relationships between year and degree days for scenarios **a** and **b** were either marginal or non-significant (p 0.06 and p 0.22 respectively). Driving the analysis with additional climate data for 2010 2012 (2010 was also a very dry winter in south-western Australia) may make the currently marginal decline significant, but daily climate surfaces for these years are not yet available. *P. umbrina* is a long lived species [11] and certainly has the capacity for persisting in a boom/bust environment, but detection of a climatically-driven downward trend in activity potential would provide a clear motivation for assisted colonization.

Figure 3. Examples of three simulations of tortoise body temperatures and activity potential at Ellen Brook Nature Reserve using AWAP climate data for 2006 when low winter rainfall severely restricted the swamp hydroperiod (grey shading). Blue lines depict the body temperature (°C) of a tortoise, pink indicates that the tortoise in is water, green indicates selected shade (10 100%) and the red panel shows the depth (cm) of the microclimate selected by the tortoise during the aestivation period. The behavioral routines in NicheMapR cause a tortoise to select a microhabitat that maintains its body temperature below its voluntary thermal maximum of 28 °C (Table 2). At high environmental temperatures the tortoise aestivates and thermoregulates by seeking cooler microhabitats in burrows in up to 80% shade. At lower environmental temperatures the tortoise aestivates just below the surface and ceases to thermoregulate. The tortoise then selects an aquatic environment once the wetland water depth is at least 5cm. (**a**) depicts a scenario where the simulated tortoise was prevented from basking, (**b**) demonstrates a more natural scenario where the tortoise was able to raise its body temperature above its voluntary minimum through ambient basking, while (**c**) presents a hypothetical scenario where basking is maximized (*i.e.*, simulated tortoises preferentially bask rather than swim/forage).

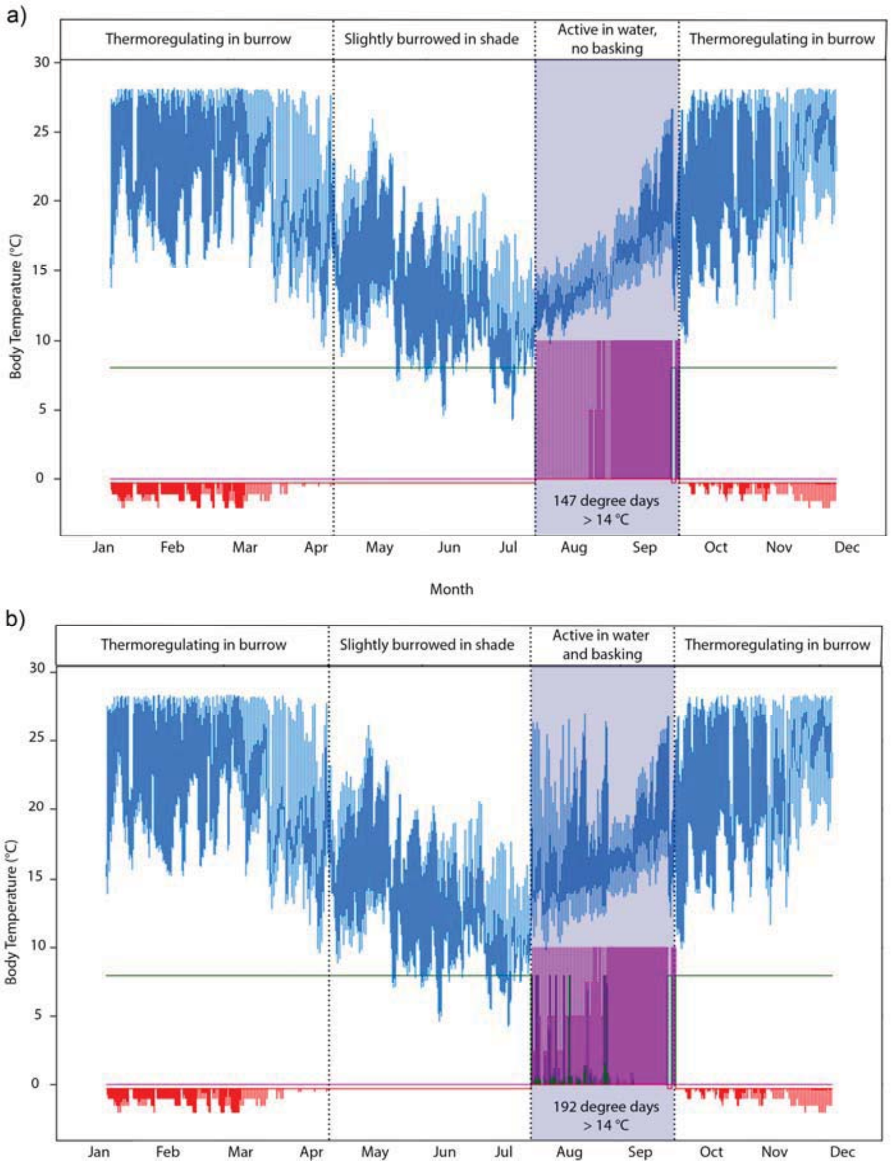


Figure 3. *Cont.*

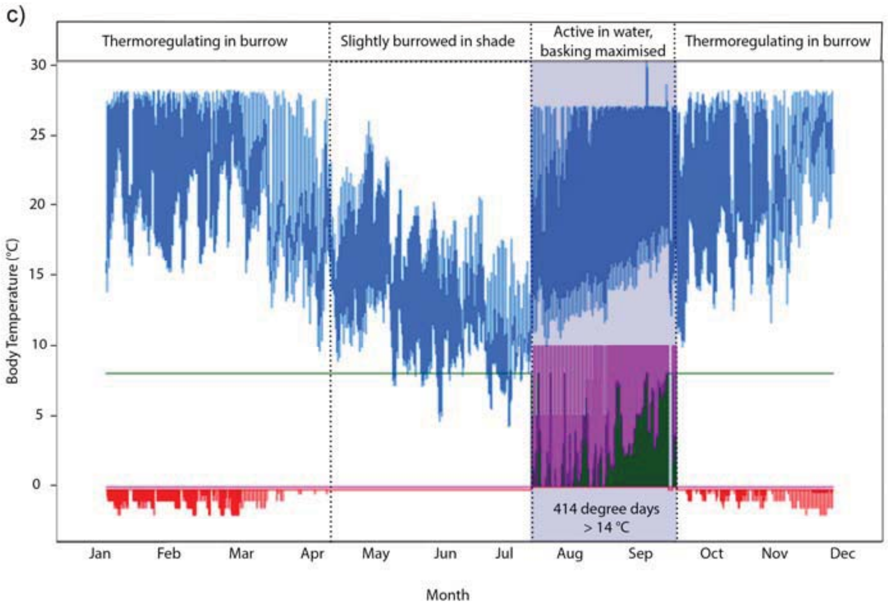
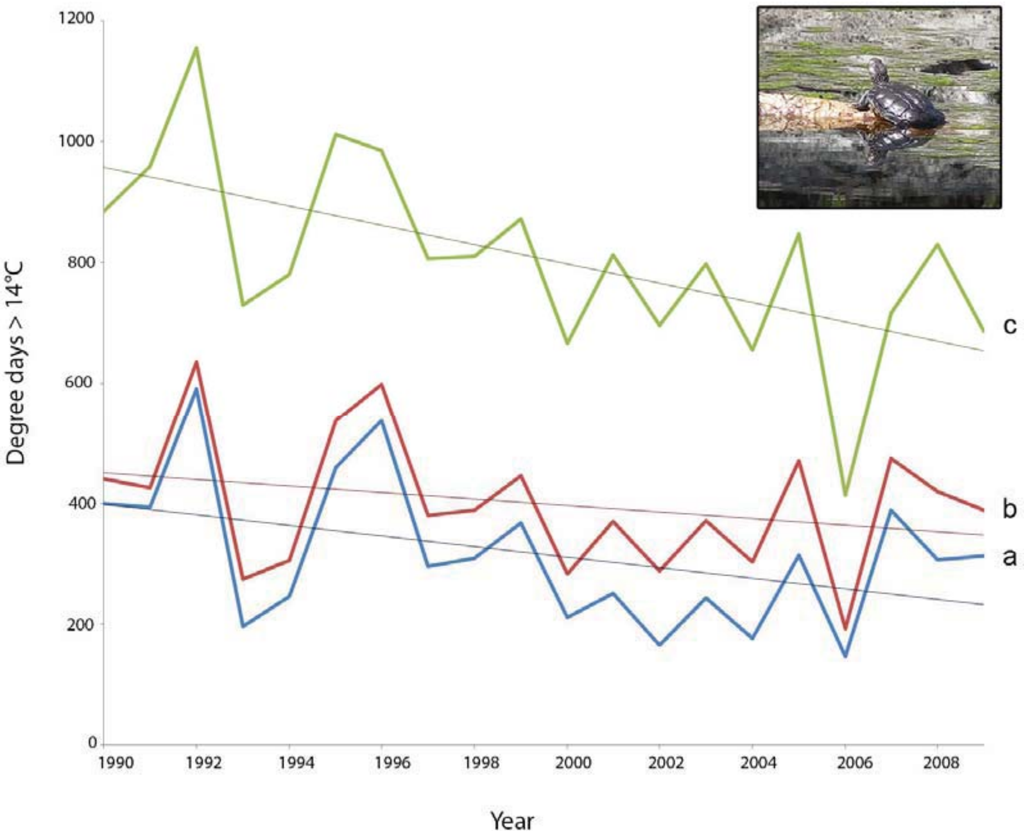


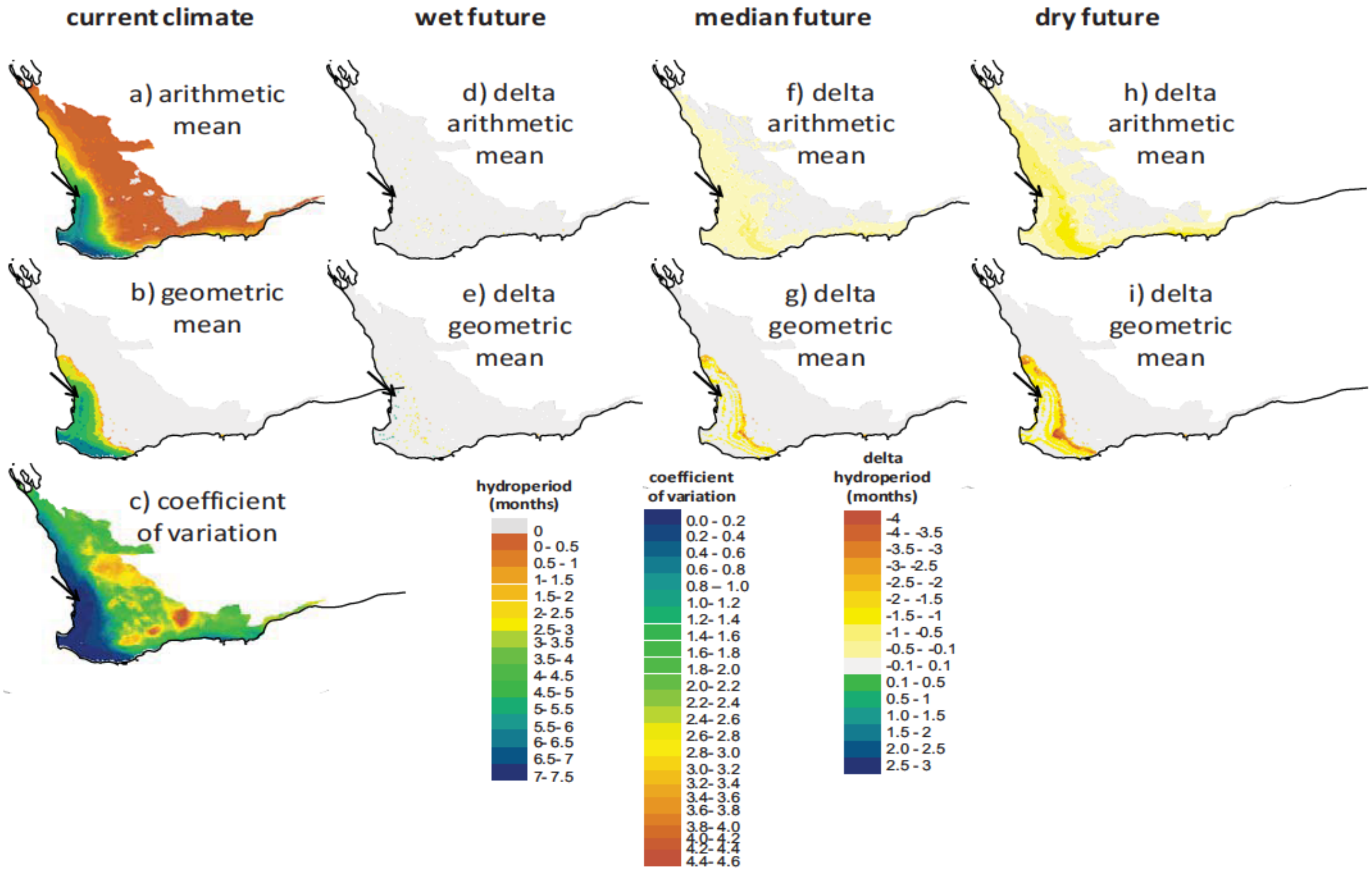
Figure 4. Sensitivity analysis showing how the structure of the behavioral subroutine in NicheMapR influences the degree day predictions over 20 years at Ellen Brook Nature Reserve. The blue line indicates no basking (scenario **a** in Figure 3), the red line indicates an option to bask when water temperatures fall below 14 °C (scenario **b** in Figure 3), and the green line indicates that tortoises always seeks the warmest thermal environment above a threshold of 14 °C, which would usually be out of the water (scenario **c** in Figure 3; e.g., inset photograph of a basking Western Swamp Tortoise by GK).



2.2. Screening of Wetland Hydroperiods under Current and Future Climates

The coupled model system was applied to the Southwest Australia Ecoregion to assess how a wetland environment identical to EBNR would perform under different climatic forcing conditions. Across the ecoregion there was a large variation in mean hydroperiod lengths under the current climatic conditions, ranging from 0 to >7 months, with a sharp transition occurring along the line from Geraldton in the north, to Albany in the south (refer to Figure 1 for locations). This is exemplified most clearly in the region defined by the geometric mean (Figure 5b), based on the strong influence of rain-bearing frontal systems influencing the coastal part of southwestern corner of Australia, and the increasing potential evaporation as a function of distance inland and latitude. Beyond the Geraldton-Albany line the coefficient of variation (Figure 5c) also increased considerably, highlighting the increased level of inter-annual variability. The region on the Swan Coastal Plain and the southern coast, extending from Perth in the north to Denmark in the south, had an average hydroperiod of six months or greater, and the current EBNR site is therefore at the northern most tip of this region.

Figure 5. Screening maps of the Southwest Australia Ecoregion showing (**a**), the arithmetic mean, (**b**) the geometric mean and (**c**) the coefficient of variation of the hydroperiod (in months) predicted by WET-R in the period 1990 2009. Models are driven by current climate (1990 2009: AWAP data, **a c**) and also indicated are the impacts on the hydroperiod of three future climates for 2030 where air temperatures increase by 0.7 1.3 °C and total annual rainfall decreases by 1% 14% (future scenario current scenario; **d i**). The black arrow indicates the location of the wild populations.



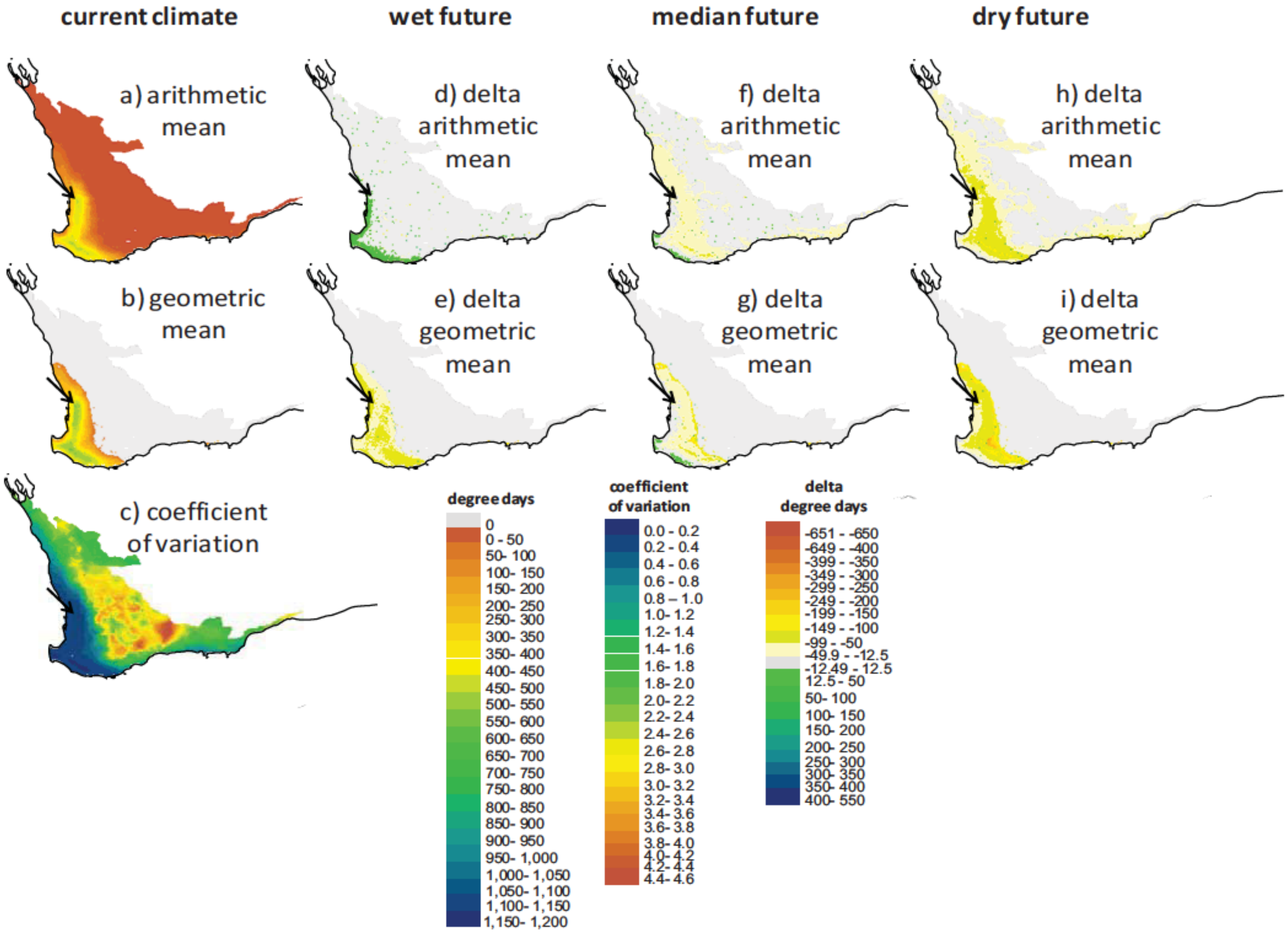
The change in hydroperiod length by 2030 varied substantially between the three future climate scenarios tested and varied from no discernible change to greater than a two month reduction. Under the wet future climate, there was no large shift with small areas improving in the southwestern tip and areas on the inland side of the six month hydroperiod contour reducing slightly (Figure 5e). Under the median future climate, there was a consistent reduction in the arithmetic mean across the ecoregion of 0.5–1 month, however the geometric mean showed a more marked change at the inland sites of up to 4 months and less significant reductions in the center of the region. Under the dry future scenario, the pattern was similar but a more extensive reduction was predicted.

2.3. Screening of Tortoise Activity Potential under Current and Future Climates

The terrestrial and aquatic temperature predictors integrated with the behavioral routine allowed us to make spatially explicit predictions of a tortoise's annual potential for activity (foraging and assimilating) by quantifying the extent that sites would allow tortoises to forage in water and attain their preferred body temperature range. Because the hydroperiod drives activity potential, there are obvious parallels between the maps that show the spatial variation in the hydroperiod (Figure 5) and the degree day maps in Figures 6–8. The key difference in these two types of screening maps is that regions that are more suitable based on thermal criteria can be distinguished. Considering the maps in the "no basking" scenarios in Figure 6 we find that for some locations, such as the coastal regions of the south west and the southern parts of the Swan Coastal Plain, the activity potential increases under the "wet future" climate, whereas there is no equivalent increase at the location of the wild populations. In this climate change scenario rainfall was reduced by only 1%, so the increase in activity is due to the projected increase in air temperature. However, under the dry future climate, the reduction of the hydroperiod length effectively offsets the increase in air temperature, with the net result being that activity potential is decreased. Under all climate change scenarios there are sites within the Southwest Australia Ecoregion where activity potential either increases relative to the present day situation (1990–2009) or decreases less than it does at the current tortoise habitat. In particular, sites in the coastal regions around Bunbury, the Scott Coastal Plain east of Augusta, and Nuyts Wilderness northwest of Walpole (see Figure 1 for locations) offer the most robust habitat (in terms of activity potential) under the three 2030 climate change scenarios we examined.

What is more notable is the effect of the assumptions made about thermoregulatory behavior (e.g., Figures 3 and 4) on the degree day outputs of NicheMapR. As shown graphically in Figure 3, activity potential is enhanced when tortoises are either allowed or forced to bask (behavioral scenarios B and C). Figure 8a illustrates the much greater predicted activity potential (degree days >14 °C exceeding 1,000 in some locations) when tortoises bask continuously during the hydroperiod, and the wide band of "improved" habitat (green shading) under the median future climate scenario. Given that the behavior of continuously basking is unlikely to be realistic, the most careful attention should be paid to scenarios mapped in Figure 7, where the optional basking behavior typical of *P. umbrina* was modeled. In these cases, outcomes are similar to those described for Figure 6 (no basking) where sites near the south west coast show either no change or improved potential activity under future climates. In contrast, there was a decline in the potential for activity at the site of the current habitat at Ellen Brook Nature Reserve.

Figure 6. Screening maps of the output of NicheMapR coupled with WET-R showing (**a**), the arithmetic mean, (**b**) the geometric mean and (**c**) the coefficient of variation of the degree days above 14 °C, assuming the tortoises will attempt to raise body temperature by basking during the hydroperiod if water temperature was unsuitable for foraging (<14 °C). The degree day metric is proportional to the potential for feeding and assimilation. Models are driven by current climate (1990 2009: AWAP data, **a c**) and the three future climates for 2030 outlined in Figure 4 (future scenario current scenario; **d i**).



