On the mechanisms of animal movement from first principles

On the mechanisms of animal movement from first principles

Matthew Malishev

Submitted in total fulfilment of the requirements
of the degree of Doctor of Philosophy

November 2017

School of Biosciences
The University of Melbourne

Declaration

This is to certify that:

(i) the thesis comprises only my original work towards the Ph.D. except where indicated in the Preface

(ii) due acknowledgement has been made in the text to all other material used

(iii) the thesis is fewer than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices or the thesis is 35,000 words as approved by the RHD Committee.

Advisory committee:

Professor Mark Burgman
Associate Professor Michael Kearney
Associate Professor Michael Bode

Keywords: Individual-based modelling, movement ecology, energetics, dynamic energy budget, biophysical ecology, home range

Copyright © 2017 by Matthew Malishev
ISBN 000-00-0000-000-0

An electronic version of this dissertation is available at
https://github.com/darwinanddavis/Thesis

Why didn't evolution make a giraffe good at carpentry so it could build a ladder?

Karl Pilkington

Contents

Acknowledgements i
Tables ii
Figures iii
Abstract 1
Introduction 2

Chapter 1 **8**
Abstract 12
Introduction 13
1.1. Small-scale displacement: Foraging and local habitat selection 16
1.1.1. Process-based models of small-scale movement 16
1.1.2. Foraging IBMs incorporating energetics 18
1.1.3. Energetics IBMs in foraging and habitat selection 27
1.2. Cognitive processes 29
1.2.1. Spatial awareness alleviates movement challenges 29
1.2.2. Cognition and energy use are complementary mechanisms 29
1.2.3. Energy use is a useful mechanism informing movement 30
1.3. Home range occupancy and dispersal potential 30
1.3.1. Explicitly modelling home range occupancy and dispersal 30
1.3.2. General individual traits link resource use to home range 31
1.3.3. Energetics IBMs as useful for modelling home ranges 32
1.4. Migration and geographic distribution 32
1.4.1. Migrants use both internal and external cues 32
1.4.2. Animals assess energy reserves for migration 33
1.4.3. Energetics link small- and large-scale movement 34
Conclusions 36
Acknowledgements 37
Funding 37
Authors' contributions 37
Data accessibility 37

Competing interests 37
Ethics approval and consent to participate 37

Chapter 2 **39**
Abstract 42
Introduction 43
Indirect movement costs as the primary constraint to movement 44
The i_{DEB} primer for modelling individual movement 47
The primary metabolic pathways 47
Maintenance 48
Growth 48
Simulating individual movement behaviour using i_{DEB} 49
Concluding thoughts and future directions 54
Acknowledgements 55
Funding 55
Authors' contributions 55
Competing interests 55
Ethics approval and consent to participate 55

Chapter 3 **57**
Abstract 61
Introduction 62
Overview 63
Purpose 63
Entities, state variables, and scales 65
Energy budget model 65
Heat budget model 68
Decision-making IBM 68
Habitat 69
Microclimate 73
Scales 73
Process overview and scheduling 73
Design concepts 74

Basic principles 74
Emergence 74
Adaptation 75
Fitness 75
Prediction 75
Sensing 75
Stochasticity 76
Observation 76
Details 76
Initialisation 76
Input data 78
Habitat 78
Microclimate 78
Submodels 78
Activity budget 78
Results 78
Does the model capture realistic home range area and behaviour? 78
How does movement strategy shape activity budgets? 81
How does movement potential affect individual metabolic outputs? 82
Does the individual heat budget model capture realistic costs? 82
Discussion 85
Limitations and future work 89
Conclusions 90
Acknowledgements 91
Funding 91
Authors' contributions 91
Data accessibility 91
Competing interests 91
Ethics approval and consent to participate 91

Chapter 4 **93**
Abstract 96
Introduction 97

Methods 99
Dynamic Energy Budget model 99
Microclimate data inputs 99
Life stage 99
Initial maturity 100
Structure 100
Mass 100
Simulations 100
Results 100
Home range area and body mass 100
Rate of T_b change and body mass 102
Activity budget and body mass 104
Metabolic properties 106
Discussion 110
Home range area and body mass 110
Rate of T_b change and body mass 112
Activity budget and body mass 112
Metabolic constraints on life stage and habitat requirements 113
Conclusions and future directions 115
Acknowledgements 117
Funding 117
Authors' contributions 117
Data accessibility 117
Competing interests 117
Ethics approval and consent to participate 117

Summary and further thoughts 119
Appendix A 125
Bibliography 175
List of Publications 194

This page is blank to fix some screwed-up formatting

Acknowledgements

Everyone doing a Ph.D. says their advisory committee is the best.