2.4. Implications of Screening on the Selection of Sites for the Assisted Colonization of P. umbrina

Translocations of *P. umbrina* to new habitats first began in 2000, and on average 20 40 captive-bred juveniles are introduced each year to one of two reserves about 50 km north of the known range of the species (Mogumber and Moore River Nature Reserves) or have been used to supplement the declining population at TSNR [11]. All current release sites are expected to provide increasingly marginal habitat because of decreasing winter rainfall and increasing groundwater abstraction [12]. For example, constant pumping of bore water has been necessary to maintain water levels at TSNR since 2003, and this site, which formerly provided good habitat for *P. umbrina* in the mid-1960s, now recruits very few juveniles into the population. The exceptionally low rainfall in 2006 prevented the species from breeding in all but EBNR and a drying climate was isolated as the major reason for the failure of previous recovery efforts to meet the key criterion of >50 adults in the wild [11]. Therefore the identification of translocation sites that will offer some stability and refuge under future climates will be integral for the planning of future conservation efforts, and will likely play a defining role towards *P. umbrina* recovery.

Figure 7. Screening maps of the output of NicheMapR coupled with WET-R showing (**a**), the arithmetic mean, (**b**) the geometric mean and (**c**) the coefficient of variation of the degree days above 14 °C, assuming the tortoises will remain in the water during the hydroperiod unless it exceeds the voluntary thermal maximum temperature. The degree day metric is proportional to the potential for feeding and assimilation. Models are driven by current climate (1990 2009: AWAP data, **a** **c**) and also indicated are the impacts of the three future climates for 2030 outlined in Figure 4 (future scenario current scenario; **d** **i**). The black arrow indicates the location of the wild populations.

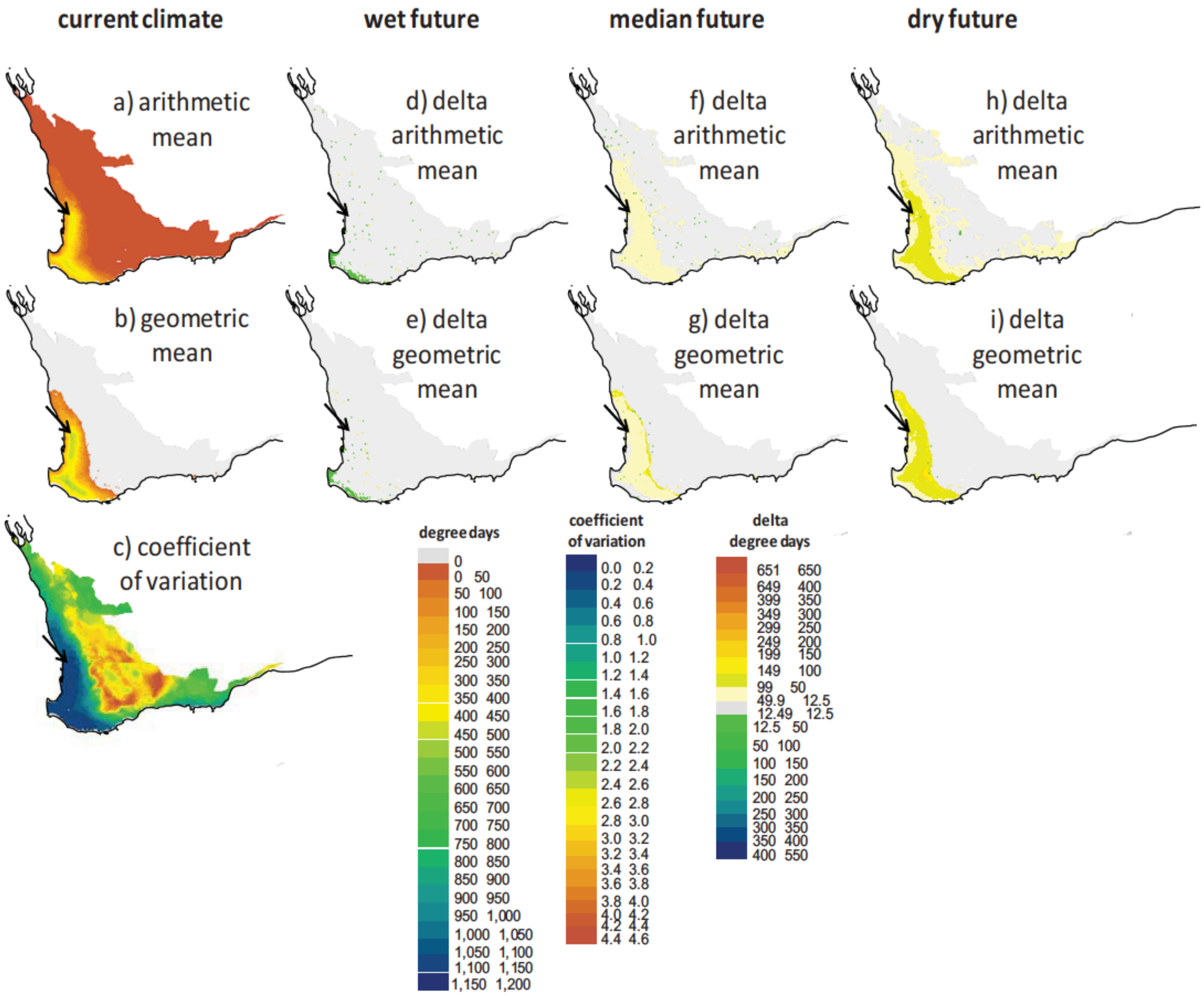
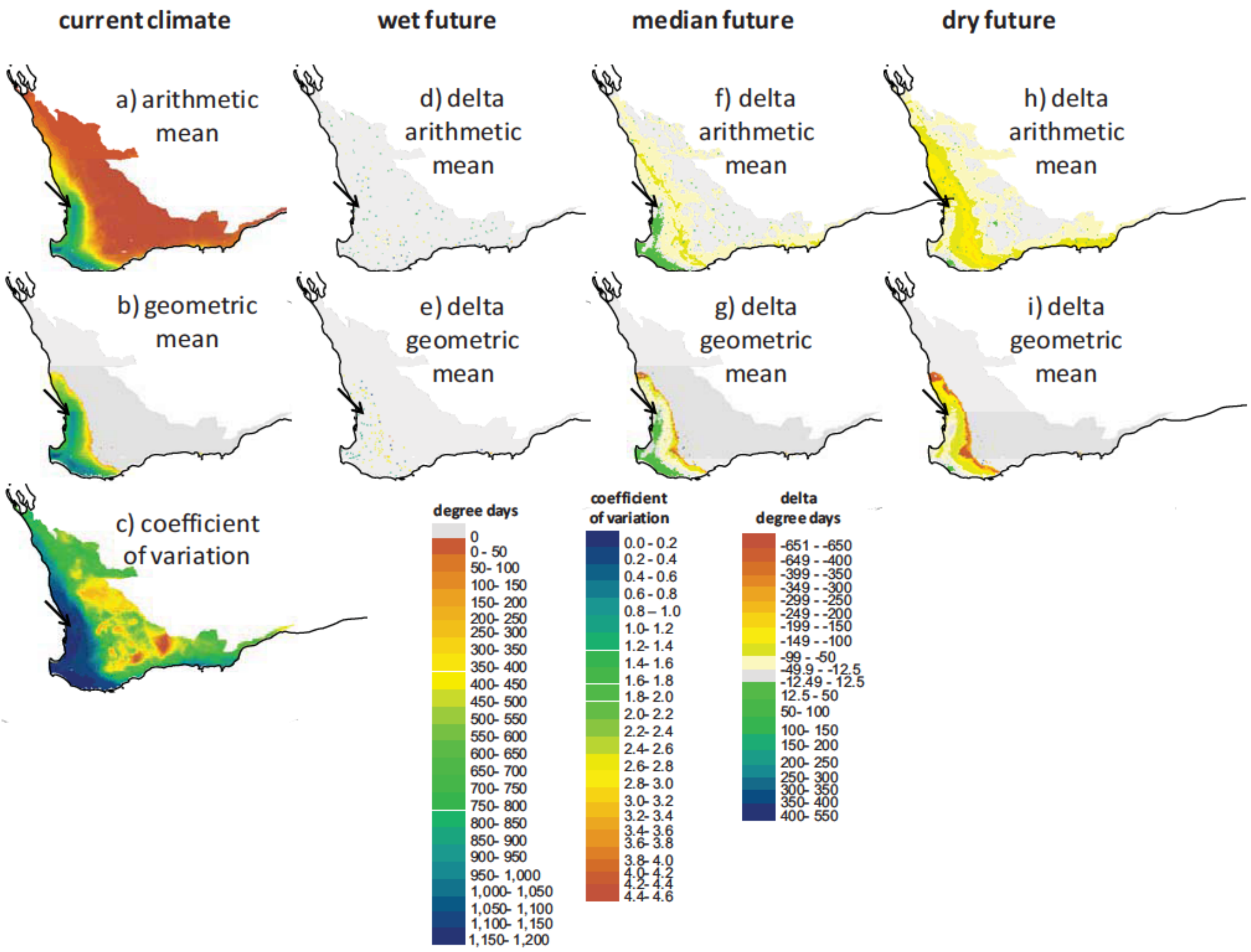


Figure 8. Screening maps of the output of NicheMapR coupled with WET-R showing (**a**), the arithmetic mean, (**b**) the geometric mean and (**c**) the coefficient of variation of the degree days above 14 °C, assuming the tortoises spend virtually all of the hydroperiod basking (*i.e.*, foraging bouts are only a small fraction of each simulated hour). The degree day metric is proportional to the potential for feeding and assimilation. Models are driven by current climate (1990 2009: AWAP data, **a c**) and also indicated are the impacts of the three future climates for 2030 outlined in Figure 4 (future scenario current scenario; **d i**). The black arrow indicates the location of the wild populations.



We have shown here that it is possible to produce a species distribution model using a process-explicit rather than a statistical approach that identifies locations in terms of multiple regressions against key environmental variables. The crucial advantage, as well as the necessity of this approach for this particular case study, is that we can look at future projections with a clear understanding of at least one constraint on the tortoises' fundamental niche. Under the three 2030 climate scenarios examined here we derive different predictions about future changes in hydroperiods and the activity potential of *P. umbrina.* The model's predictions of the regions where suitable growth conditions occur highlights that the current population is at the northern-most margin of a large area where the climatic niche is similar, and that translocation sites north or inland of the current location are going to be unsuitable in the future under forward climate projections.

Our model projections occur within a global biodiversity hotspot [32], where numerous species compete for conservation attention. A limitation of our climatically-driven screening model is that it does not account for a range of other typically local scale factors that will be important in selection of a translocation site for *P. umbrina*. Tools such as Multiple Criteria Analysis [33] can be used to further refine site selection, by ranking sites against criteria weighted by their importance in decision-making. Criteria relevant to translocation site selection in *P. umbrina* include soil type, vegetation composition, predator control, land tenure and anticipated land-use change, food resources, local scale hydrology and size [34] which can be assessed by liaison with stakeholders. The intersection of our spatial model outputs with sites scoring highly in relevant criteria can provide a quantified means of refinement during the final stages of selecting sites for translocations.

2.5. Caveats of the Existing Framework and Future Directions

This paper presents an outline or framework, and not a conclusive implementation of translocation decisions for the Western Swamp Tortoise. Refinements in the form of improvements to the climatic, eco-hydrological and physiological assumptions underlying the model must be made in order for the models to be implemented with certainty sufficient to justify a change in current practice.

The climate data used for the current data analysis is from the AWAP dataset, which interpolates daily meteorological data onto a continuous surface. In this study the daily data used at each point was further disaggregated to hourly for the microclimate and wetland models by simply assuming the daily rainfall was spread evenly over the day, however, it is well known that sub-daily patterns of rainfall distribution can vary over the ecoregion assessed here [35]. Since runoff generation in the wetland region is essentially a threshold process often governed by sub-hourly patterns of rainfall intensity and antecedent conditions, spatial and temporal variability in the nature of rainfall delivery may impact on the overall frequency of wetland filling and should be further considered as part of a local scale hydrological assessment.

Spatial changes in the temporal character of rainfall delivery may also occur under future climate scenarios. For example, an increase in dominance of the rainfall from summer thunderstorm activity versus winter frontal systems may significantly impact on the nature of runoff generation and overall hydroperiod length. In the present analysis we adopted a simple increase in temperature and decrease in rainfall based on 2030 conditions [8], which were average regional changes based on the ensemble prediction of 15 GCM’s. Alteration to the seasonal character and sub-daily intensity patterns of rainfall delivery have therefore not been considered in our assessment and may significantly impact on the timing of wetland filling, the lake water balance and length of the hydroperiod. Similarly, our approach does not consider heterogeneity in the spatial response of the region to a changing climate; meso-scale changes in land surface topography and condition may locally amplify or dampen projected shifts in rainfall and temperature. Therefore, we propose to use appropriate GCM downscaling approaches [36] to account for these changes. Further, we propose also to account for uncertainty in GCM predictions by running a Montecarlo simulation of the combined effects of declining rainfall and increasing air temperatures, sampled from assumed normal distributions parameterized from the percentiles of the GCM predictions.

A key assumption of our screening is that the characteristics of the Ellen Brook wetland are transferrable throughout the southwest of Western Australia. Here we have assumed identical features of the wetland hydrological processes; that is, the claypan nature of the wetland with limited surface water and groundwater, its soil and vegetation properties, as well as the wetland depth-area-volume relationship. This is a logical approach as it is likely to be the most pessimistic case. Calibration of our model has showed that hydroperiod is very sensitive to soil hydraulic properties as well as variations in the wetland geometry, and Coletti *et al*. [28,37] has also demonstrated the sensitivity of different morphologies, soil and vegetation properties to wetland inundation under different climatic conditions, to which the reader is also referred. Local variables may create better or worse microclimatic and wetland conditions and should be considered in addition to screening based purely on climatic differences application of the model to specific wetlands would require site specific data and individual calibration. Alternatively, it may be possible to optimize the claypan wetland geometry to maximize the performance of *P. umbrina* in each climate. Such an assessment may help limit the number of potential release sites or provide a design for an engineered wetland could that be a viable option for assisted colonization if natural sites are limited.

Our physiological analysis centers on the heat budget and how it interacts with the hydroperiod and water temperatures to permit aquatic activity at suitable body temperatures. While our predictions for degree days of foraging time provide key insights into the relative suitability of different parts of southwestern Australia as potential habitat for *P. umbrina*, they do not provide a means to identify key thresholds of suitability. The latter will require the development and integration of energy and water budgets to quantify the consequences of different hydroperiods for growth and reproduction potential as well as the consequences of the dry periods for loss of body condition in terms of energy/nutrient and water stores. In this context, Dynamic Energy Budget (DEB) theory [38], a formal theory and model for metabolism, will play a key role in integrating heat, water and mass budgets across the entire life cycle. It will provide a means to capture the effect of different climatic histories on future growth and reproduction and to capture phenological constraints in the context of the full life cycle [23,39]. This in turn will allow us to predict how recruitment and survival respond to annual variation in temperature and rainfall, especially in terms of the energy available to females for egg production and the potential for growth in the hatchlings' first season and its influence on survival through their first summer. Such predictions can then act as input to population viability models. The merger of DEB with NicheMapR has already been demonstrated for an ectotherm model [23] and, whilst beyond the scope of this paper, the integration of DEB into our existing model is a logical next step for improving the predictions generated here.

The requirements of the terrestrial phase of the annual lifecycle of *P. umbrina* have largely been ignored here for the purposes of explaining our framework for coupling eco-hydrological and ecoenergetic models. Nonetheless, understanding the constraints of the terrestrial environment will be as critical as understanding the spatial variation in activity potential. Tortoises spend around half of the year (more in dry years) in terrestrial environments that fringe the wetlands. Eggs develop in underground nest chambers [40] and juvenile and adult tortoises seek out cool microclimates during this period and aestivate under leaf litter or in existing burrows or crevices. During this period eggs and tortoises are vulnerable to energy depletion, hyperthermia and desiccation. Both NicheMapR and WET-R have existing capacity to predict soil temperature and water potential, and a database of soil properties across Australia at 5 km resolution offers further avenues to make such predictions spatially explicit. Modeling the heat and energy balance of tortoises when in terrestrial habitat, and integration of DEB theory in NicheMapR, will ultimately allow us to model processes such as allocation of energy to the reproductive buffer (eggs) during aestivation.

3. Experimental Section

3.1. Wetland Water Balance and Thermodynamic Model: WET-R

The wetland model applied here is based on Coletti *et al*. [37] which divides the wetland into different zones of hydrological function and simulates partitioning of water between the zones as mediated by climate, soil and vegetation controls. As a result, the model predicts the changes in the extent of surface water inundation, soil moisture and vegetation, and captures the various eco-hydrological feedbacks that mediate wetland response to changes in rainfall delivery and air temperature [28]. In this analysis, the above model was adapted to operate on a sub-daily (hourly) time-step and to simulate wetland thermodynamics.

Water temperature is computed based on a heat budget considering solar heating, longwave radiation and standard bulk aerodynamic flux parameterizations for sensible and latent heat. The budget is driven by the prevailing meteorological conditions provided by the microclimate model of NicheMapR, and the heat balance is calculated as:

$$\left(L\rho_w c_p\right)\frac{dT_w}{dt} = \rho_w c_p\left(I\ T_i - O\ T_w + R\ T_{sky} A_L\right) + \left(H - E - S + \phi_{LW} + \phi_{SW}\right)A_L \tag{1}$$

where T_w is the lake temperature, T_i is the inflow temperature, T_{sky} is the air temperature (all in °K), p_w is the density of water (kg/m^3), c_p is the specific heat capacity of water (J/kg/K), L is the lake volume (m^3) and I, O and $(A_L R)$ are the inflow, outflow and rainfall volume fluxes respectively (m^3/d), where A_L is the lake surface area (m^2) used to multiply the rainfall depth (m/d). H, E and S are heat fluxes (W/m^2) for sensible heat, evaporation and soil heat conduction, respectively, calculated according to:

$$H = \rho_a c_p C_H u_2\left(T_{sky} - T_w\right) \tag{2}$$

$$E = \rho_a \lambda C_E u_2\left(e_s - e_a\right) \tag{3}$$

$$S = \frac{C_S}{z_s}\left(T_s - T_w\right) \tag{4}$$

where C_H, and C_E are bulk transfer coefficients for sensible and latent heat respectively (-), λ is the latent heat of vaporization (J/kg), ρ_a is the density of air (kg/m^3), and C_S is the diffusivity of heat into the soil below the water (W/m/K), and z_s is the active soil depth over which heat diffusion occurs. ϕ_{LW} is the net longwave radiation (W/m^2) and ϕ_{SW} is the solar insolation (W/m^2), calculated from:

$$\phi_{LW} = \varepsilon_a \sigma\left(T_{sky}\right)^4 - \varepsilon_w \sigma\left(T_w\right)^4 \tag{5}$$

$$\phi_{SW} = \left(1-\alpha\right)\widehat{\phi}_{SW}\left[\frac{A_L}{A_{MAX}} k_s\right] \tag{6}$$

where ε is the emmisivity of air or water, σ is the Stefan-Boltzman constant, α is the shortwave radiation albedo, $\widehat{\phi}_{SW}$ is the incident solar radiation above the vegetation (W/m^2). The last term of Equation 6 accounts for the effect of wetland vegetation shading on the incident solar intensity, with k_s defined as a constant to increase the shading effect, and A_{MAX} is the maximum area of inundation extent (m^2).

3.2. WET-R Setup and Calibration

The wetland morphology, soil, vegetation and initial conditions were based on application of the model to the wetland system at EBNR. A digital elevation model of the area at one meter resolution was obtained from the Western Australian Department of Environment and Conservation (DEC) and was used to derive the area-depth-volume curve for the model. The hydrological and vegetation parameters were applied as in Coletti *et al.* [37], where the model was similarly applied across the range of environments representative of the region. The wetland has previously been identified as a claypan system, with no significant inflows from surface waters or ground waters, but historically surface water and groundwater have likely contributed [41]. Rather, it is considered to be a bowl, which fills seasonally from direct rainfall and due to the low permeability of the sediments, it drains slowly to groundwater and more rapidly due to evaporation. Weirs installed at a height of 450 mm above the base of the wetland limited the depth of inundation. These factors greatly simplified the WET-R model and reduced the number of uncertain parameters.

Water level observations taken at EBNR for the years 1999–2009 were used to calibrate the water balance sub-model. Observations were derived from visual inspection of up to eight level gauges installed in the center of deeper pools throughout the wetland, and were made at approximately monthly intervals. Calibration of WET-R involved adjustment of three hydraulic parameters and five thermal parameters. The three hydraulic parameters calibrated included the saturated hydraulic conductivity of the lake sediments (h_c, 0.1 mm/h), the adjacent sandy sediments controlling internal water redistribution (h_{cu}, 0.11 mm/h) and the exponent on infiltration rate relation to saturation (k_i, 3.0). A simulated annealing algorithm was used to obtain the best-fit of these hydraulic parameters by reducing the root mean square error (RMSE) between observed and modeled water levels [42,43].

Water temperature was been logged every 15 minutes at EBNR since early 2009 using an automated weather station (Unidata 6540V) with a linear temperature probe positioned in the deepest part of the wetland. For this period (2009) we also ran WET-R using the locally measured meteorological data generated by the on-site weather station (rather than the AWAP climate surface) to provide the most accurate assessment of the performance of the model in predicting wetland water temperatures. Assumed values for C_S, C_H, C_E, ε_a, k_s were 0.5, 0.0013, 0.0013, 0.99 and 0.25, respectively.

3.3. Modeling the Heat Budget and Activity Constraints of P. umbrina

Available physiological and behavioral data for *P. umbrina* (Table 2) was used as input for a biophysical model within the software package NicheMapR (an R version of the package Niche Mapper™ [44]) which solves heat and mass budgets under different microclimatic scenarios for given behavioral strategies [23,44–46]. The problem of defining the microclimates available for a particular species can be tackled by combining weather station data with microclimate models. For the

P. umbrina case study here we can drive the microclimate model (described in [45]) of NicheMapR with historical continent-wide 0.05° grids of daily minimum and maximum temperature, vapor pressure, rainfall and daily solar radiation available through the Australian Water Availability Project (AWAP, [29]). The microclimate model calculates the clear sky solar radiation from first principles, and we can account for cloud cover effects on solar (and infrared) radiation exposure through the AWAP daily solar estimates (*i.e.*, observed daily solar over calculated clear sky solar). In the absence of interpolated daily wind speed data we use gridded long-term average wind speed obtained from ANUCLIM [47]. The microclimate model runs for two extremes of shading. We used a fixed value of 80% shade as the maximum value and characterized the minimum available shade using daily interpolations of monthly long-term average (1995 2008) values of the satellite derived Fraction of Available Photosynthetically Active Radiation (FAPAR) [48,49]. The minimum shade values derived from FAPAR influenced the soil heat budget but we assumed that basking tortoises could find patches of full sun. In sum, these microclimate calculations provide realistic hourly estimates of the microclimatic conditions above and below ground available to *P. umbrina* over a 20-year period from 1990 to 2009. However, because the microclimate model in NicheMapR does not explicitly consider microclimates available in a wetland setting, we derive predictions of water availability and temperature from the eco-hydrological wetland model (WET-R outlined above). Further environmental information gained from this approach includes the wetland hydroperiod, water temperature, and feedbacks of the wetland on soil temperature, soil moisture and vegetation changes.

Table 2. Parameters for the biophysical model of *P. umbrina* that were used to predict the thermodynamic niche.

Parameter	Value	Source
Morphological Traits		
Insulative fat layer thickness	0	Default value
Thermal conductivity of flesh	0.5 W/mC	Default value
Specific heat of flesh	4,185 J/(kg-K)	Default value
Density of flesh	1,000 kg/m3	Default value
Maximum solar absorptivity	0.85%	Default value
Minimum solar absorptivity	0.85%	Default value
Emissivity of animal	1	Default value
Reflectance of animal	0.9	Assumed
Proportion of body surface area in water while basking	30%	Assumed
Configuration factor to sky	0.4	Default value
Configuration factor to substrate	0.4	Default value
Physiological Traits		
Voluntary thermal maximum (upper body temperature for foraging, leaving pond, seeking deeper burrows)	28 °C	[31,50–52]
Voluntary thermal minimum (lower body temperature for foraging)	14 °C	[50,52]
Temperature difference between expired and inspired air	0.1	Default
Proportion of surface area acting like a free water surface	1%	Default
Behavioral Traits		
Daily activity	Diurnal *	[51], this study
Retreat underground in 80% shade	Yes—max depth of 1 m	GK unpublished
Shade seeking	Yes—0 to 80%	[53]
Allometric Respiration		
Typical mass of an animal	6 g (hatchling)	[11]
Metabolic Rate	$Q = 0.013\ M^{0.8}10^{(0.038*Tb)}$	[54]

* *P. umbrina* was confirmed to be diurnal by overnight video surveillance of 16 individuals at Perth Zoo for a total of 14 surveillance nights during late spring [55].

Outputs from both the microclimate model and wetland model then drive a steady-state biophysical model that solves the heat and mass balance for *P. umbrina* based on morphological, physiological and behavioral traits entered by the user (Table 2). In this study we calculated the heat budget only. The behavioral subroutine within NicheMapR was configured for *P. umbrina* by including thermal thresholds for basking and swimming (where the latter would allow foraging). We assumed that a tortoise would enter the wetland and begin activity if water depth exceeded a threshold of 0.05 m. Because heat exchange under water is dominated by convection, aquatic organisms such as *P. umbrina* will assume the temperature of the water when feeding or basking aquatically, but can elevate their body temperature by basking above the water surface or on land. If water temperatures are too low, tortoises can remain within their active temperature range by seeking out basking microclimates to raise their body temperature above the voluntary thermal minimum (14 °C; Table 2). We therefore implemented this behavior as a subroutine in the model, and further assumed that, in the absence of a suitable basking microclimate, tortoises would remain (inactive) in the water until the next hourly time-step, when they could surface to seek a basking microclimate once more. However, we also appraised two other less likely scenarios. The second scenario assumed tortoises would not bask but remained in the water at all times. The third scenario was that tortoises basked 100% of the time on the assumption that only very short bouts of foraging in the water were needed to fill the gut and that the rest of the time was spent basking to maximize assimilation rates. These additional behavioral scenarios allowed us to assess the sensitivity of our assumptions regarding basking behavior on our predictions of the thermodynamic niche.

When the water temperatures predicted by WET-R caused tortoises to exceed their voluntary thermal maximum of 28 °C, they could seek shade on land until the next hourly time-step, at which point they could return to the water if it had cooled sufficiently to reduce body temperatures to within the voluntary thermal range. Once either the hydroperiod ended or water temperatures permanently exceeded 28 °C, tortoises were terrestrial and entered aestivation, while continuing to defend an upper preferred body temperature by seeking cooler microclimates up to one meter underground in shaded burrows. We set a shade value of 80% to reflect the observation that the aestivation sites of *P. umbrina* are frequently beneath small trees or bushes [56].

3.4. Regional Screening for Suitable Translocation Sites

The coupled model was initially applied across the Southwest Australia Ecoregion for the period 1990 2009 using daily climate data from AWAP. These daily data were disaggregated to an hourly time step by assuming air temperature and wind speed peaked one hour after local solar noon and reached a minimum at dawn (vapor pressure and cloud were assumed to be constant through the day but to vary between days). Rainfall for a given day was spread evenly across 24 h. The simulations were run at 5 km resolution representing 13,169 locations and performed on a supercomputer (Victorian Life Sciences Computation Initiative) that allowed up to 200 sites to be processed simultaneously such that a 20-year run across the whole ecoregion took approximately 1 h.

Hourly predictions of water level and temperature from the wetland model were passed to the NicheMapR ectotherm model at each location in the screening assessment. The NicheMapR system then computed, on an hourly time step, the degree days that were within the hydroperiod and above the threshold activity body temperature of 14 °C (with an upper cap at 28 °C) during daylight hours. These were summarized per year of simulation and we then calculated the arithmetic and geometric means of hydroperiod and degree days across years as well as the coefficient of variation of the arithmetic mean.

To compare how the spatial extent of the activity potential varied under future climate conditions we ran the above analysis for the year 2030 by adjusting the AWAP data with projected future climates based on 16 Global Climate models each driven by one of three future greenhouse gas emission levels [8]. The three scenarios were a "Wet future" climate (0.7 °C air temperature increase, 1% rainfall decrease), a "Median future" climate: (1 °C air temperature increase, 7% rainfall decrease) and a "Dry future" climate: (1.3 °C air temperature increase, 14% rainfall decrease). Daily air temperature data from the AWAP database were simply increased by the appropriate increment before running the microclimate model, and AWAP daily rainfall data were reduced by the appropriate amount. We then computed the differential between the current and future conditions for each metric.

4. Conclusions

Planning for assisted colonization demands rigorous methodologies for selecting release sites, with risk assessment being foremost among a range of potential considerations [57]. Despite the fact that assisted colonization will be most often motivated by climate change, little effort has been expended in developing methodologies to forecast the future climatic suitability of a release site. Correlative SDMs have limited potential for identifying future habitats for range-restricted species, but the framework that we have demonstrated here offers a methodology for guiding the assisted colonization of any species dependent upon ephemeral wetlands. Further, our eco-hydrological model could be simplified for organisms inhabiting perennial wetlands, and our eco-energetic model can be driven by parameters for analogous species' if the required physiological data are unavailable, provided the model outputs can be tested against a known location and population.

In the *P. umbrina* case study developed here we have located regions of suitable habitat under a range of likely future climates. Ultimately our methodology will be expanded to explicitly include the energy/mass budget of the tortoises, and local scale hydrology, to allow quantitative statements about growth, development, starvation risk and reproduction. We will also consider not only longer term climate changes as predicted by global climate models, but also the natural climate variability across a range of temporal and spatial scales relevant to the prediction of wetland hydroperiods. Such approaches can be used to determine how sensitive the suitability of a particular translocation site will be to future predictions of climate changes.

Acknowledgments

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APPENDIX B:
SUPPLEMENTARY TABLES FOR CHAPTER 2

Table B1 – Factors assigned to the theme ‘assessment of alternatives’, as derived from the assessment of 24 decision tools on assisted migration. Refer to Figure 2.5 (Chapter 2, main text) for reference key.

Category	Reference	Factor
In General	1	Are […] barriers predicted to disappear under the effect of climate change?
	8	The emergence of novel or non-analogue climates.
	9	Climate change is predicted to bring about new suitable areas for the species.
	11	Other: Consider ex-situ conservation (in context of recovery objectives).
	18	What are the limits of less dramatic alternatives to managed relocation, such as increasing habitat connectivity?
	18	What is adequate evidence that alternatives to managed relocation are unavailable and that the probability that managed relocation will succeed is adequate?
	18	To what extent do local adaptation, altered biotic interactions, no-analog climate space, and the persistence of suitable microhabitats within largely unsuitable landscapes mitigate the extinction risk (and managed relocation need) of species listed as vulnerable?
	19	Assess connectedness.
	21	Are movement pathways adequate or can they be restored?
	21	Are there adequate internal refugia?
	21	Are there adequate external refugia?
	23	Is it possible to facilitate natural migration?
	24	Consider improving […] connectivity, reduce local stressors, enhance genetic diversity within existing range.
	24	Consider ex situ conservation.
	24	Is short distance range expansion sufficient?
	24	Can habitat be created to accommodate natural altitudinal or latitudinal shifts?

Table B2 – Factors assigned to the theme 'practicality and feasibility', as derived from the assessment of 24 decision tools on assisted migration. Refer to Figure 2.5 (Chapter 2, main text) for reference key.

Category	Reference	Factor
In General	10	Are translocation and establishment of species technically feasible?
	11	If we have the practical know-how for moving a particular species safely (e.g., with minimal risk of disease transmission) and with a high probability of establishing a new population, then the project will be more acceptable.
	12	Strategies for assisted colonization: Methods of establishment.
	16	Degree to which the target can be captured, propagated, transported, transplanted, monitored, or controlled.
	19	Species Assessment: Feasibility assessment.
	23	Is establishment possible?
	24	Is translocation and establishment technically needed and/or feasible?
Costs	2	Funding: Identify the source of funds for the translocation and demonstrate that long term management and monitoring.
	11	Who should bear these costs?
	16	Feasibility: Economic cost.
	18	Who pays for managed relocation, including the studies needed to support an action, monitoring, and the outcomes of the management action?
	19	Socio-economic analysis: Assess costs.
Source Population	2	Population(s) from which individuals will be removed, effect of removing individuals on source population(s).
	3	Which population (if n > 1) can be the source for the translocated individuals?
	3	Is the source population negatively affected by the removal of individuals?
	22	Prioritise collection of taxa that are only locally abundant.
Co-Dependants	7	Dependence on interspecific interactions.
	8	Do threatened species have distinctive assemblages of dependants?
	14	Do […] host specific dependant species occur on translocated hosts? (Consider likelihood of dependents reaching the translocated host).

Co-dependants (continued)	14	Do threatened host species have dependent species restricted (host specific) to that host and therefore have high probabilities of extinction?
	14	Consider managing dependants as a threatened ecological community on that host species.
Engagement	2	Consultation and communication: Define stakeholders. Define the stakeholders. Have they been consulted and what has been the response? Provide evidence of support for the translocation.
	16	Social Criteria: Acceptability: Willingness to support action.
	16	Social Criteria: Acceptability: Aesthetic, cultural and moral attitudes towards focal and collateral units.
	16	Social Criteria: Acceptability: Concern that a focal units protection will restrict land in the recipient region from being managed or developed.
	19	Socio-economic analysis: Engage stakeholders.
	19	Institutional procedures: Involve stakeholders.
	19	Stakeholder engagement: Assess community concerns.
	19	Social environment: Stakeholder engagement.
	19	Socio-economic analysis: Assess public sentiment.
	19	Socio-economic analysis: Assess institutional capacity.
Legalities	16	Legal or regulatory obstacles (permits etc.) that would hinder or restrict the capacity to conduct assisted migration.
	16	Regulations or laws that facilitate assisted migration.
	16	Acceptability: Willingness to support new laws and policies that encourage or enable assisted migration.
	18	Do existing laws and policies enable appropriate managed relocation actions?
	18	Do existing laws and policies inhibit inappropriate managed relocation actions?
	18	Do the existing implementation policies of environmental laws provide the guidance for resource managers to fulfil their obligations for climate change adaptation?
	18	What is the process for managers, stakeholders, and scientists to work collaboratively to make managed relocation decisions?

Table B3 – Factors assigned to the theme 'ethics', as derived from the assessment of 24 decision tools on assisted migration. Refer to Figure 2.5 (Chapter 2, main text) for reference key.

Category	Reference	Factor
In General	10	Do the benefits of translocation outweigh the biological and socioeconomic costs and constraints?
	18	What is the ethical responsibility of humans to protect biodiversity (genotypic, population, species, ecosystem)?
	20	Will the experimental release further the conservation of the species?
	20	Is the experimental population essential to the continued existence of the species?
	23	Will the species survive on their own?
	23	Do benefits outweigh costs?
	24	Do the benefits outweigh the biological social and economic costs and constraints?
Confidence in Knowledge	3	Are the projections made for the translocated population correct?
	8	Species information.
	11	Other: Adequate research.
	13	Confidence in ecological understanding.
	16	Social Criteria: Acceptability: Trust and acceptance of ecological information.
	18	How well can we predict when management must address interacting suites of species rather than single species?
	18	How well can we predict when relocated species will negatively affect host system species or ecosystem functioning (e.g., nutrient flux through food webs, or movement of individuals)?
	18	How well can we predict the likelihood of a species' successful long-term establishment in light of a changing climate?
Humane-ness	2	Translocation methodology: Describe how individuals will be moved. For animals describe how the animals' welfare will not be compromised.
	2	Approvals: Include endorsement by proponent's institution, approvals by owner of source and target locations. For vertebrates other than fish, approval of an Animal (Experimentation) Ethics Committee must be obtained, noting that specialists with knowledge about translocations may need to be added to such committees.
	11	Feasibility: Humaneness (the public may find it much more acceptable to do this [assisted migration] for plant propagules than for highly sentient animals).

Humaneness (continued)	16	Social Criteria: Collateral Impact: Concerns about the harm to individual organisms subjected to assisted migration.
	16	Social Criteria: Focal Impact: Concerns about the harm to individual organisms subjected to assisted migration.
	18	What constitutes an acceptable risk of harm and what are adequate assurances for the protection of recipient ecosystems?
Action vs. Inaction	13	Perceived risk of no assisted migration.
	16	Financial loss whether focal unit declines in abundance or goes extinct.
	16	Consequence: loss of uniqueness (phylogenetic, functional) cultural importance of the target and its community (i.e. is the target a flagship or iconic species? Is the historic integrity of the community important?
	16	Consequence: effect on existing conservation efforts.
	18	Which conservation goals take ethical precedence over others and why?
	18	Is there an ethical responsibility to refrain from activities that may cause irreversible impacts, even if restraint increases the risk of negative outcomes?
Acceptance	16	Social Criteria: Acceptability: Willingness to accept potentially irreversible consequences (cultural, aesthetic, economic).
	16	If no action were taken and the species went extinct in the wild, are there ex situ individuals available for population reestablishment?
	18	Who is empowered to conduct managed relocation, and what is their responsibility in the event that the consequences are not those predicted?

Table B4 – Factors assigned to the theme 'risks', as derived from the assessment of 24 decision tools on assisted migration. Refer to Figure 2.5 (Chapter 2, main text) for reference key.

Category	Reference	Factor
In General	8	Risks (Consideration must be given to minimizing the risks and consequences of failure).
	8	Completion of comprehensive pre-translocation assessments for each species, the use of the principles of adaptive management to tailor the design, implementation and ongoing monitoring of projects, and/or the use of existing frameworks and guidelines to inform specific aspects of assisted colonization.
	13	Perceived risk of assisted migration.
	19	Risk Assessment: Target Species.
	19	Risk Assessment Exit Strategy.
Invasiveness	1	Are the identified differences likely to affect the survival/invasiveness of the species?
	2	Risk analysis: Describe the risk analysis undertaken and its outcomes. In particular, state why the taxon is considered unlikely to become invasive.
	3	Risk assessment of the likelihood the introduced species will become invasive using knowledge on intrinsic traits that promote invasiveness, laboratory and field tests, or community-based modelling.
	8	Learn from invasive species research.
	19	Post Release Management: Dispersal.
Disease	2	Disease: Disease transmission risk.
	19	Individual Release: Describe procedures for minimising the risk of death due to parasites and pathogens being moved with the taxon.
Threats to Humans	2	Does the translocated taxon pose any risks to human life or property or to other taxa resident at the target site?
	19	Individual release: Behavioural concerns.

Threats to Recipient Region	16	Ecological Criteria: Likelihood: decline or loss of ecological functions in recipient region.
	16	Ecological Criteria: Likelihood: decline or extinction of native species in recipient region.
	19	Risk Assessment: Recipient ecosystem.
	19	Population genetic issues.
Reversal	16	Degree to which effects are reversible (e.g. whether the focal unit could be easily controlled or managed once established in the recipient region).
	19	Post Release Management: Culling/removal.
General Traits	15	Intracontinental > intercontinental.
	15	Fish & crustacean < all others.

APPENDIX C:
ESTABLISHING GUT PASSAGE TIME FOR TWO SPECIES OF WESTERN AUSTRALIAN TURTLES

INTRODUCTION

A species' gut passage time is an important physiological measure that is useful for understanding how efficient a species is at acquiring and utilising energy. To measure gut passage times in chelonians, an indigestible marker is introduced with food, and the time taken to eliminate the marker is equal to the gut passage time (with the retention time being the time taken to completely eliminate the marker; e.g. Nagy 1986; Nagy 1998). X-ray technology is often used to track indigestible markers through the various organs of the digestive system to get a precise measure of gut passage time (e.g. Hailey 1997). However, this method is no longer recommended due to the potential negative effects of x-ray technology on the reproductive output of chelonians (Kuchling 2012). Though less precise, simply recording the entry and expulsion of indigestible markers gives a reliable indication of gut passage time in most species of turtles and tortoises.

Quantification of gut passage time was necessary for facilitating the measurement of standard metabolic rates in the Critically Endangered western swamp turtle (*Pseudemydura umbrina*), where fasted animals were required for metabolic experiments (Chapter 3). However, as gut passage times in this species were unknown, animal ethics considerations required me to demonstrate a proof of concept using a sympatric, less threatened turtle species.

Accordingly, here I report the outcomes of a pilot study of gut passage time on the oblong turtle (*Chelodina colliei,* previously *Chelodina oblonga;* Kuchling 2010), housed at the University of Western Australia (Crawley, Western Australia). This species is broadly distributed through wetlands in the south-west of Western Australia, where it inhabits both ephemeral and permanent wetlands (Clay 1981). I trialled three different indigestible markers, and report on the outcome of these, as well as provide the values for gut passage time in this species, and subsequently also for *P. umbrina*.

METHODS

Six male and two juvenile *Chelodina colliei* were trapped at Lake Goolellal during October 2010 in Perth, Western Australia (31°4'29 "S, 115°47'38 "E). Turtles were trapped using baited modified funnel traps, and were weighed, measured for carapace length, and marked with nail polish upon capture. Masses were measured using a Compact HL2000i 0.1g resolution digital scale, and length was measured to the nearest millimetre using Vernier callipers.

Turtles were transferred to the University of Western Australia and housed individually under natural photoperiods in outdoor enclosures for a period of three weeks (Plate C1). Turtles were given access to live prey (mosquito larvae, bloodworms) in addition to the experimental food during this time.

Capture of *C. colliei* was conducted under permit issued by the Department of Biodiversity, Conservation and Attractions, Parks and Wildlife Services to S.G. Arnall and A.R. Rafferty, who assisted with collection of the animals (Regulation 17; permit number SF007654). Protocols were approved under the Perth Zoo (2010-8) and UWA (RA/3/100/966) animal ethics committees. Turtles were released at their point of capture upon completion of the pilot study.

For testing gut passage time, three indigestible markers were trialled: 1) 1.2mm plastic spherical beads (Carst & Walker; Malaga, Western Australia), 2) rounded craft glitter,

Plate C1 – Sub-adult *C. colliei* housed outdoors at the University of Western Australia animal yards, showing various available microclimates and hides (e.g. basking log, sheltered tunnel). Photograph: S. Arnall.

and 3) food dye. *P. umbrina* held at Perth Zoo are fed ‘turtle pudding’ (minced beef, skinned rat, crayfish, white fish, egg yolk, gelatine, calcium carbonate and Herptivite^{TM}; Rep-Cal Research Laboratories, Australia) as part of routine husbandry practises. To provide consistency for future *P. umbrina* protocols, each marker was mixed into a batch of turtle pudding prior to being frozen, and was then thawed and fed to *C. colliei.* Dye was subsequently found to not be retained in the pudding and so was eliminated from further testing.

Following one week of acclimation to housing conditions, *C. colliei* were fed a random treatment of 2.5g of turtle pudding mixed with either plastic beads or craft glitter. All individuals were fed on the same day at around 2.30pm (in accordance with Perth Zoo protocols). Any uneaten food was removed after 6 hours, and feeding was reattempted the following day(s) until the turtle pudding was consumed.

To track expulsion of the markers, a simple collecting device was used to collect faeces. Similar to that described in Spencer *et al.*(1998), the device was a small (individual-specific) portion of light plastic and gauze netting taped over the tail and on to the carapace and plastron. The design appeared to have little effect on the movement of turtles. After feeding, turtles were checked every hour (including overnight) until the markers could be visually detected in the catching device.

RESULTS AND DISCUSSION

Male *C. colliei* ranged in mass between 597g and 989g (mean 817g ± 0.056g SE, n =6), while the two sub-adults were 127g and 162g respectively. All individuals maintained weight during the pilot study. Carapace lengths ranged from 10.22 cm to 22.07 cm. Food uptake was moderate, with just over half the turtles consuming the turtle pudding diet (n=5), though this took up to week for some individuals. Three individuals failed to eat any turtle pudding across the duration of the pilot study and were removed from the analyses.

Glitter was better retained within the turtle pudding than the plastic beads, which often separated out of the turtle pudding once cubes were placed in the water. Glitter markers were consumed by three of the turtles, and turtle pudding containing beads was attempted to be consumed by two individuals (in the latter, consumption was only confirmed in one). Gut passage time ranged from 3.2 to 5.3 days, with mean retention being 8.9 days (Table C1). However, it is likely that retention time was underestimated, as retention periods of over several months have been recorded in other species (e.g. in the much larger green sea turtle *Chelonia mydas*; Lutz 1990) and markers can sometimes be expelled together after several months of absence (Lutz 1990). Gut passage time was shorter in the juvenile *C. colliei* than the adult individuals, though sample sizes were inadequate for any statistical comparison. Mean minimum and maximum ambient temperatures across the pilot study were 10°C ± 0.55° C and 25.1° C ± 0.97° C respectively (6^{th} – 21^{st} of October 2010; Station 009225: BOM), though numerous microclimates were available within enclosures, including basking areas (Plate C1).

Turtles tolerated the collection devices well, and a combination of rigid strapping tape (Elastoplast^{TM}; New South Wales, Australia) and waterproof first aid tape (Nexcare 3M^{TM}; Minnesota, United States) was found to hold best in the water medium. Collection devices proved to be necessary because both glitter and plastic beads separated from the turtle pudding upon contact with the water. An alternative method

Table C1- Gut passage time and retention time for *Chelodina colliei* fed turtle pudding mixed with glitter (A) or rounded plastic beads (B), where retention time was taken as the earliest point at which two consecutive days were recorded with an absence of markers (provided defecation occurred). All individuals were adults with the exception of 'individual 1' which was a juvenile.