My one was a faultless combination of knowledge, expertise, and mentorship that surpassed the most critical of expectations from any budding researcher.

To my advisors, Mark, Mike, and Mike (M^3). Thank you for pushing me in every aspect of my work, thinking, and research acumen. I was privileged to have the most perceptive, critical, and inspiring thinkers as mentors.

My two labs, the Centre of Excellence for Biosecurity Risk Analysis (CEBRA) and the Climate and Metabolic Ecology Lab (CAMEL). No research problem of mine was too great, diverse, or untimely to solve from the unmatched expertise available to me from my colleagues. I was never short of help, guidance, or hedonistic lunchtime conversations.

To my colleagues for hosting me during my research visits: Bas Kooijman and Bob Kooi at the Vrije Universiteit, Amsterdam, the Netherlands; and Volker Grimm and Jürgen Groeneveld at the Helmholtz Centre for Environmental Research UFZ, Leipzig, Germany. Thank you for helping me improve this thesis, write papers, and learn to code.

Finally, I thank my family for their support and patience.

Tables

Table 1. Literature synthesised for the review showing the relationship between the time and space scales that current individual-based models on animal movement operate and the corresponding time and space scale referenced in Figure 1. The table also details the purpose of the model, the species considered, the time and space scale of the simulation/study site, and the extent each model considers energy use at the individual level.

Table 2. Primary metabolic processes occurring at each model time step of an hypothetical simulated animal moving in space and time as it interacts with its environment. The internal energetic state of the animal is governed by the DEB theory equations, which drives its movement decisions in response to direct and indirect movement costs.

Table 3. Individual variables and parameters of the DEB model (Kooijman 2010) parameterised for the sleepy lizard, *Tiliqua rugosa*. Parameters are estimated from available animal data (Table 6). Dimensions: — dimensionless; *J* Joules; *L* structural length; *t* time. Unit: *d* days; *cm* centimetres. Square [*] and curly {*} parentheses denote parameters per volume and surface area, respectively; dot accents denote rates.

Table 4. Individual variables and parameters of the transient heat budget model. Units: — dimensionless; *C* Celsius; *J* Joules; *kg* kilograms; *m* metres; *s* seconds; *t* time; *W* watts.

Table 5. State variables and parameters of model individuals, habitat, and microclimate. Units: — dimensionless; *C* Celsius; *J* Joules; *m* metres; *s* seconds; *t* time; *T* temperature; *W* watts. As in 'Entities, state variables, and scales'.

Table 6. Organism data for parameterising the standard Dynamic Energy Budget model of Tiliqua rugosa. Unit: *d* days; *g* grams; *K* Kelvin. All data are from Kearney, M. R., Munns, S. L., Moore, D., Malishev, M. and Bull, C. M., unpublished data (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Tiliqua_rugosa_res.html), except life span, which is from (Snider & Bowler 1992).

Table 7. Individual variables and parameters of the DEB model (Kooijman 2010) for simulating juvenile and adult sleepy lizards, *Tiliqua rugosa*. Units: *J* Joules; *cm* centimetres; *g* grams.

FIGURES

Figure 1. Conceptual hierarchy of individual movement spanning (1) fine, (2) intermediate, and (3) coarse time and space scales. Each section (Displacement, Dispersal, Migration) represents the common processes at each scale and the width and height represent the time and space scale, respectively. The central individual unit *i* with its internal state and dynamic energy budget *DEB* fluctuates with basic energy requirements, costs, and gains (i_{DEB}), ultimately linked to individual fitness. At each scale, thicker, coloured arrows represent emerging processes, boxes represent the end processes from movement, and plus signs denote dominant complementary behaviours or processes.