Treatment	**Individual**	**Mass (kg)**	**Carapace Length (cm)**	**Gut Passage Time (days)**	**Retention (days)**
A	1	0.162	10.66	3.2	6.4
B	2	0.597	19.22	5.3	10.2
A	3	0.858	20.73	4.1	8.6
A	4	0.909	22.07	4.6	11.6
A	6	0.701	21.15	3.9	7.8
Mean		0.645 ± 0.133	18.77 ± 2.08	4.2 ± 0.4	8.9 ± 0.9

would be to feed turtles in one location and then house them in another, sifting the water for presence of the markers hourly. This would further prevent results from being confounded by the additional effort (energy use) required by turtles during activity when swimming with the collection devices on. While plastic beads have many advantages in dietary studies (e.g. they can be easily recovered from faeces, are able to be counted, and are not chewed into smaller pieces; Van Soest 1994) here the smaller and flatter nature of glitter made it easier to feed within the turtle pudding, and this was deemed preferable to introducing plastic beads to the animals through tube feeding (e.g. Amorocho & Reina 2008).

GUT PASSAGE TIME IN *P. UMBRINA*

Having demonstrated that glitter added to turtle pudding was an appropriate and safe indigestible marker, and that the collection devices trialled on *C. colliei* were suitable for visualising these markers for the measurement of gut passage time, the same method was applied to *P. umbrina*. Gut passage time was measured in 16 adult and sub-adult *P. umbrina* during November and December 2010. I followed the method described for *C. colliei* for collection devices, and used glitter as the indigestible marker. Individual *P. umbrina* were housed outdoors under fluctuating conditions in enclosures at the Perth Zoo, as described in Chapter 3, and were fed as per normal husbandry protocols before and after the introduction of the marker. Mean minimum and maximum ambient temperatures across the pilot study were 15.4°C ± 0.5° C and 27.6°C ± 1.1° C respectively (23 November – 14 December 2010; Station 009225: BOM), but as with *C. colliei*, numerous microclimates were available within enclosures (Plate C2).

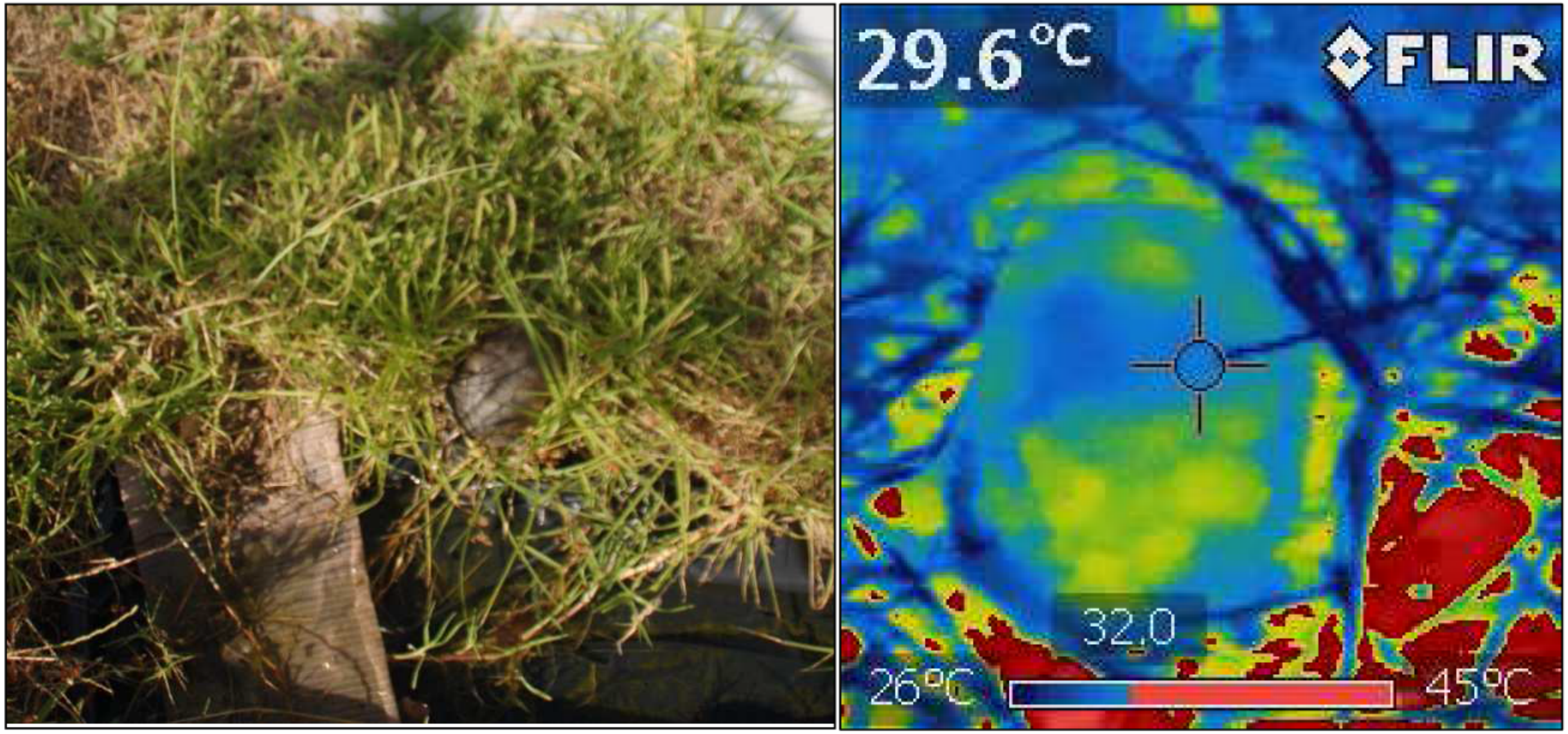

Plate C2 –*P. umbrina* housed outdoors at the Perth Zoo, showing mesh strip hide and basking behaviour. Right panel shows thermal infrared image of the same individual taken with an FLIR Systems i7 thermal camera, demonstrating a spot reading of body temperature (32.0°C) that is higher than the ambient temperature (29.6°C). Photographs: S. Arnall.

Sub-adults (81g-142g; n = 8) had a mean gut passage time of 33.68 hours (± 4.16 hours) and adults (260g-369g; n = 8) had a shorter gut passage time of 23.45 hours (± 4.06 hours). However, this was not significantly different (t_{14} = 1.759, P = 0.545). All individuals consumed the turtle pudding. Retention time ranged from 3 to 9 days (age classes pooled).

As *P. umbrina* (maximal size 13.8cm; Chapter 4) are smaller than *C. colliei* (male 17.1cm ± 11.3cm, female 19.4cm ± 21.3cm; Bonnet *et. al* 2010), it was expected that their gut passage time would be less than that of *C. colliei* due to a lesser gut volume and size. For both species, gut passage times and retention times were similar to that reported elsewhere for chelonians (Table C2; though note that these data are impacted by numerous factors including food type and water temperature, and the two species in this study experienced diurnally fluctuating natural conditions, which further confounds comparisons). There appeared to be a weak cursory relationship between body mass (y) and gut passage time (x) in the testudine species reported (R^2 = 0.39), where larger species had longer gut passage times (midpoints taken; y = 0.0494x + 3.8582). As the purpose of this study was the facilitation of experimental work, many variables which would benefit the understanding of scaling relationships in both *P. umbrina* and *C. collei* were not recorded (e.g. body temperature, food digestibility, and food intake). For example, Meinenberger *et al.* (1993) found daily mean food intake scaled with body mass in the desert tortoise (*Xerobates agassizii*), and this in turn influenced gut passage time (where the higher the food intake, the shorter the gut transit time). However, in other species, no relationship has been found (Bjorndal 1987; Bjorndal 1989). Comparisons within and between species for which measurements of mass, length,

Table C2 – Gut passage times recorded in some Testudine species.

Scientific Name	Common Name	Adult/Sub-adult: Mass	Gut Passage Time (Hours)	Retention Time (Hours)	Reference
Caretta caretta	Loggerhead Turtle	4.4 kg - 22.2 kg	217.2 (± 73.2)	316.56 (± 111.3)	Valente *et. al* (2008)
Chelodina colliei	Southwestern snake-necked turtle	Adult: 0.597 kg - 0.989 kg Sub-adult: 0.127 kg - 0.162 kg	107.5 (± 7.4) 76.8	229.2 (± 20.4) 153.6	This study
Chelonia mydas agassizii	East pacific green turtle	26-48 kg	528 (± 151.2)	592.8 (± 144)	Amorocha & Reina (2008)
Emydura macquarii	Australian short-necked turtle	Not reported	Fish Diet: 89 (± 6) - 20°C 70 (± 3) - 30°C Plant Diet: 260 (± 10) - 20°C 118 (± 8) - 30°C	115 (± 9) - 20°C 89 (± 51) - 30°C 310 (± 30) - 20°C 158 (± 12) - 30°C	Spencer & Thompson (1998)
Geochelone carbonaria	Red-footed tortoise	0.4 kg - 4.8 kg	Guava Diet: 62.4 (± 24 day) Mango Diet: 158.4 (± 28.8) Lantana Diet: 228 (± 40.8)	Not Reported	Bjorndal (1989)
Geochelone denticulata	Yellow-footed tortoise	0.5 kg - 6.6 kg	Guava Diet: 86.4 (± 21.6 day) Mango Diet: 115.2 (± 31.2) Lantana Diet: 208.8 (± 45.6)	Not Reported	Bjorndal (1989)
Geochelone pardalis	Leopard Tortoise	3.4 kg	91.2 (± 36)	141.6 (± 36)	Hailey (1997)
Gopherus polyphemus	Gopher tortoise	3.3 kg - 7.9 kg	312 (± 67.2)	Not Reported	Bjorndal (1987)
Kininys spekii	Speke's hinge-back tortoise	1.1 kg	52.8 (± 9.6)	108 (± 24)	Hailey (1997)

Scientific Name	Common Name	Adult/Sub-adult: Mass	Gut Passage Time (Hours)	Retention Time (Hours)	Reference
Pseudemydura umbrina	Western Swamp Turtle, Western Swamp Tortoise	Adult: 0.26 kg- 0.369 kg Sub-adult: 0.081 kg - 0.142 kg	23.45 (± 4.06) 33.68 (± 4.16)	72 - 216	This study
Pseudemys nelsoni	Florida red-bellied cooter	Adult: 3.04 kg (± 0.29 kg) Hatchling: 0.0123 kg (± 0.002 kg)	81 (± 19) 56 (± 4)	Not Reported Not reported	Bjorndal & Bolten (1992)
Testudo pardalis	Leopard Tortoise	Male: 3-5 kg Females: 11 kg - 21 kg	144 - 166	Not reported	Taylor *et. al* (1996)
Trachemys scripta scripta	Yellow-bellied slider	1.4 kg - 1.6 kg	85 (± 7)	Not Reported	Bjorndal (1991)
Xerobates agassizii	Desert Tortoise	Male: 1.9 kg - 2.68 kg Female: 3.1 kg - 1.3 kg Juvenile: 0.751 kg - 0.249 kg	Plant Diet: 24.5 (± 2.6) 18 (± 3.7) 15.4 (±0.9) Grass Diet: 25 19.33 (±3.06) 24 (±1.58)	Not Reported	Meienberger *et. al* (1993)

feeding history, digestibility, food intake, temperature, and phylogeny are known would facilitate a better understanding of scaling relationships in testudines.

CONCLUSION

The gut passage time of *P. umbrina* was successfully measured by introducing an indigestible glitter marker to their food, after demonstrating proof of concept in *C. colliei*. Gut passage time was longer in *P. umbrina* than *C. colliei*, though measurement conditions were not identical. The information from this pilot study can be used to inform fasting protocols required for future experimental work, such as the measurment of standard metabolic rates in *P. umbrina* (Chapter 3).

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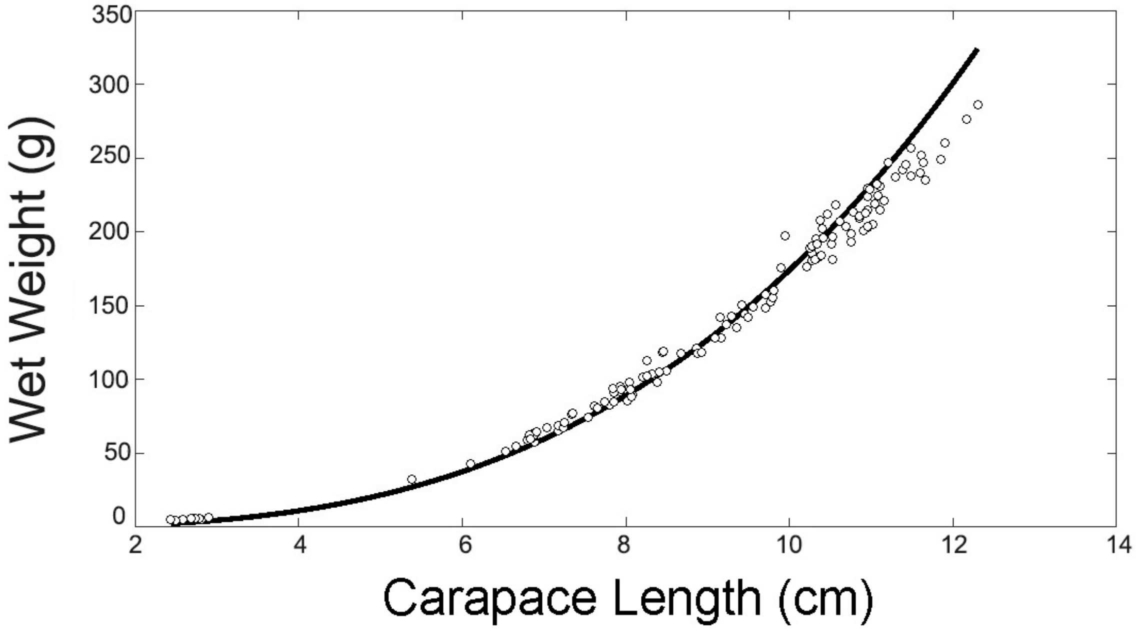
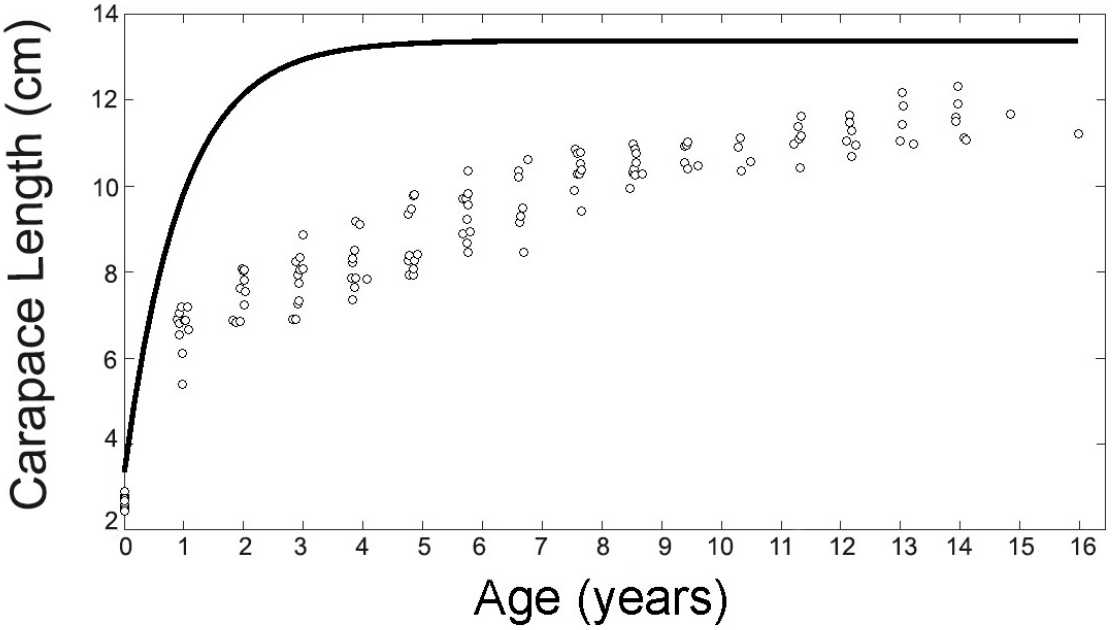
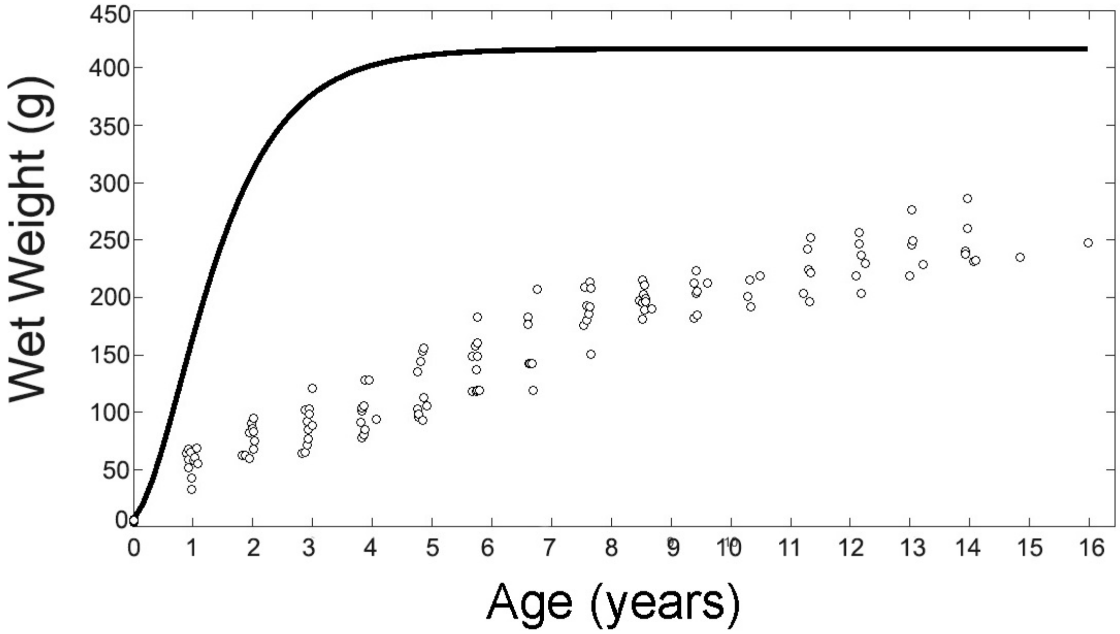
APPENDIX D:
SUPPLEMENTARY TABLES AND FIGURES FOR CHAPTER 4

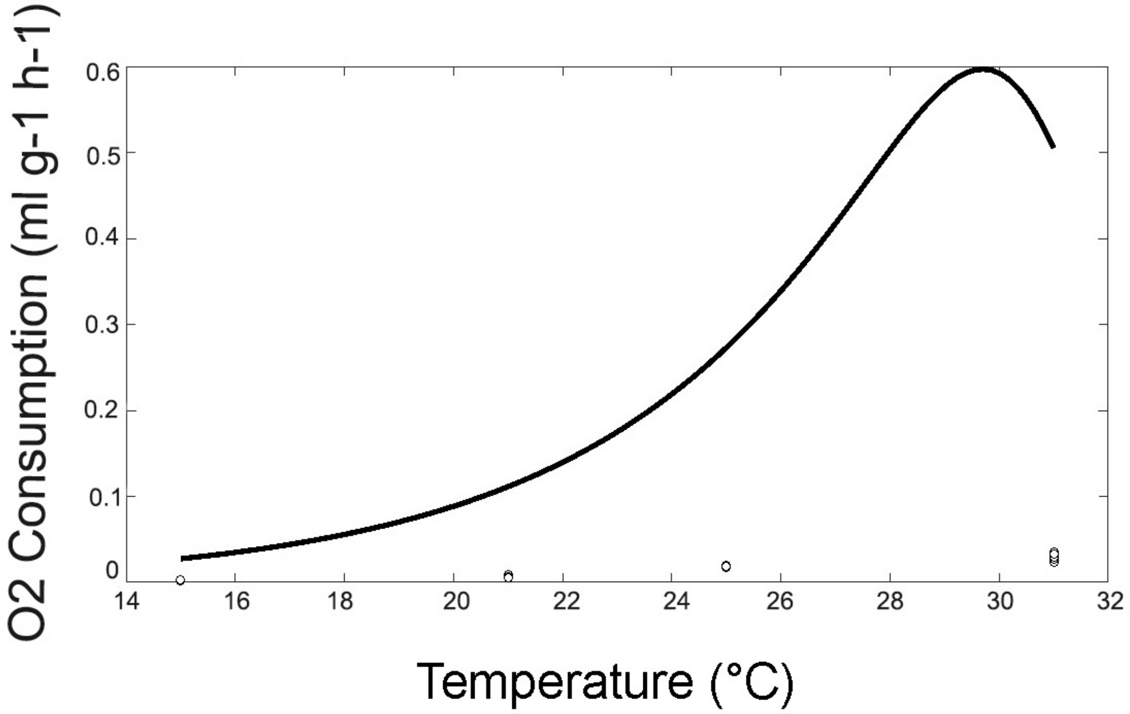
Here I provide high-resolution figures for the three model fitting strategies, MF1 (which takes the midpoint f to approximate the yearly fluctuations between an f of 1 during wet periods, and 0 during aestivation periods), MF2 (which fits the model with a splining function to explicitly derive f and c_T across time), and MF3 (which applies a depression factor to MF2 during aestivation (refer 4.2.4 main text for details). I also provide the outputs of MF3 when a typical testudine somatic maintenance cost was prioritised (referred to below as the 'Typical [$\dot{p}_M$] Model').

MF1

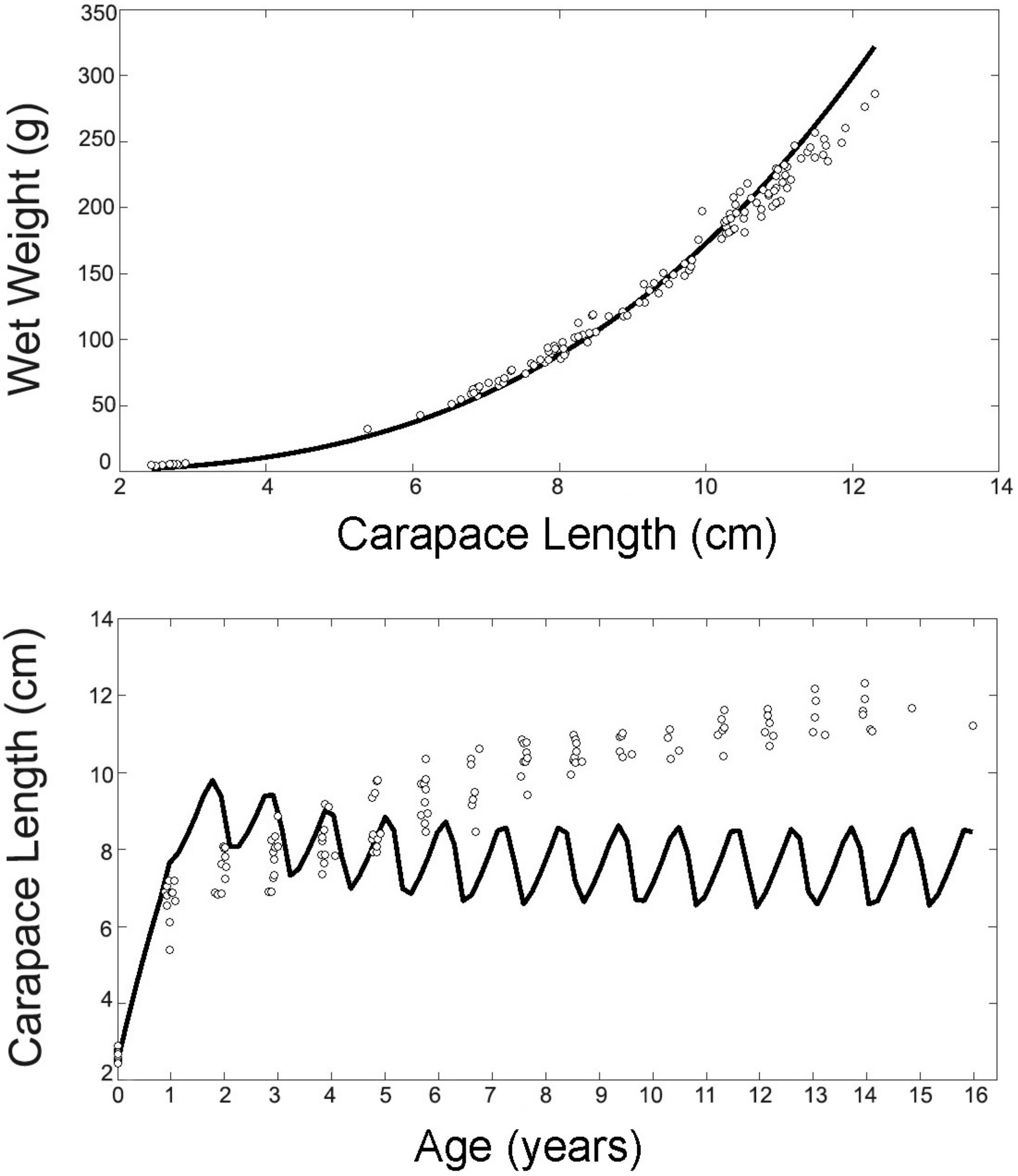

Wet Weight (g)
350
300
250
200
150
100
50
0
2
4
6
8
10
12
14
Carapace Length (cm)

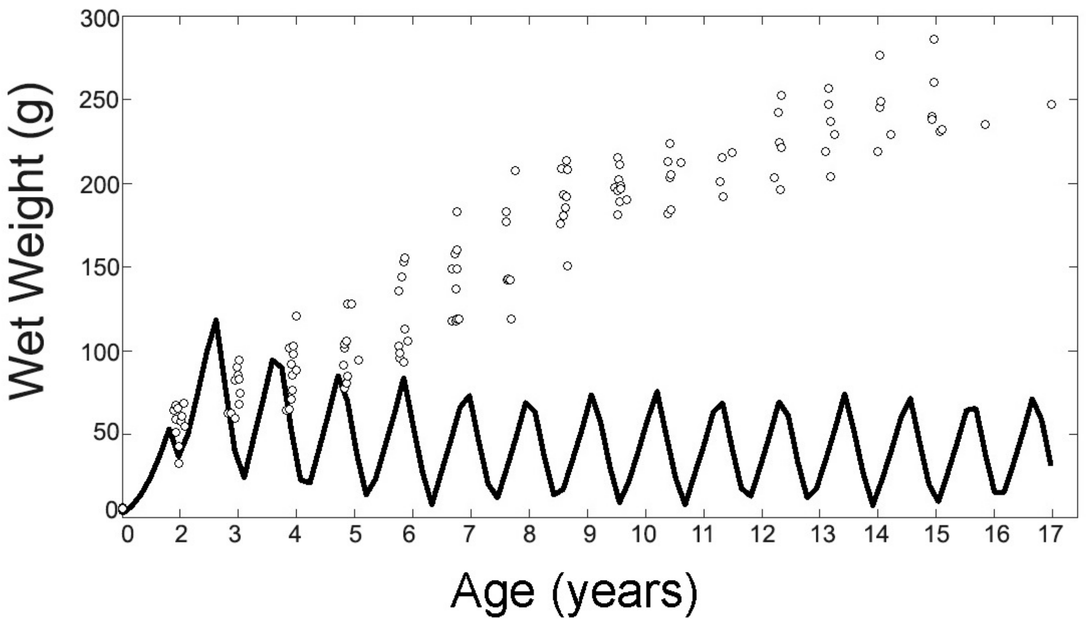

Carapace Length (cm)
14
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Age (years)

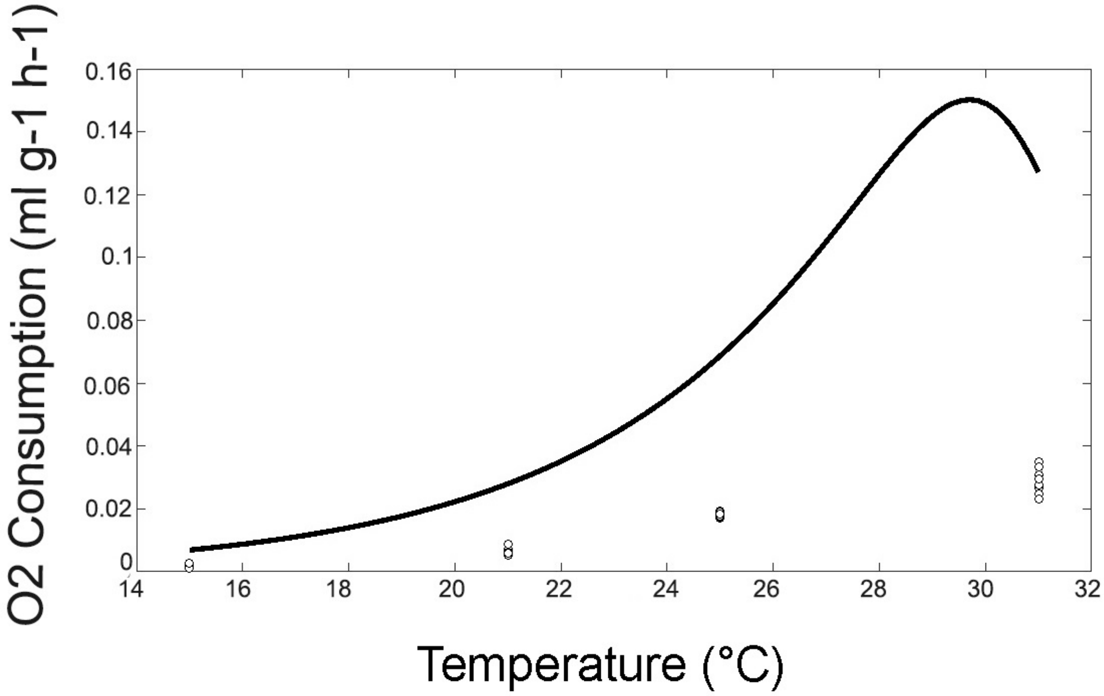

Wet Weight (g)
450
400
350
300
250
200
150
100
50
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Age (years)


O2 Consumption (ml g-1 h-1)
0.6
0.5
0.4
0.3
0.2
0.1
0
14
16
18
20
22
24
26
28
30
32
Temperature (°C)

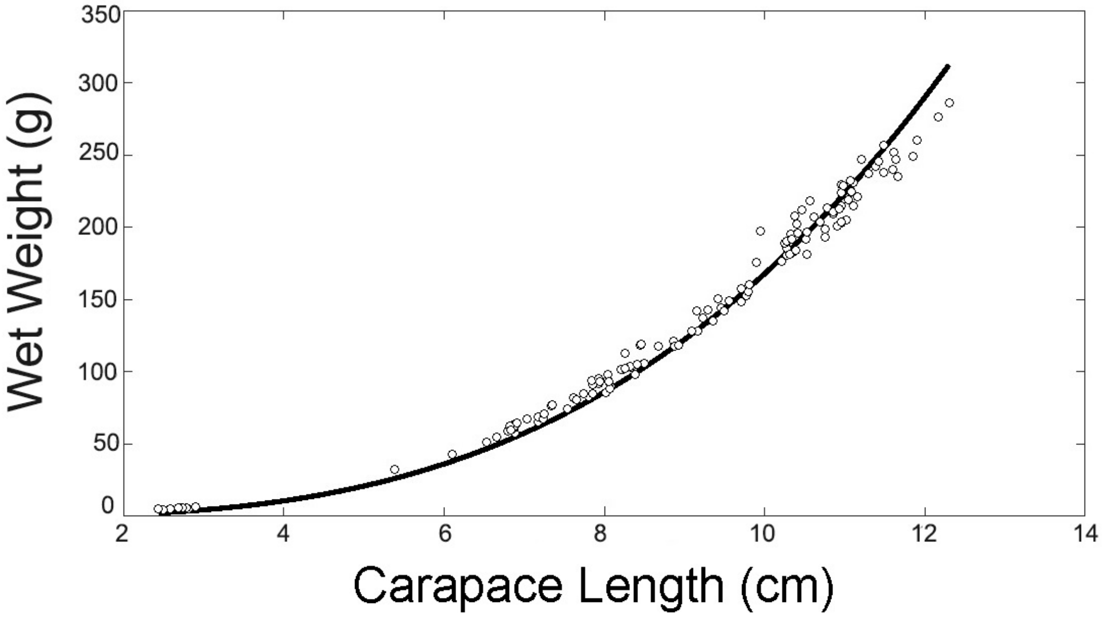
MF2

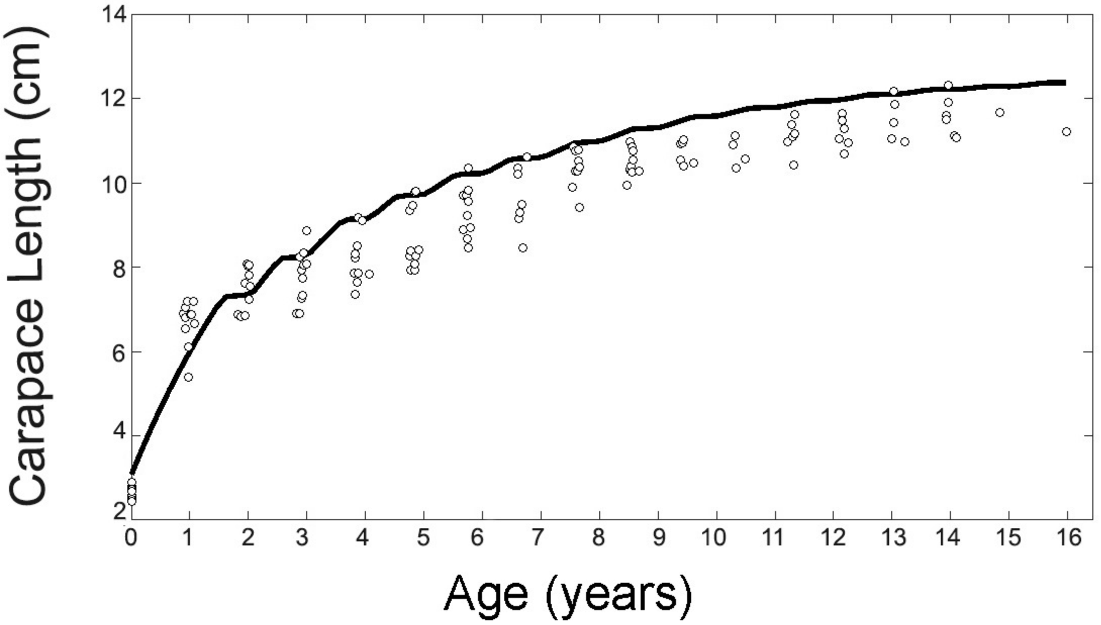

Wet Weight (g)
350
300
250
200
150
100
50
0
2
4
6
8
10
12
14
Carapace Length (cm)
Carapace Length (cm)
14
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Age (years)

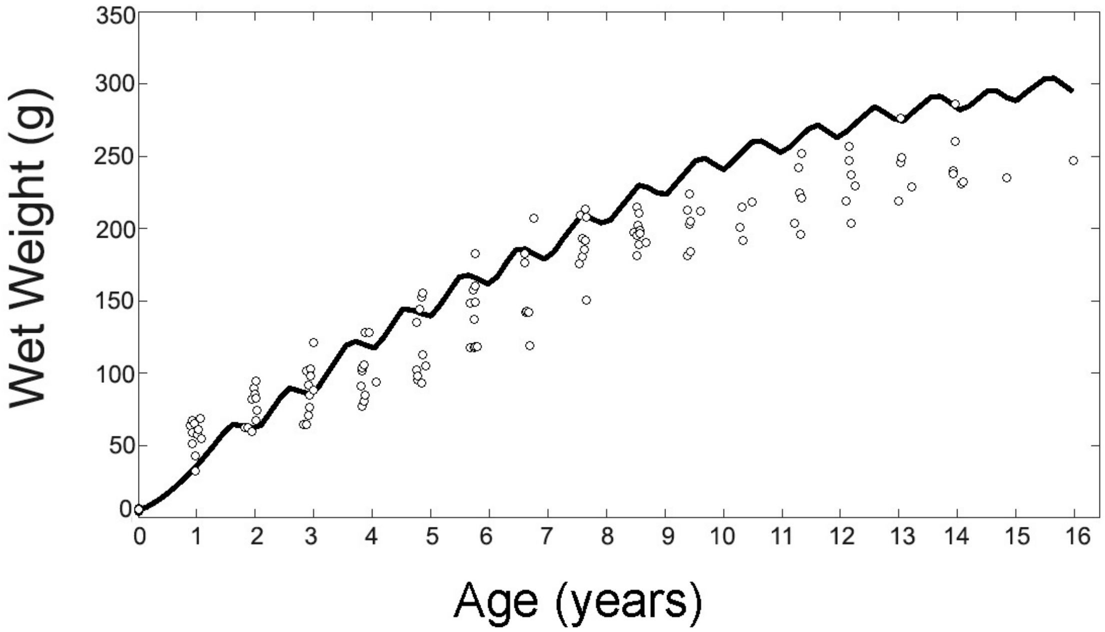

Wet Weight (g)
300
250
200
150
100
50
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Age (years)

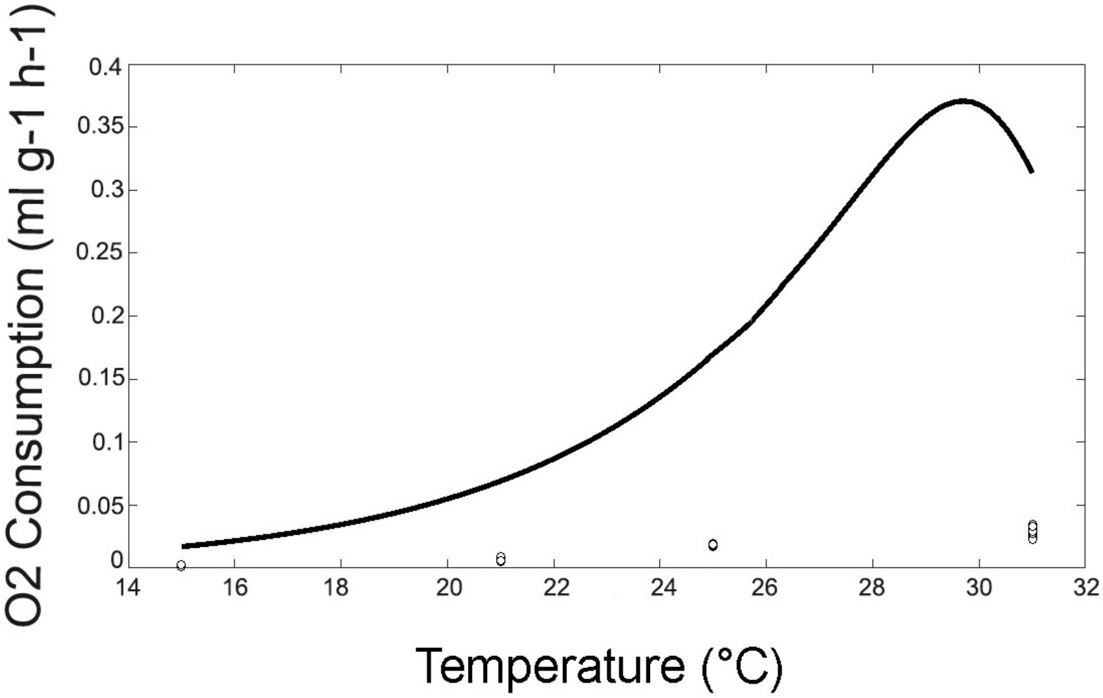

O2 Consumption (ml g-1 h-1)
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
14
16
18
20
22
24
26
28
30
32
Temperature (°C)

MF3

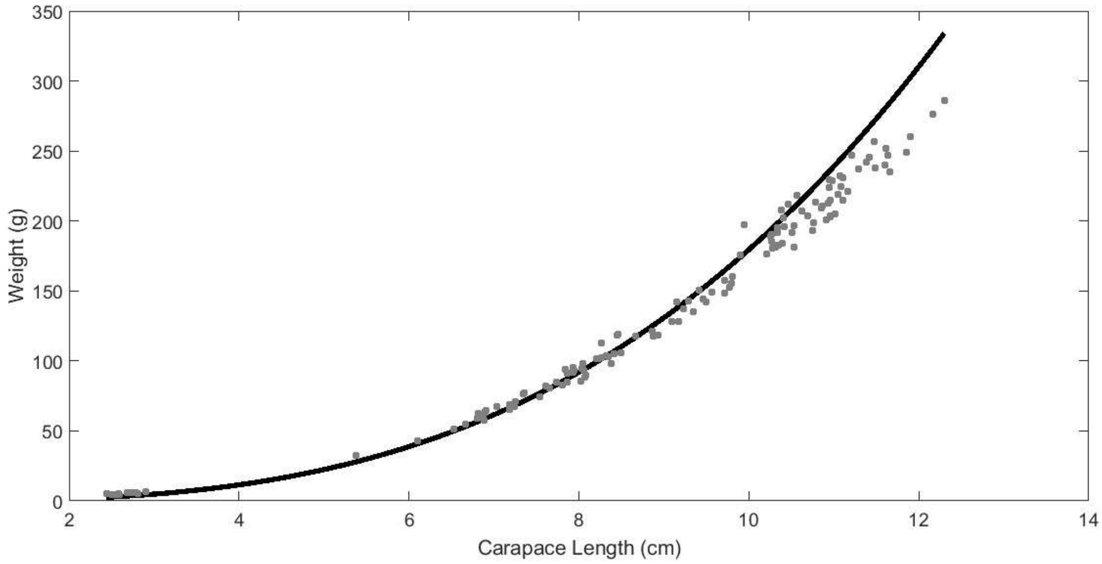

Wet Weight (g)
0
50
100
150
200
250
300
350
2
4
6
8
10
12
14
Carapace Length (cm)

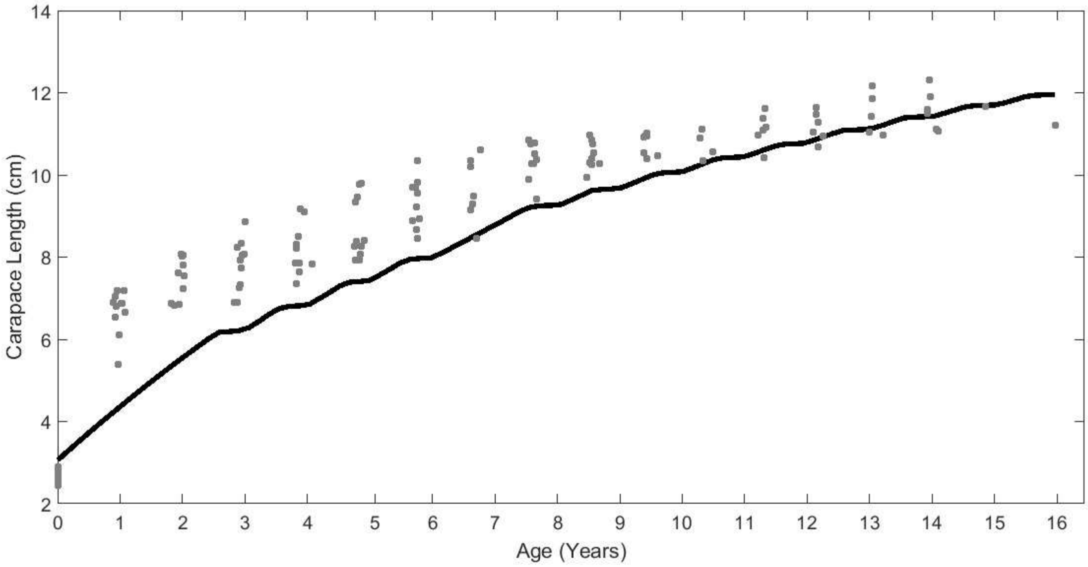

Carapace Length (cm)
2
4
6
8
10
12
14
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Age (years)

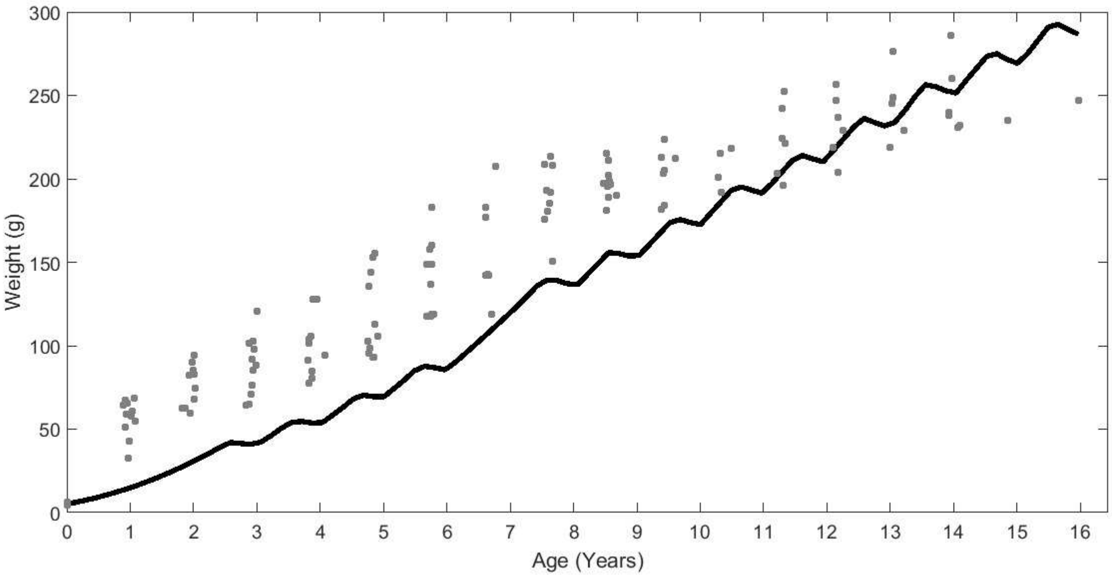

Wet Weight (g)
350
300
250
200
150
100
50
0
Age (years)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16