Figure 2. Stylised conceptual diagram of direct and indirect movement costs in time and space throughout the individual life cycle. Circles represent individual body mass of offspring, juvenile, and adult. Direct movement costs (A, green) form a proportion of somatic maintenance costs (B, blue) across growth. Indirect movement costs (C, pink) change as the individual interacts with its environment over time due to increasing movement trade-offs associated with different behaviour, such as foraging, mating, and defending. Hatched polygon represents points in time and space where the individual may anticipate how indirect movement costs influence performance, i.e. consciously change strategy in response to previous maladaptive behaviour, where E_H^P signifies the shift in maturity from offspring to juvenile and the onset of adaptive movement, e.g. dispersal events. Numbers represent different behavioural events (described in main text).

Figure 3. Examples of contrasting landscape and habitat structures that animals must negotiate in space and time. Top: Light Detection and Ranging (LIDAR) data of an arid, terrestrial environment in South Australia (139º21'E, 33º55'S) highlighting A) large vegetation in contrast to B) available small vegetation for the same site that acts as available refuges for animals throughout the day. Middle: Examples of simulated model landscapes showing C) low and D) high resource (food and shade) density to emulate the conditions seen in A) and B). Insets show simulated animal movement paths using a spatial movement framework that incorporates the i_{DEB} primer. Bottom: Field images of the study site in A) and B) showing the visible differences between E) low and F) high resource density within a habitat.

Figure 4. Schematic of data and model inputs of the IDEBM model. Examples of weather data: monthly to annual temperatures microclimate; Microclimate: local solar and infrared radiation temperature, ground and air temperature (Table 4); DEB model: See Tables 3 and 6; Heat budget model: See Table 4; Habitat data: food and shade patches (Table 5). The DEB and heat budget models update with the time steps of the decision-making IBM to form feedback loops. All weather and habitat data are modelled on the sleepy lizard habitat (139º21'E, 33º55'S). Animal data are for the adult sleepy lizard.

Figure 5. Schematic of decision-making IBM simulation runs. Solid boxes are processes, dashed boxes are individual decisions, and ellipses are individual actions. Searching refers to either searching for food, shade, or socialising, depending on the current thermal or metabolic state or movement strategy of the animal. Hungry refers to whether the gut fullness threshold is <75%.

Figure 6. (A) Distributions of home range area (km^2) of real (pink) and seeded simulated optimising (orange) and satisficing (blue) movement strategies under dense resource distribution (food and shade). Home range polygons in space showing overlap of seeded simulated (B) satisficing and (C) optimising individuals and (D) real individuals. Home ranges in (D) appear more scattered due to different starting locations of real animals, whereas (B) and (C) have seeded starting locations in the centre of the landscape. The vegetation layer in (D) is generated from LIDAR data of the habitat site, showing the thermal mosaic of the landscape.

Figure 7. Activity budget for all optimising and satisficing animals throughout the breeding season showing proportion of time spent (A) feeding, (B) searching, and (C) resting, as well as (D) proportion of number of transitions between activity states. Radius = time spent in activity state; circumference = days throughout the breeding season. Black arrows indicate a 5-day period where environmental conditions were not conducive to activity, so animals spent this time resting in shade.

Figure 8. Movement path and home ranges of real versus simulated sleepy lizards. (A) Individual #11885, a real sleepy lizard showing active movement and (B) individual #11533, a real sleepy lizard showing passive movement, throughout the breeding season. (C) A random simulated optimising individual representing the maximum potential movement and (D) a random simulated satisficing individual representing the minimum movement necessary throughout the breeding season based on its physiological limits. (C–D) green = food patches, black = shade patches, and polygons represent home ranges. Patch size in simulations represents time elapsed on patch.

Figure 9. Energetic outputs showing differences in maximum (optimising) and minimum (satisficing) potential movement. (A) Cumulative movement costs (kJ) for a random simulated optimising (orange) and satisficing (blue) individual throughout the breeding season. (B) Difference in mean structural volume (g^{-1} cm^3; green), wet mass storage (g; blue), converted food mass (g; black), and reproductive organ wet mass (g; pink) between optimising and satisficing movement strategies throughout the breeding season.

Figure 10. (A) Hourly T_b for individual #11885 (orange), a real sleepy lizard showing active movement and individual #11533 (blue), a real sleepy lizard showing passive movement, throughout the breeding season. (B) Hourly T_b for a simulated optimising animal (orange) and satisficing animal (blue). (C) Example of daily T_b profile for the same optimising animal during the hottest (orange curve) and coldest (blue curve) day of the breeding season. Dashed horizontal lines show thermal limits of activity period (26ºC–35ºC) and black graphics atop (A) represents the sun cycle.

Figure 11. Distribution of home range area (km^2) against differences in mass (g) of simulated adults and juveniles. A) Adults and juveniles under high resource density; B) juveniles under low resource density; C) adults under low resource density.

Figure 12. Kernel utilisation distribution of simulated home ranges from a random individual under high resource density. Top panel: A) Optimising and B) satisficing adults (green). Bottom panel: C) optimising and D) satisficing juveniles (blue).

Figure 13. Kernel utilisation distribution of simulated home ranges from a random individual under low resource density. Top panel: A) Optimising and B) satisficing adults (green). Bottom panel: C) optimising and D) satisficing juveniles (blue).

Figure 14. Mean rate of T_b (ºC) change against mean T_b (ºC) of simulated adults (left) and juveniles (right) for A) optimising and B) satisficing movement strategies under high resource density and C) optimising and D) satisficing movement strategies under low resource density. Vertical dashed blue, orange, and red lines represent basking temperature (14ºC), lower activity range temperature (T_{lower}, 26ºC), and upper activity range temperature (T_{upper}, 35ºC), respectively.

Figure 15. Example of T_b (ºC) in the morning (09:00 hours) throughout the breeding season comparing simulated adults and juveniles under high resource density. A) Optimising adult, B), optimising juvenile C), satisficing adult, and D), satisficing juvenile. Horizontal dashed blue, orange, and red lines represent basking temperature (14ºC), lower activity range temperature (T_{lower}, 26ºC), and upper activity range temperature (T_{upper}, 35ºC), respectively.

Figure 16. Example of T_b (ºC) in the morning (09:00 hours) throughout the breeding season comparing simulated adults and juveniles under low resource density. A) Optimising adult, B), optimising juvenile C), satisficing adult, and D), satisficing juvenile. Horizontal dashed blue, orange, and red lines represent basking temperature (14ºC), lower activity range temperature (T_{lower}, 26ºC), and upper activity range temperature (T_{upper}, 35ºC), respectively.

Figure 17. Time simulated optimising A) adults and B) juveniles take to reach their activity range (T_{lower}, 26ºC) from 06:00 AM (orange) and 09:00 AM (blue) throughout the breeding season. As a comparison, C) and D) show the time adults and juveniles, respectively, take to reach activity range throughout the breeding season when surrounding microclimate conditions are near optimal (12:00 PM; purple).

Figure 18. Relative structural volume to initial structural volume (V) of a random simulated adult (dark colours) and juvenile (light colours) under high (#) and low resources across the breeding season.

Figure 19. Relative total wet mass to initial wet mass (structural volume V and reserve storage E) of a randomly simulated adult (dark colours) and juvenile (light colours) under high (#) and low resources across the breeding season.

Figure 20. Body condition, measured as the ratio of reserve storage E to total wet mass (structural volume V and reserve storage E) of a random simulated adult (dark colours) and juvenile (light colours) under high (#) and low resources across the breeding season.

Figure A1. Distributions of home range area (km^2) of real animals (pink) and simulated optimising (orange) and satisficing (blue) movement strategies under (A) dense and (B) sparse resource distribution (food and shade). Insets (L–R): Home range polygons in space showing overlap of simulated satisficing (blue) and optimising (orange) movement strategies, and examples of (upper) dense and (lower) sparse resource distributions in the study site.

Figure A2. Rates of T_b change (ºC 2 min^{-1}) comparing (A) observed active (orange; #11885) and passive (blue; #11533) movement and (B) simulated optimising (orange) and satisficing (blue) movement for the morning hours (heating period; 06:00–12:00). (C) Observed active (orange) and passive (blue) movement and (D) simulated optimising (orange) and satisficing (blue) movement for the afternoon hours (cooling period; 12:00–18:00) throughout the breeding season. Animal graphics represent the most probable activity state of the animal (from Fig. 5).

Abstract

From shifts in air temperature on the scale of seconds to blooms of food growth across landscapes, animals directly experience environmental change across vast time and space scales. A prevailing challenge in ecology is to accurately predict how animals respond to these changes at the habitat scale. At the individual level, animals are directly linked to environmental change by their physiology. Exploring the physical links animals share with their surrounding environment can reveal the limits to their movement decisions, habitat use, and ecology.