O2 Consumption (ml g-1 h-1)
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Temperature (°C)
14
16
18
20
22
24
26
28
30
32

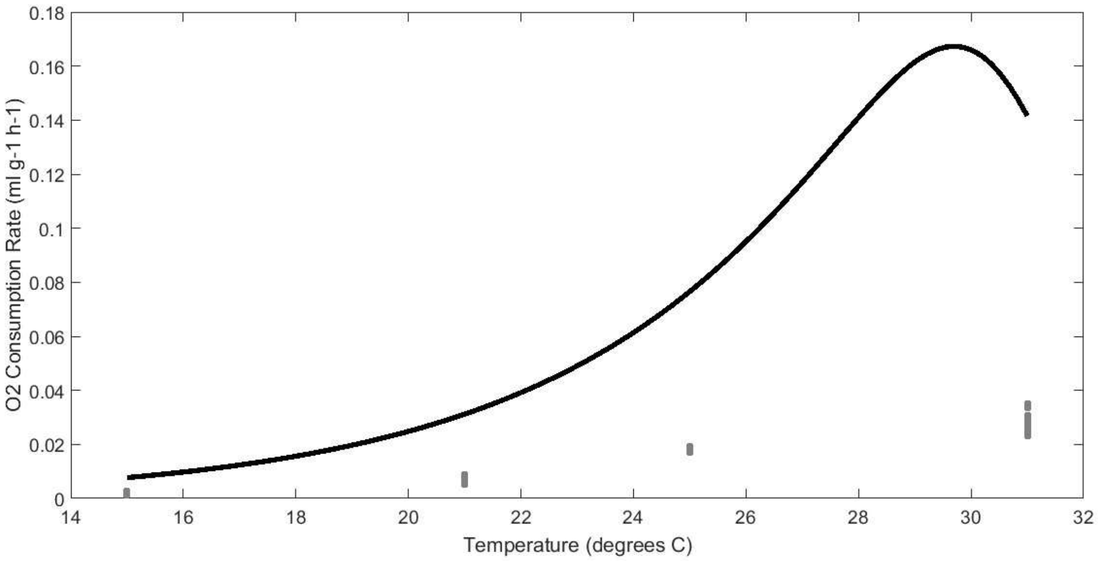
Typical $[\dot{p}_M]$ Model







Weight (g)
300
250
200
150
100
50
0
Age (Years)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16



O2 Consumption Rate (ml g-1 h-1)
0.18
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
Temperature (degrees C)
14
16
18
20
22
24
26
28
30
32

Zero-variate data	**Observed**	**Expected – Typical p_M**	**Expected – MF3**
a_b, age at birth (days)	153	69.9	55.0
a_p, age at puberty (days)	3767	4542	2960
a_m, life span (days)	36500	35890	32920
L_b, length at birth (cm)	2.6	3.06	3.06
L_p, length at puberty (cm)	10.7	9.86	10.10
L_i, ultimate length (cm)	13.8	17.78	13.68
W_b, wet weight birth (g)	5.2	5.15	4.92
W_p, wet weight puberty (g)	236.5	171.9	178.60
W_i, ultimate wet weight (g)	417.0	1010.0	443.6
R_i, max. reproduction rate (# day^{-1})	0.0137	0.0084	0.0089
Fit Score – Mean Absolute Relative Error MRE	-	0.542	0.781

Parameter values	Unit	Typical p_M	MF3	Source
z, zoom factor	-	7.6	2.7	Estimated
δM, shape coefficient	-	0.43	0.20	Estimated
v, energy conductance	cm d^{-1}	0.02	0.01	Estimated
$\varkappa$, allocation fraction to soma	-	0.65	0.72	Estimated
$\varkappa_R$, reproduction efficiency	-	0.95	0.95	Default
$[\dot{p}_M]$, vol-specific somatic maintenance	J d^{-1} cm^{-3}	18.96	504.1	Estimated
k_J, maturity maintenance rate coefficient	d^{-1}	0.002	0.002	Estimated
$[E_G]$, spec cost for structure	J cm^{-3}	8292	7965	Estimated
e_H^b, energy maturity at birth	J	1042	2275	Estimated
e_H^p, energy maturity at puberty	J	5.46E+05	5.57E+05	Estimated
h_a,Weibull aging acceleration	d^{-1}	9.55E11	6.30E11	Estimated
T_A, Arrhenius temperature	K	19731	19731	Chapter 3
T_L, lower bound for T_A	K	278.15	278.15	Chapter 3
T_H, upper bound for T_A	K	304.15	304.15	Chapter 3
T_{AL}, value of T_A below lower bound	K	50000	50000	Chapter 3
T_{AH}, value of T_A above upper bound	K	90000	90000	Chapter 3
s_M, metabolic depression factor	-	0.0735	0.0518	This study

APPENDIX E: SUPPLEMENTARY TABLES AND FIGURES FOR CHAPTER 5

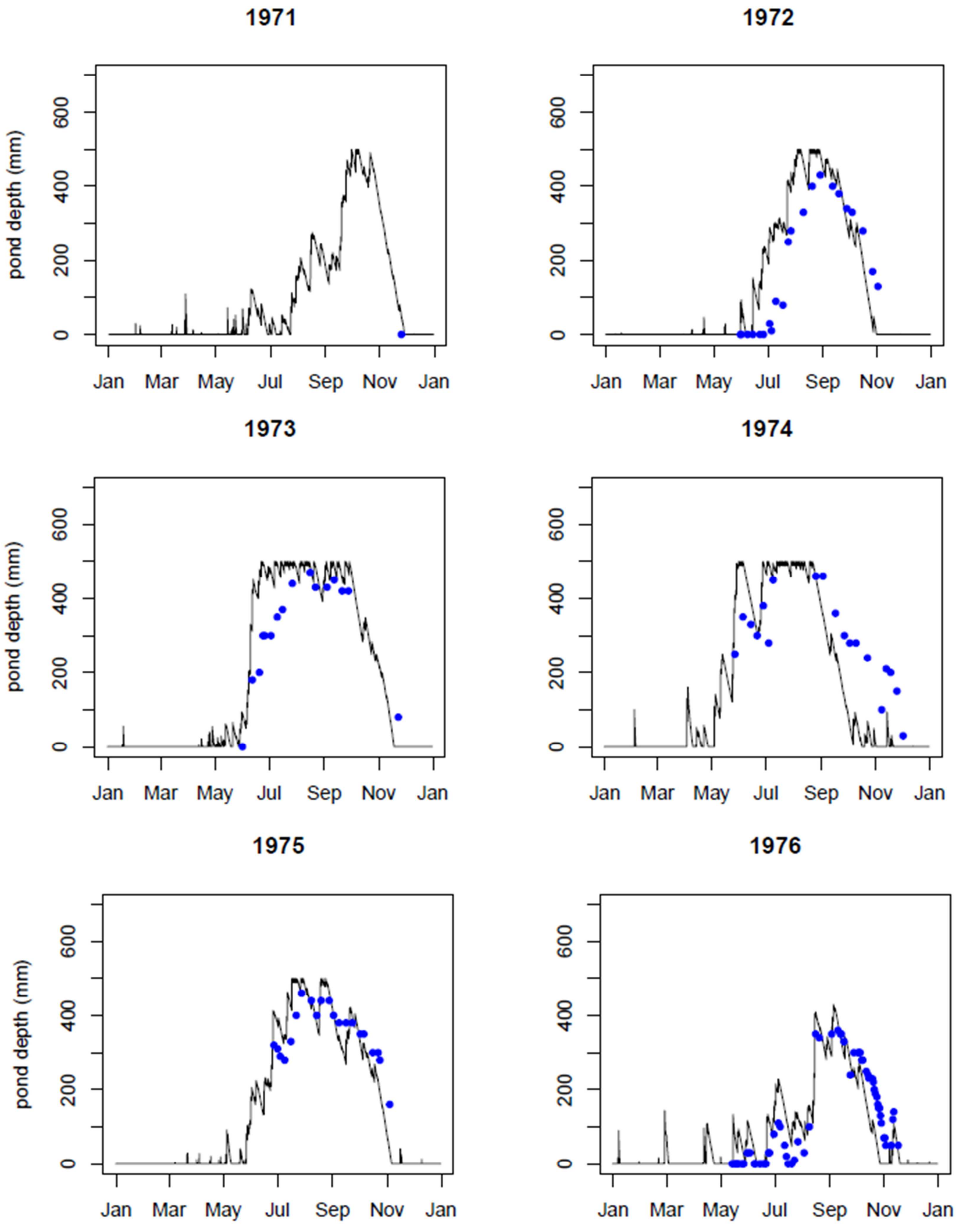
Table D1 - Index of year classifications where ‘good’ years are those with the longest hydroperiods and the warmest projected water temperatures, ‘poor’ years are years with the shortest hydroperiods and the coldest temperatures, ‘medium-poor’ years are those with long hydroperiods but cool temperatures and ‘medium-good’ years are years with short hydroperiods and warm temperatures (N=11 per category).

Individual Born	Year Classification
1972	Medium-Poor
1973	Good
1974	Medium-Poor
1975	Medium-Poor
1976	Poor
1977	Poor
1978	Medium-Poor
1979	Poor
1980	Good
1981	Medium-Good
1982	Medium-Good
1983	Medium-Good
1984	Good
1985	Medium-Good
1986	Poor
1987	Medium-Poor
1988	Good
1989	Medium-Poor
1990	Medium-Good
1991	Good
1992	Medium-Poor
1993	Poor
1994	Medium-Poor
1995	Good
1996	Good
1997	Medium-Good
1998	Medium-Good
1999	Good
2000	Medium-Poor
2001	Medium-Good
2002	Poor
2003	Good
2004	Medium-Poor
2005	Poor
2006	Medium-Good
2007	Medium-Poor
2008	Poor
2009	Poor
2010	Poor
2011	Good
2012	Medium-Good
2013	Medium-Good
2014	Good
2015	Poor

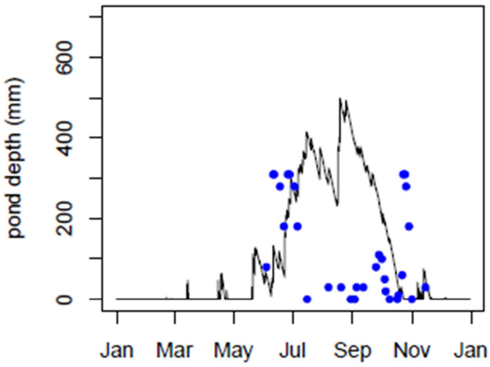
Table E 2 – Mean hydroperiod length and water temperature for each year type classification.

	Hydroperiod Length	Temperature
Good	175.443	13.217
Medium-good	155.061	12.716
Medium-poor	128.830	12.974
Poor	111.856	12.232
Pr > F	< 0.0001	< 0.0001
Significant	Yes	Yes

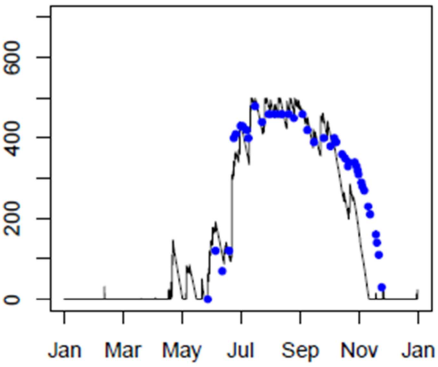
Figure E1 – Predictions (black lines) against observations (blue dots) for hydroperiod at Ellen Brook Nature Reserve, as generated by the microclimate model of NicheMapR, and tested against visual water depth guages.