Food and climate are common, interacting constraints on animal movement. As we improve data resolution and build better models, we continue to make more informed forecasts of how changing constraints directly influence animal movement. Individual-based models offer a useful bottom-up approach connecting the internal, individual state with the external environment. Drawing from metabolic theory and biophysical ecology, this thesis integrates the basic, physical principles of energy, mass, and heat exchange in an individual-based movement framework to forecast animal movement potential, activity budgets, and home range patterns.

I tested this movement framework using an ectotherm case study, the Australian sleepy lizard, *Tiliqua rugosa*. I applied a general metabolic theory, Dynamic Energy Budget (DEB) theory, of resource uptake and use that computes the individual energy and mass state, including maintenance, growth, and reproduction. Using a microclimate modelling engine (*NicheMapR*), I then combined this with established biophysical principles of heat exchange to define the metabolic and thermal state of the animal in space and time. This was then packaged into a decision-making model—the Individual Dynamic Energy Budget Movement (IDEBM) model—and applied to simulate movement in a landscape populated with climate and habitat data of a semi-arid study site in southern Australia.

I simulated movement of adult individuals in a model landscape using two different movement strategies (optimising and satisficing) under contrasting densities of food and shade (sparse and dense) across the summer breeding season (Sep–Dec, 2009). I then simulated both juvenile and adult life stages to explore how the interacting biophysical and metabolic effects of body size influence movement and home range patterns.

The results show how 1) the constraints on movement behaviour correspond to feeding requirements and thermal costs on the animal, 2) the IDEBM model can realistically capture movement potential and home range size of the wild population, 3) different movement strategies vary in their energetic consequences and fitness outputs, such as movement costs and mass properties, and 4) the smaller-bodied juvenile life stage is more at risk of thermal stress and metabolic movement costs under environmental extremes.

The IDEBM model is a general, theory-based movement framework capturing the constraints on individual movement and home range patterns suited to explore similar questions in a wide range of organisms and terrestrial habitats.

Introduction

The field of movement ecology is a growing subfield of ecology that shows potential in its technology, models, and application of data to global issues, including biodiversity, conservation, and predicting responses of animals to environmental change. Recent innovative work has improved our understanding of how physical processes from the external environment influence animal physiology, behaviour, and activity ranges (Bauer et al. 2009; Kearney & Porter 2009; Kearney et al. 2010; Borger 2016). A large proportion of Earth's animals are ectotherms that respond directly to changes in environmental temperature through physical processes, such as heat exchange. This direct link between the individual and its habitat can influence the animal's movement potential. This presents opportunities to formulate ecological phenomena, such as animal movement, within a predictive framework based on how individuals respond to external conditions, such as changing food and climate (Bauer et al. 2009; Giuggioli & Bartumeus 2010; Bauer & Klaassen 2013; Bauer & Hoye 2014).

Food and climate are common, interacting constraints to movement that animals must negotiate across different scales (Buckley et al. 2010). By estimating how these interacting constraints influence animal movement, we can build a realistic picture of habitat use, movement ecology, and the impact of environmental change on species. An explicit understanding of these limits in space and time allows us to pinpoint the common, individual mechanisms driving movement (Börger et al. 2008; Kearney & Porter 2009; Buckley 2010; Reynolds 2014; Bastille-Rousseau et al. 2015; Hirsch et al. 2016).

Food and temperature interact in fundamental ways to shape an animal's energy budget, which we can use to summarise individual metabolic and thermal states and thus provide a bottom-up way of capturing movement decisions (Kearney et al. 2010). Framing individual movement in an energetics context using food and temperature as energy currencies offers a general way to represent how individual physiology, behaviour, and ecology interact to drive behaviour and habitat use (Martin et al. 2012; Martin et al. 2013; Sibly et al. 2013; Kearney et al. 2013; Shepard et al. 2013). The challenge thus becomes turning this approach into a usable modelling framework to make reliable forecasts under uncertainty, such as environmental change.

Individual-based models offer a bottom-up approach for predicting complex processes using localised behaviour and interactions (Grimm et al. 2005; Grimm & Railsback 2005; Stillman et al. 2015). Building the behavioural aspect of these models on general principles of energetics unifies the study of animal movement across species and scales (Huse & Giske 1998; Buckley 2010; Kearney et al. 2010; Sibly et al. 2013; Kułakowska et al. 2014), thus offering a flexible, process-based framework for forecasting species responses in current and future environments in space and time. With this approach, we can avoid making forecasts based on correlations with coarse environmental data or limited information on essential individual traits (Fitzpatrick & Hargrove 2009; Dormann

et al. 2012; Guillera-Arroita et al. 2015; Briscoe et al. 2016). These coarser methods are useful for predicting events and processes at large scales, but can lack the appropriate organism and habitat resolution for predicting movement under changing conditions.

In contrast to these methods, individual-based models are accessible and useful tools under these scenarios for several reasons. First, correlative models often suffer from a mismatch in the resolution of the space and time scales between the animal and its changes in behaviour and activity patterns, as well as habitat constraints that reflect the physical movement and dispersal limits of the animal (Buckley 2010; Fordham et al. 2012). Second, correlative models use a statistical approach to describe patterns between the probability of an animal occurring in the landscape and data on its environment. In contrast, mechanistic models aim to predict individual responses to habitat use, such as fitness components of the individual or population, based on mechanisms driving movement and dispersal potential. Finally, movement is inherently linked to behaviour, which is difficult to capture when relying solely on statistical correlations (Bauer & Klaassen 2013). Conversely, bridging the individual-environment interface using mechanisms, such as basic biological principles of energy use, into an individual-based framework makes 1) the model robust to fine scale environmental change and 2) creates opportunities to predict movement from decision-making and behaviour (Bauer & Klaassen 2013; Kearney et al. 2013; Borger 2016).

The main thrust of this thesis is to explore what constrains the movement of species under changing environments. In particular, I aim to summarise these limits in a modelling framework using the basic principles of energy use and available climate and habitat data. I use this framework as a general means to forecast dispersal limits and fitness consequences under environmental change to identify any common mechanisms to home range emergence. Translating these ideas into a modelling platform requires knowledge of the physical constraints upon the individual niche in both space and time. These change across the life cycle of the individual, with time of day and year, and under different environmental scenarios, such as weather, resource, and habitat availability. Here, the concept of movement trade-offs becomes the focus, where animals must balance their survival requirements in the face of competing constraints. Applying this framework to environments with different climate, resource arrangements, and topography, for example, allows us to explore constraints on movement in novel habitats that may exist in the future under environmental change. I aim to explore the capacity for individual-based movement models driven by the individual energy and heat budget to predict movement, activity, and home range patterns in space and time. This type of model uses the constraints acting directly upon the individual-environment interface to predict how animals move and displace, generate and adapt their activity patterns, form home ranges and range shifts, and respond to changing resources patterns in space and time.

An explicit understanding of how environmental constraints on the animal interact with individual physiology to influence habitat requirements has markedly progressed how we interpret animal movement and environmental change on fitness consequences. I identify two primary challenges of modelling movement behaviour where individual-based models have been useful.

The first is identifying how space use by animals influences the internal, individual state, such as the energy, mass, and heat balances of the animal. Exploring movement costs, such as thermal costs, through the individual energy budget allows us to link the physiology of the animal with its fitness outcomes. Only by formulating movement costs through the basic processes defining the individual state, such as heat balances, are we able to assess the direct impact of habitat change on the individual. Temperature and climate extremes can reduce ectotherm growth rates and consequently increase mortality and delay maturation (Sears & Angilletta 2004). Recent work integrating the individual heat budget with individual-based modelling has identified the critical aspects of the individual-environment interface needed to successfully link the individual state with habitat requirements. For example, habitat quality changes in space, where using refuges to escape climate extremes allows animals to improve their access to resources and reduce energetic costs (Sears & Angilletta 2015). Further, spatial structure of the habitat defines how animals tolerate temperature change (Sears et al. 2011) and thus mediate movement costs (Jetz et al. 2004). Therefore, models on habitat use and movement behaviour by the individual need to consider how space use by the individual influences movement and fitness trade-offs.

The second challenge is formulating the internal state of the animal on general and well-tested biological principles that can be scaled to other species, systems, and higher levels of biological complexity. A major barrier to progressing this type of modelling has been understanding and applying a suitable and general theory of the processes defining the internal state, but from common currencies, such as energy use. One such theory is Dynamic Energy Budget (DEB) theory (Kooijman 2010), a general, metabolic theory of resource uptake and use by organisms that computes the individual energy and mass state, including maintenance, growth, and reproduction, throughout the individual life cycle. The theory formulates the primary metabolic functions, such as maintenance costs, growth curves, and reproductive output from feeding responses to food intake, to estimate fitness consequences. Previous work has successfully integrated DEB theory with individual-based models to estimate life history trade-offs at the population level (Bacher & Gangnery 2006; Martin et al. 2012; Martin et al. 2013); these works begin to highlight how individual-based models provide a useful and flexible platform to gain more detailed knowledge of habitat constraints on individuals.