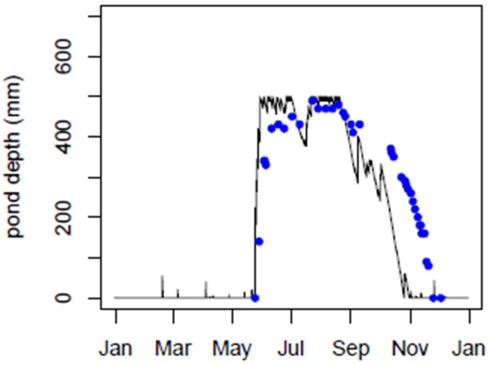
1979



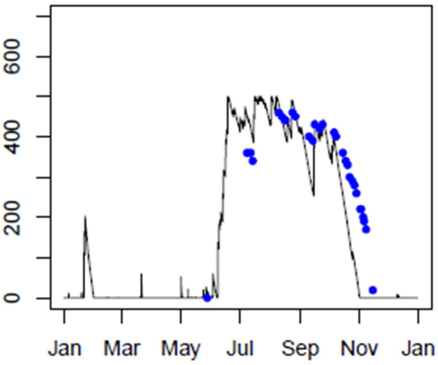
1980



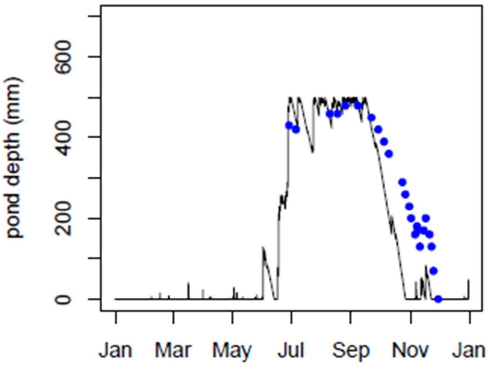
1981



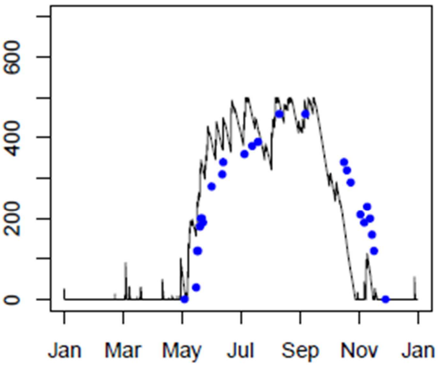
1982



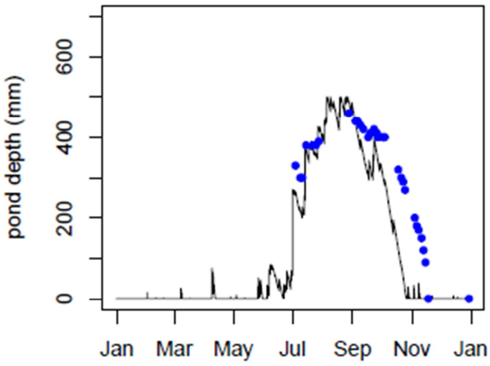
1983



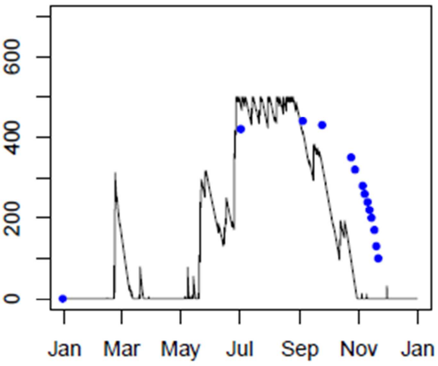
1984

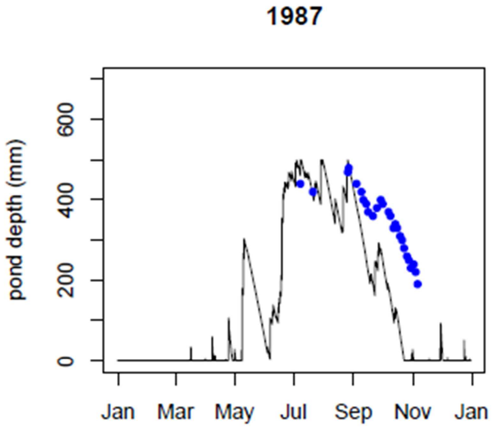


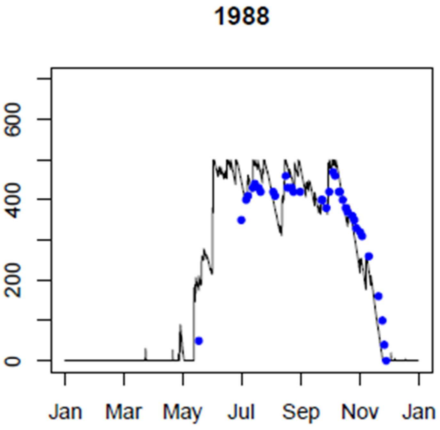
1985

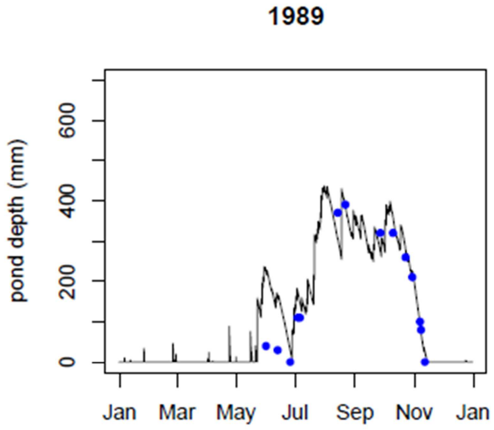


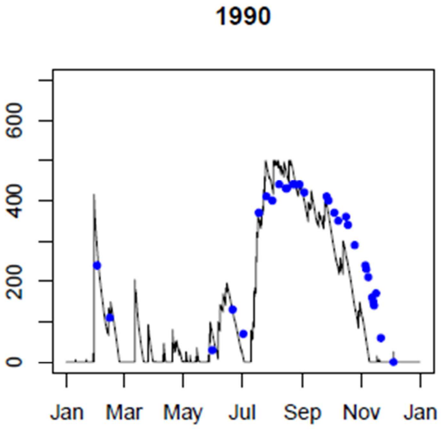
1986

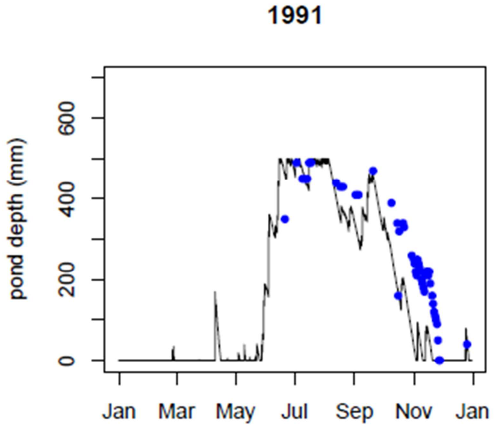


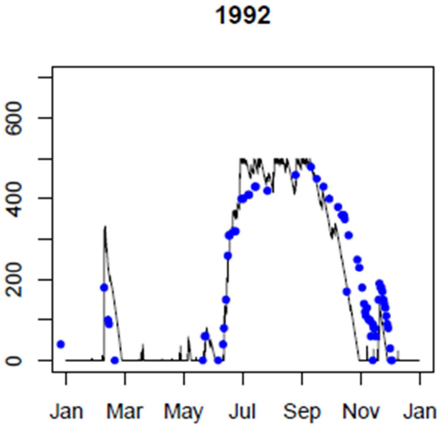

1987
pond depth (mm)
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan

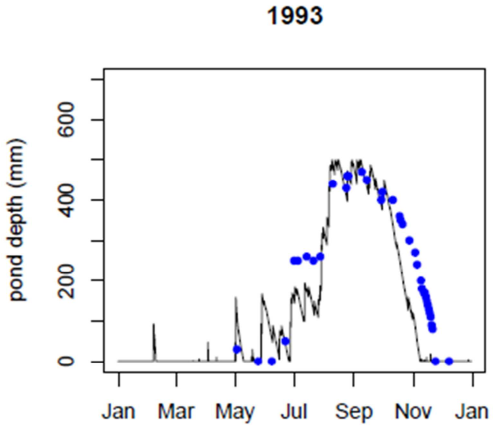

1988
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan

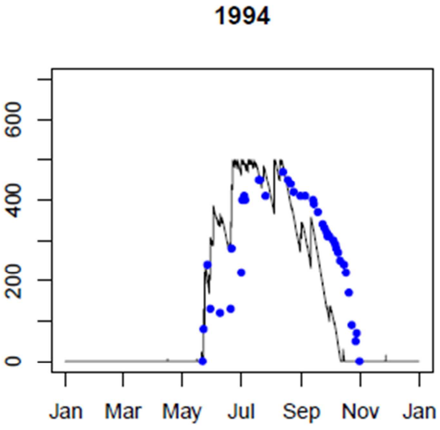

1989
pond depth (mm)
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan

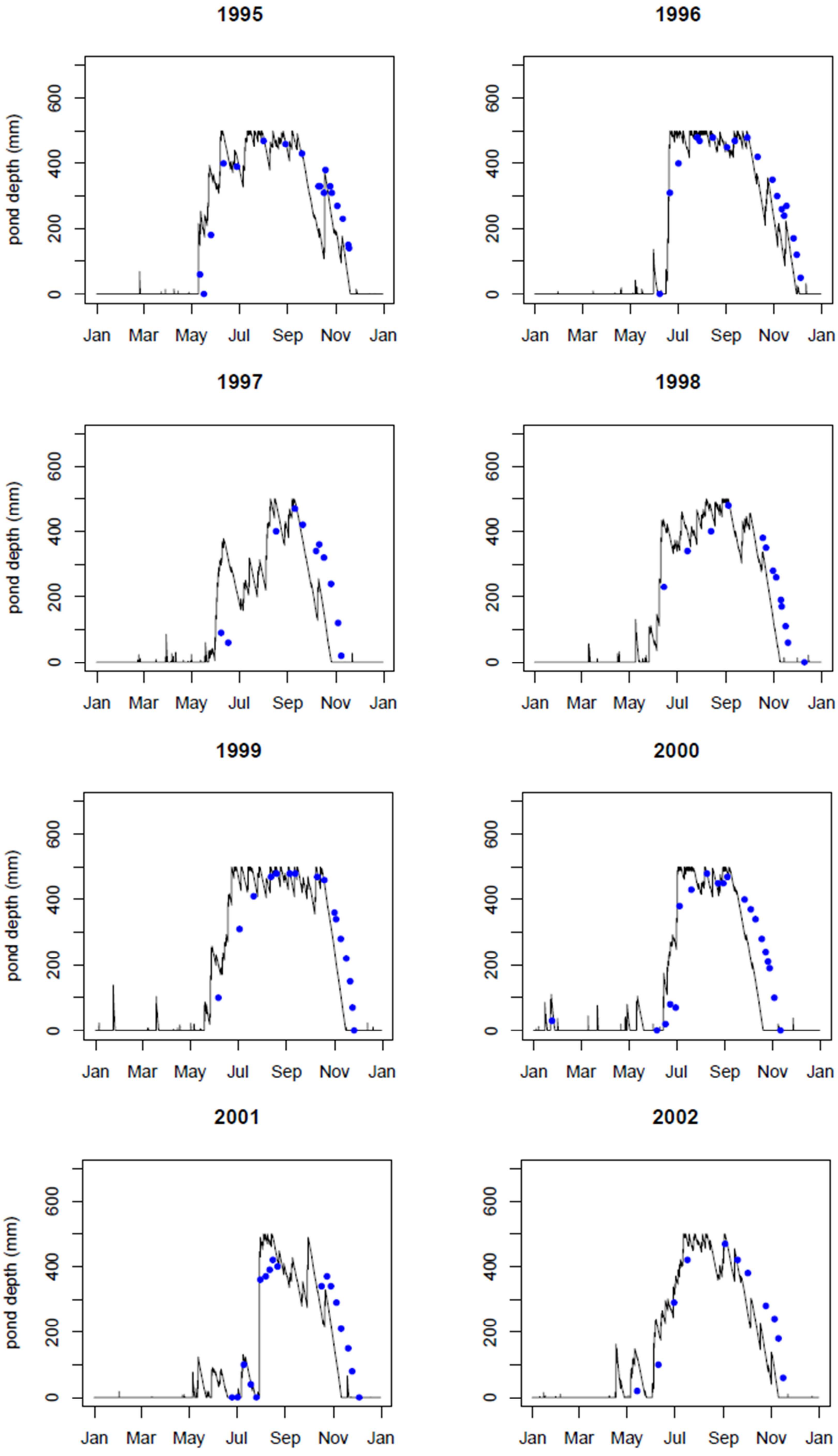

1990
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan

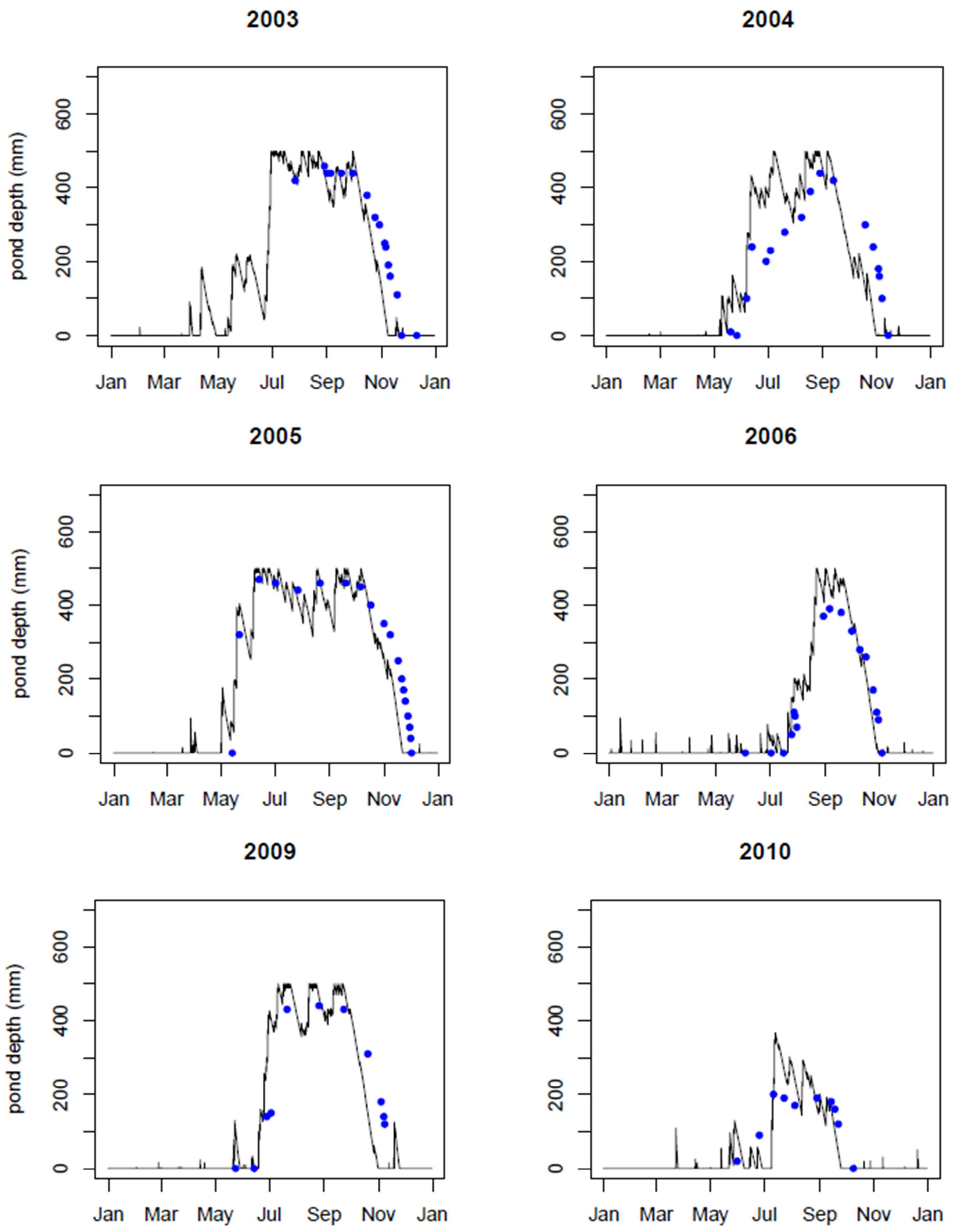

1991
pond depth (mm)
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan


1992
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan


1993
pond depth (mm)
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan


1994
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan


1995
1996
1997
1998
1999
2000
2001
2002
pond depth (mm)
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan


2003
2004
2005
2006
2009
2010
pond depth (mm)
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan

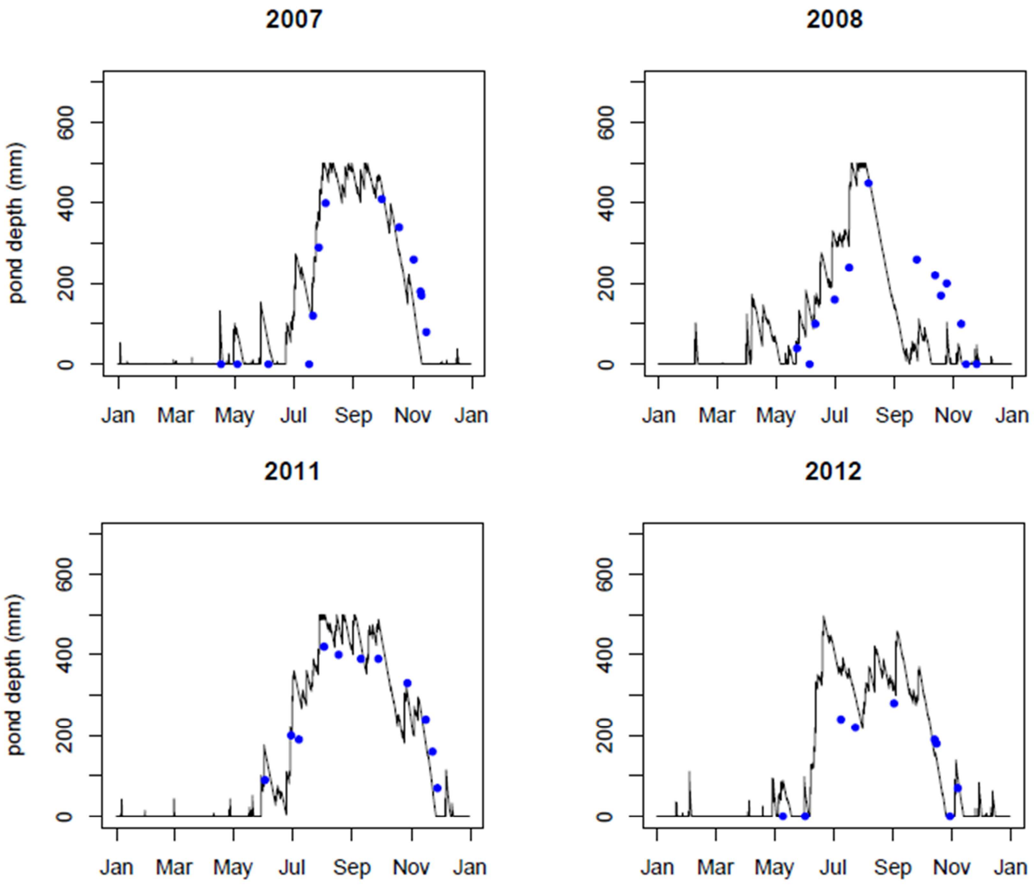
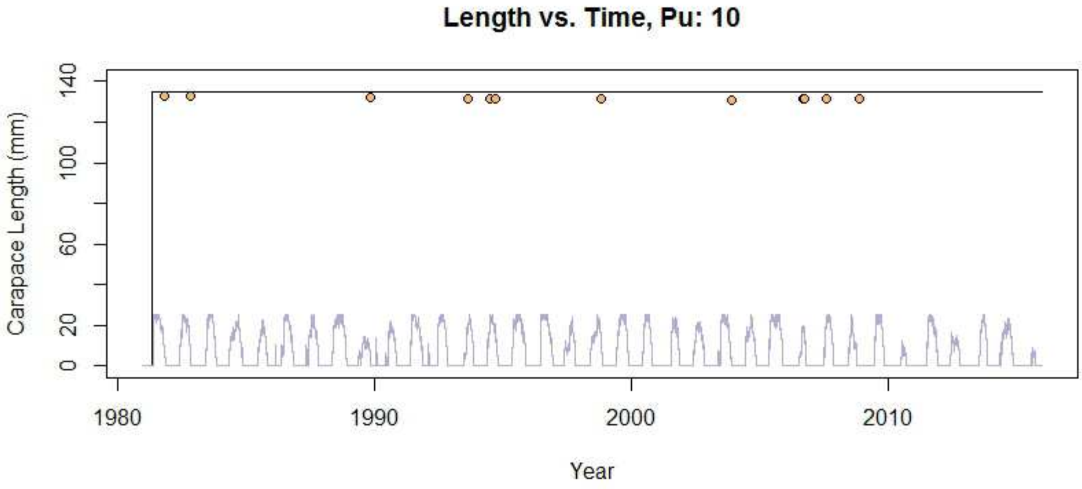
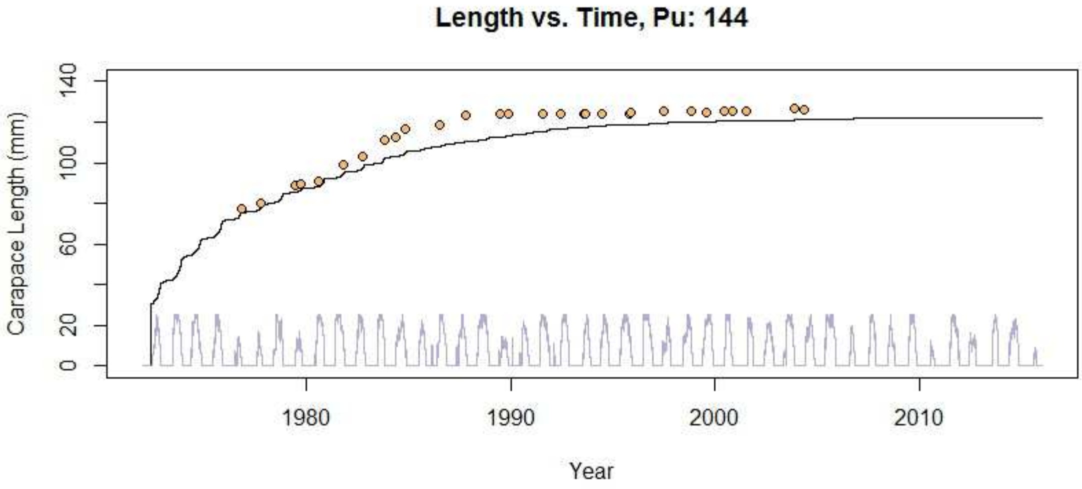
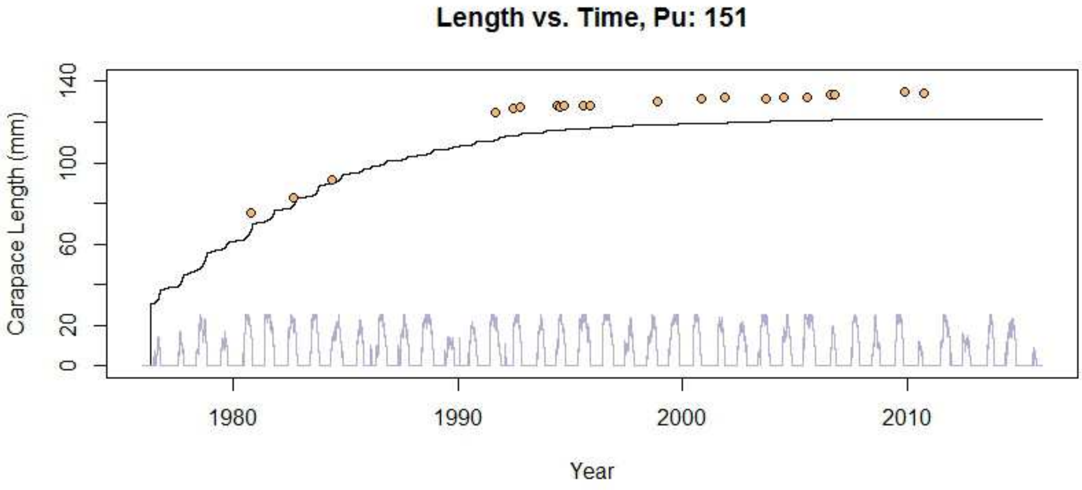
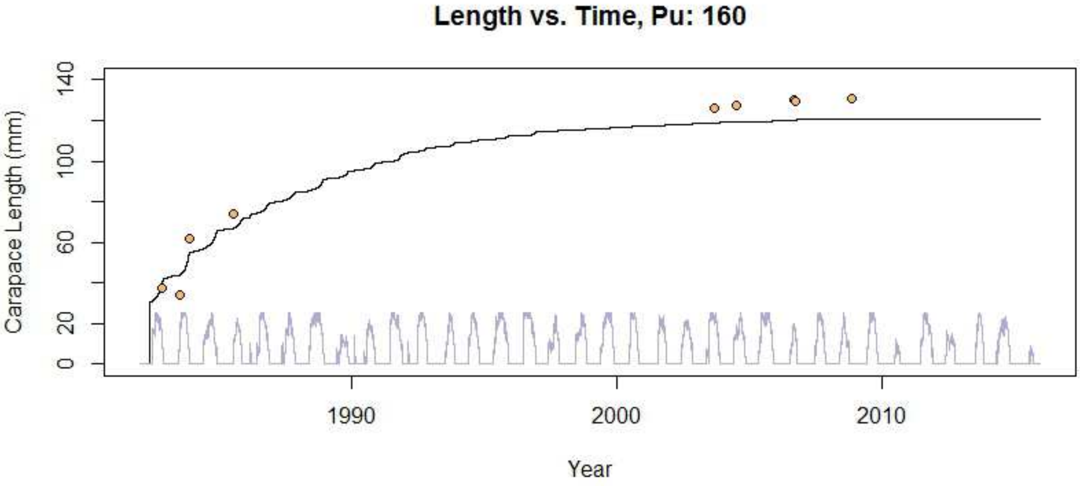

2007
2008
2011
2012
pond depth (mm)
0
200
400
600
Jan
Mar
May
Jul
Sep
Nov
Jan

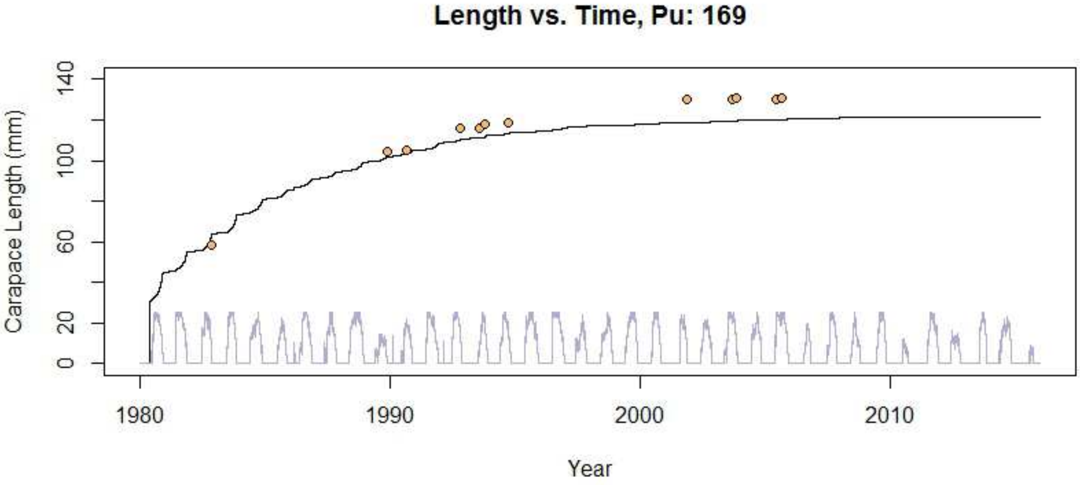
Figure E2 - Length predictions (black lines) against observations (yellow dots) for individual *P. umbrina* at Ellen Brook Nature Reserve. Blue lines depict the annual predicted hydroperiods.

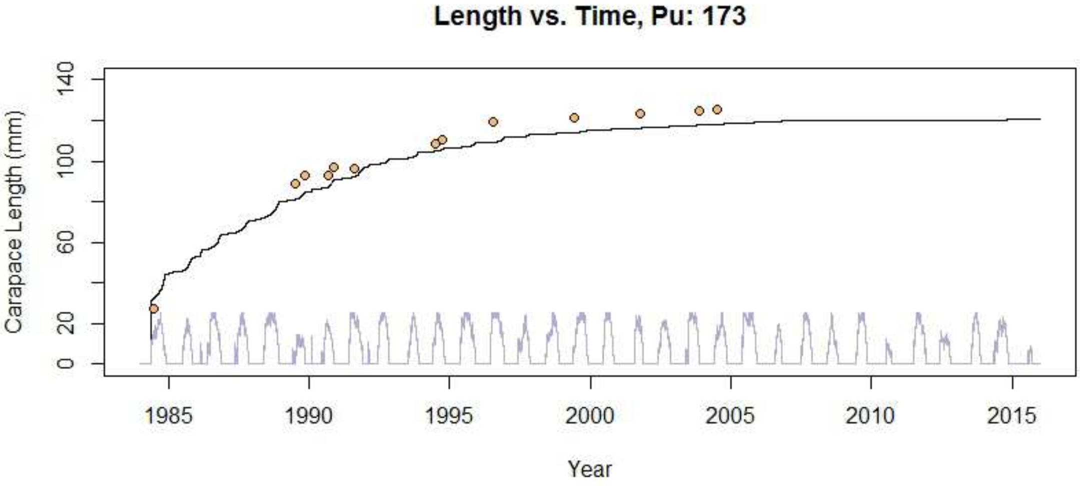


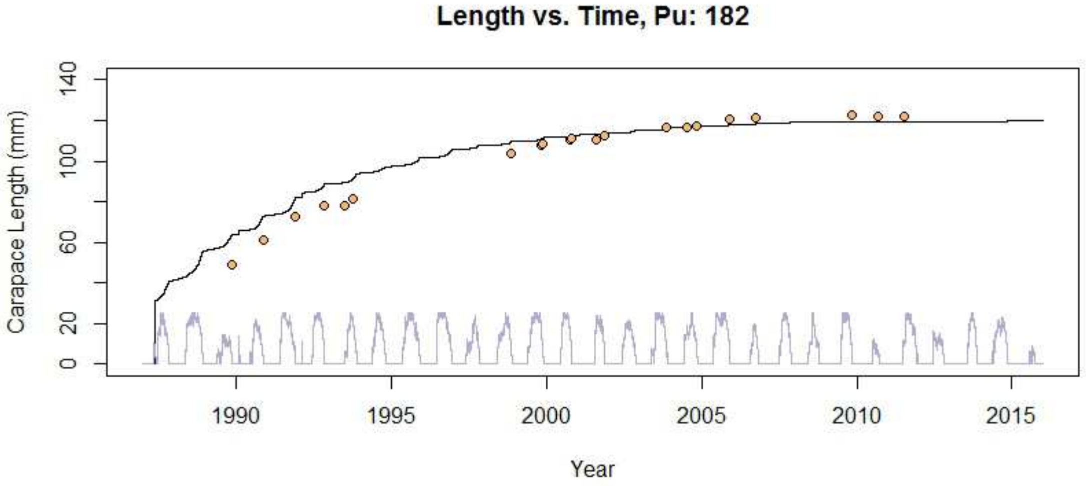


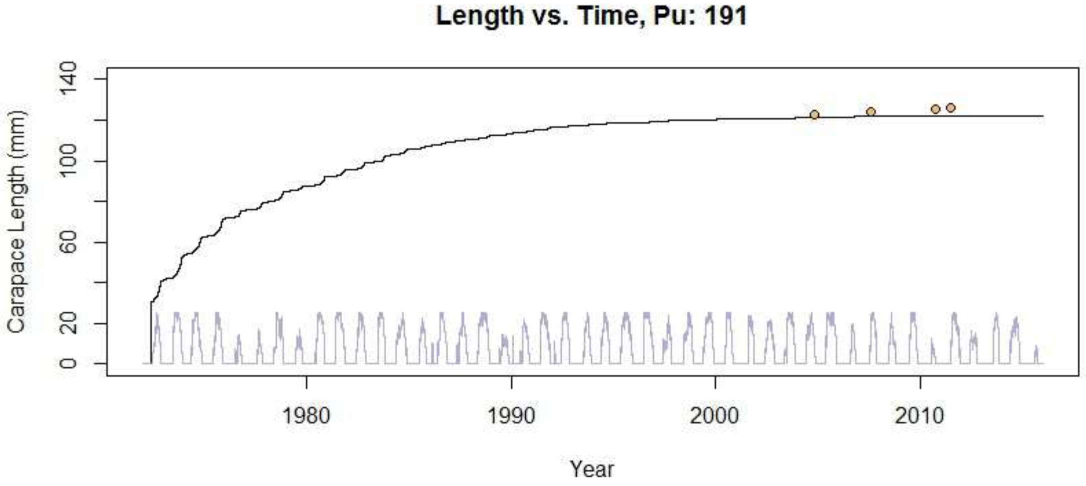


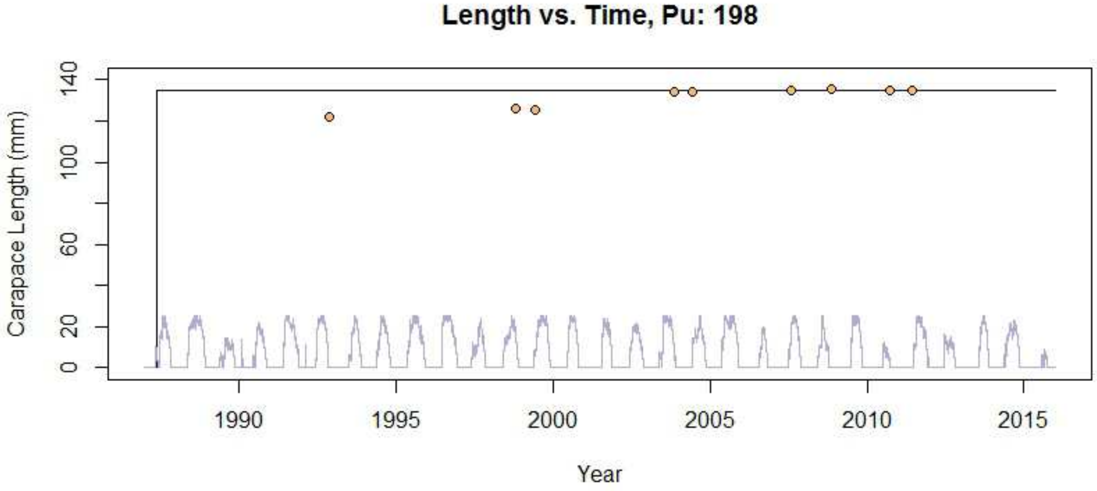

Length vs. Time, Pu: 160
Carapace Length (mm)
0
20
60
100
140
1990
2000
2010
Year


Length vs. Time, Pu: 169
Carapace Length (mm)
0
20
60
100
140
1980
1990
2000
2010
Year


Length vs. Time, Pu: 173
Carapace Length (mm)
0
20
60
100
140
1985
1990
1995
2000
2005
2010
2015
Year


Length vs. Time, Pu: 182
Carapace Length (mm)
0
20
60
100
140
1990
1995
2000
2005
2010
2015
Year


Length vs. Time, Pu: 191
Carapace Length (mm)
0
20
60
100
140
1980
1990
2000
2010
Year


Length vs. Time, Pu: 198
Carapace Length (mm)
0
20
60
100
140
1990
1995
2000
2005
2010
2015
Year

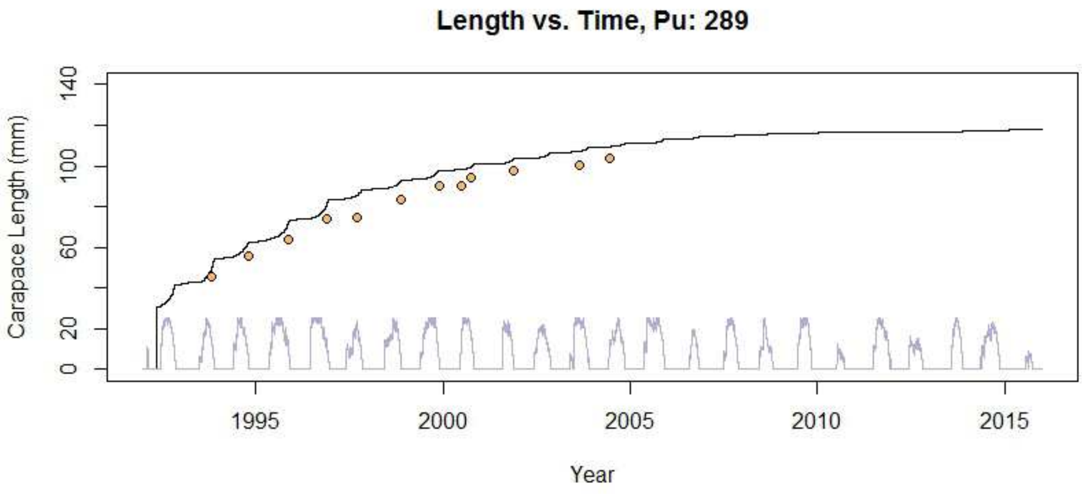
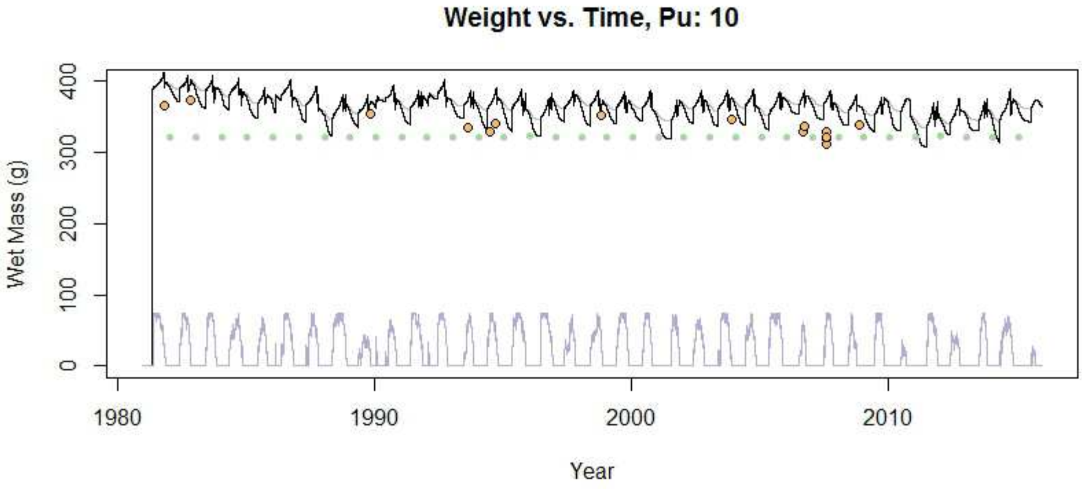
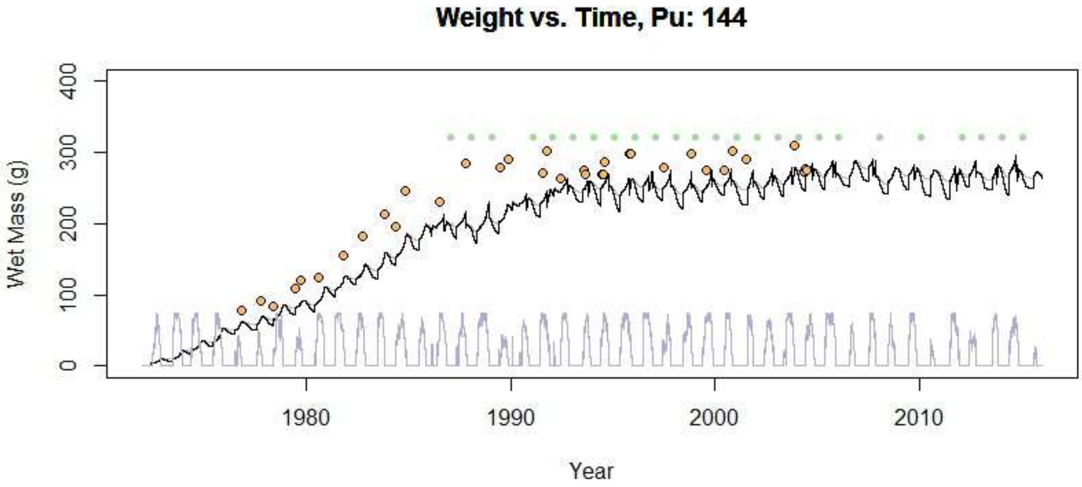

Length vs. Time, Pu: 289
Carapace Length (mm)
0
20
60
100
140
1995
2000
2005
2010
2015
Year

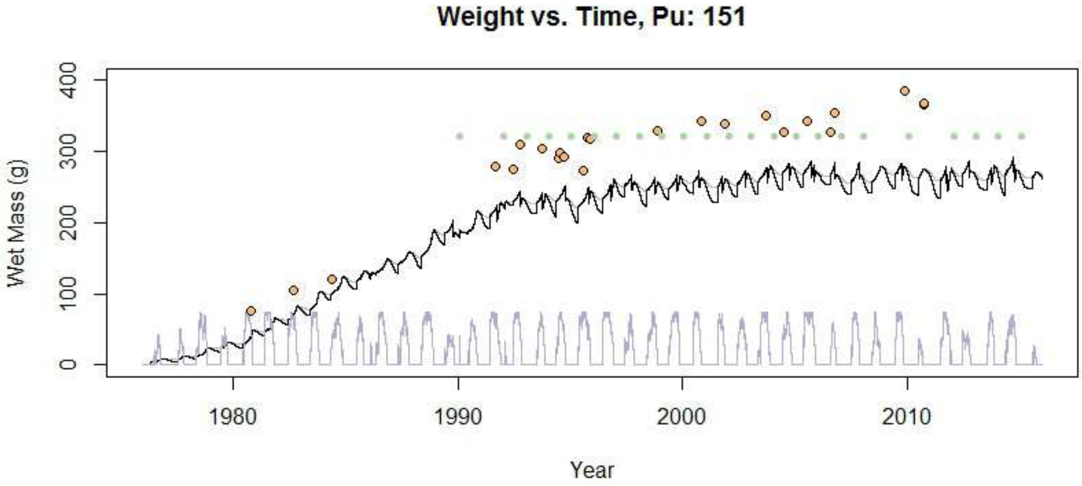
Figure E3 – Mass predictions (black lines) against observations (yellow dots) for individual *P. umbrina* at Ellen Brook Nature Reserve. Blue lines depict the annual predicted hydroperiods and green points represent predicted instances of egg laying.



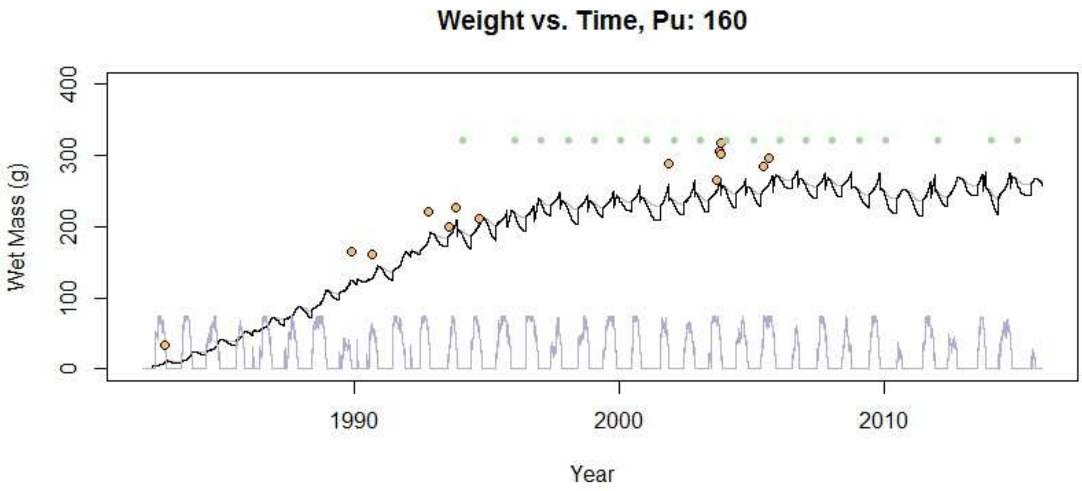
Weight vs. Time, Pu: 10

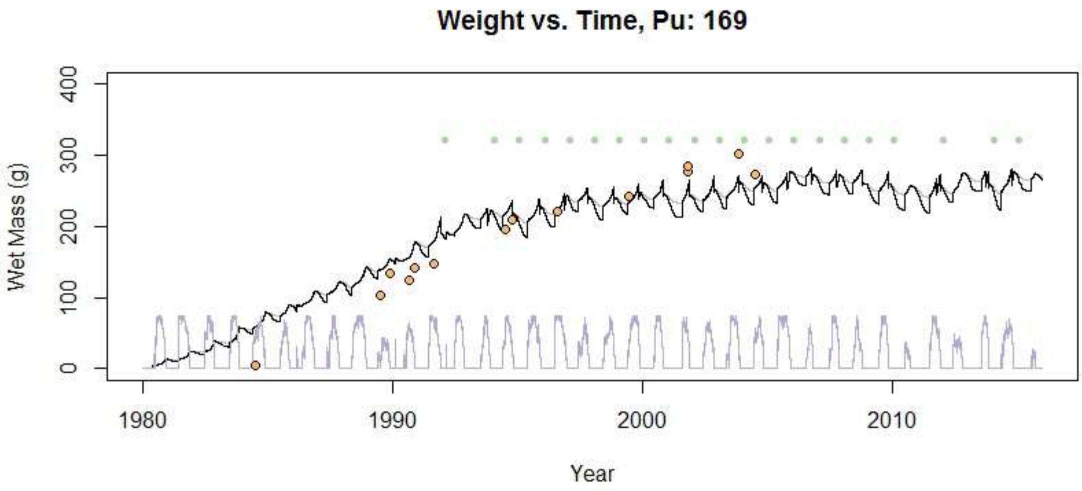


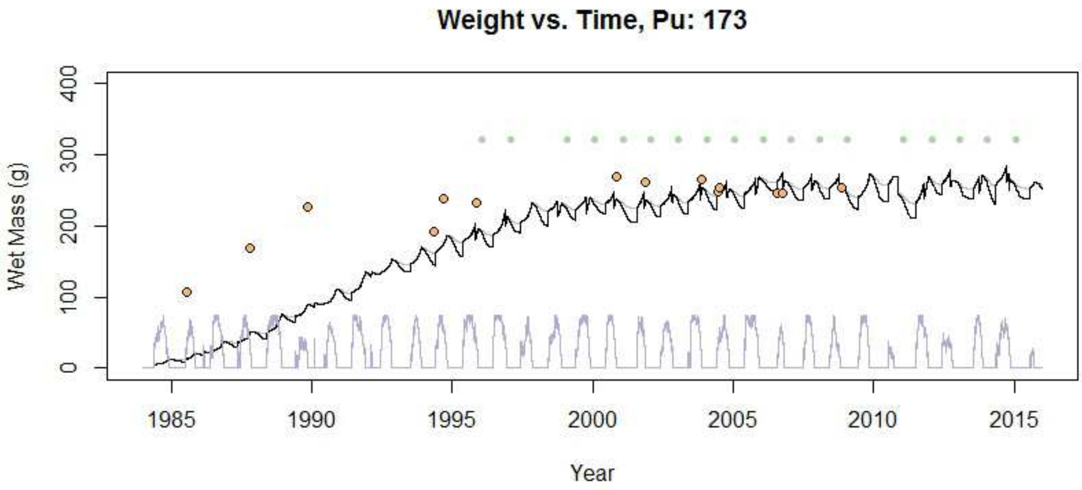
Weight vs. Time, Pu: 144

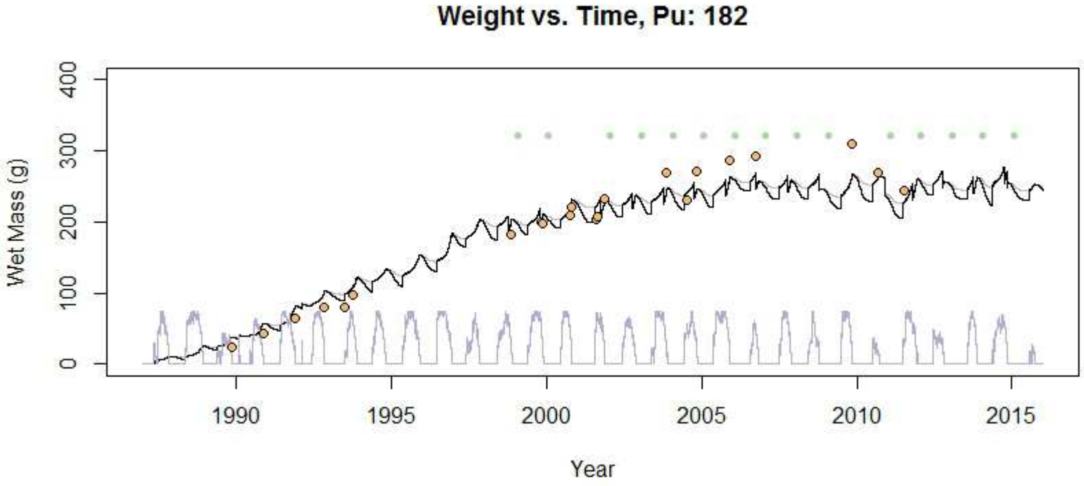


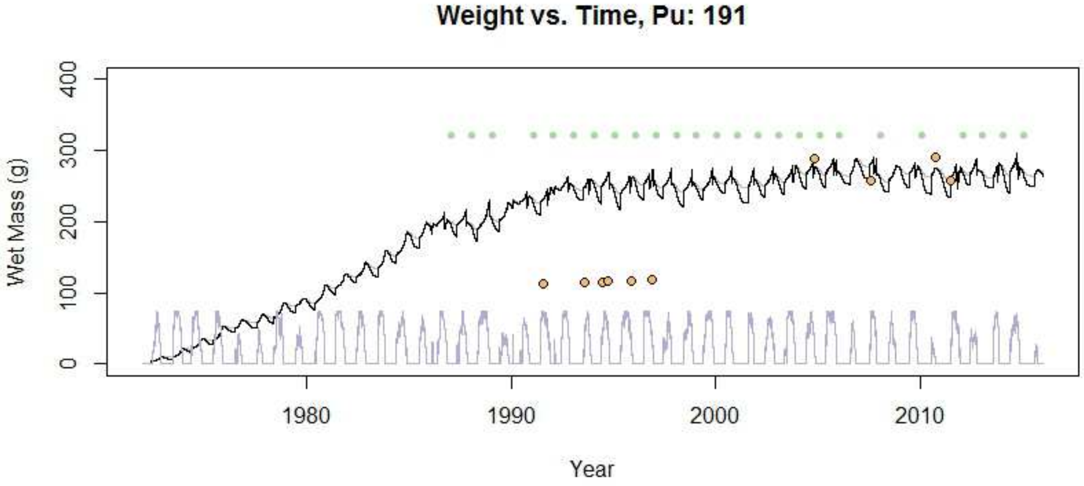
Weight vs. Time, Pu: 151

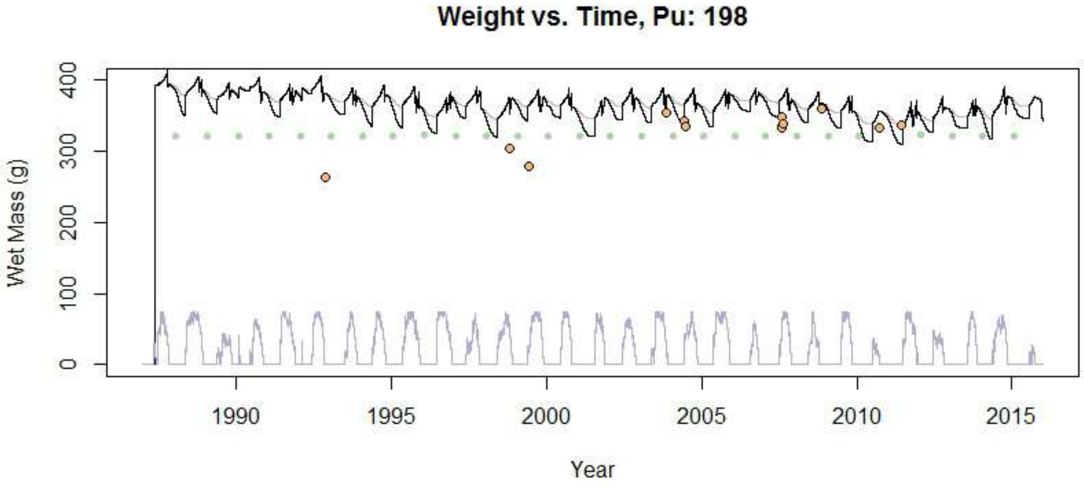

Weight vs. Time, Pu: 160

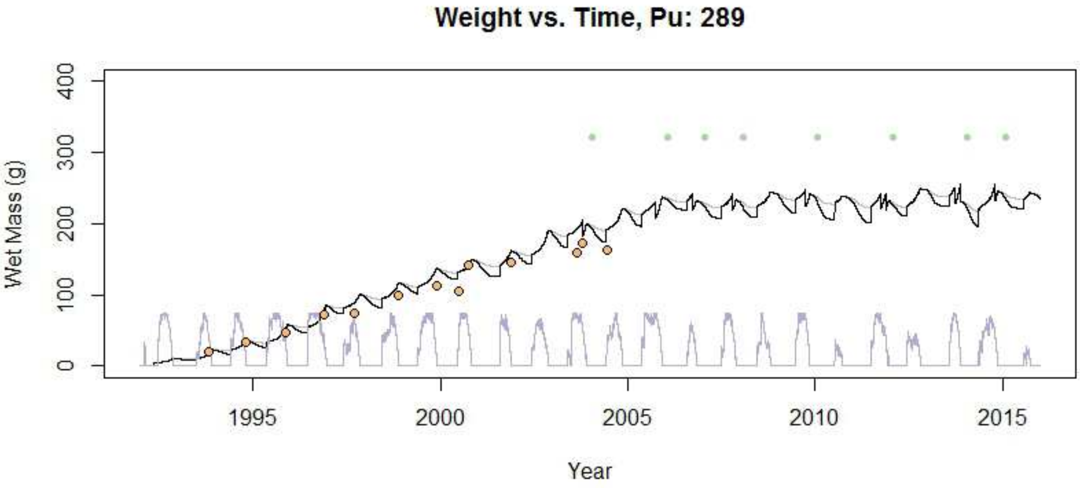

Weight vs. Time, Pu: 169


Weight vs. Time, Pu: 173


Weight vs. Time, Pu: 182
Wet Mass (g)
0
100
200
300
400
1990
1995
2000
2005
2010
2015
Year


Weight vs. Time, Pu: 191
Wet Mass (g)
0
100
200
300
400
1980
1990
2000
2010
Year


Weight vs. Time, Pu: 198
Wet Mass (g)
0
100
200
300
400
1990
1995
2000
2005
2010
2015
Year


Weight vs. Time, Pu: 289
Wet Mass (g)
0
100
200
300
400
1995
2000
2005
2010
2015
Year