Identifying these challenges emphasises the need to build a modelling framework that uses the internal, individual state to inform movement decisions and habitat use in both space and time. Individual-based models offer a solution. I use DEB theory of resource uptake and use (Kooijman 2010) together with established biophysical principles of heat exchange (Christian et al. 1983; Kearney & Porter 2009; Kearney 2012) to update the individual, internal state and drive the decision-making part of the animal. I then generate spatial movement models using the individual energy budget as an engine driving dispersal potential and fitness consequences. This generates simulations at the habitat level that link the internal state with the external, physical environment. I currently explore these questions using a terrestrial ectotherm model, the Australian sleepy lizard *Tiliqua rugosa*. Through this framework of metabolic theory-based movement, I simulate animal movement and home range emergence in landscapes of varying food and climate. From an energetics perspective, how animals budget their activity time at fine scales

translates to movement trade-offs, including the time available for feeding, escaping predators, and mating, linked to fitness consequences, such as growth and reproduction (Werner & Anholt 1993; Zollner & Lima 2005; Kearney 2012; Mitchell & Powell 2012; Travis et al. 2012; Bastille-Rousseau et al. 2015). Using general metabolic theory based on unifying principles, we can begin to make reliable forecasts of movement potential from physical movement limits, including how activity ranges shift in space and time in different environments (Kearney 2012; Malishev et al. in press).

Chapter 1 reviews the field of movement ecology, focussing on the central modelling framework of this thesis: individual-based simulation models. In this chapter, I focus on energetics as the main driver of individual movement, decision-making, and behaviour. Here, energetics refers to the energy and mass budget of the animal and how animals update their internal metabolic state in response to their changing environment, such as how food intake rates affect available reserves. The internal state then acts as an engine driving future movement potential. There are several advantages of using individual-based energetics. First, energy use operates on the individual level, so its consequences on behaviour are flexible to changes in external habitat conditions (Sibly et al. 2013; Malishev et al. in press). Second, with its central focus on energy use as a mechanism, the framework uses a fundamental understanding of the common processes driving movement among individuals (Wilson et al. 2012; Buckley et al. 2014; Van Moorter et al. 2015). Finally, animal movement pervades ecology and biodiversity, which means there are opportunities to explore it with universal principles (Bauer et al. 2009; Van Moorter et al. 2015; Borger 2016). I elaborate on how the current literature addresses these strengths in Chapter 1, then interpret them further in Chapter 2 by showing how to integrate the lessons learned from the literature in a simulation movement primer in time and space.

Chapter 2 discusses how we can integrate metabolic theory in the individual-based simulation model to update the internal state of the animal and drive movement decisions in time and space. Specifically, I apply the theoretical concepts from DEB theory of energy and mass exchange to estimate how individuals metabolise their energy uptake and use for essential metabolic processes, such as maintenance, growth, and reproduction. By integrating this theory into individual-level simulations, the model translates the consequences of changes in energy uptake and use into ecological outcomes of animal movement. This chapter first introduces the key metabolic processes defining the internal, individual state and how these processes influence movement potential and decisions, such as movement costs. These include temperature-dependent energy (including heat) and mass fluxes for assimilating food, mobilising energy reserve, somatic maintenance, growth rates of body mass and length, maturation rates, and reproductive potential, including gonad and offspring development. The chapter then introduces a movement primer for capturing the feedback between metabolic activity and movement decisions by integrating these key metabolic processes into a simulation model that predicts animal movement explicit in space and time.

Chapter 3 applies the i_{DEB} primer described in Chapter 2 by integrating its microclimate and energy- and mass-budget modelling functions to available movement data of *Tiliqua rugosa* across the breeding season. This movement model, the Individual Dynamic

Energy Budget Movement model (IDEBM), explicitly incorporates the physiology and morphology of the animal, physical response rates of the individual to its external environment, behaviour and movement strategies, and movement costs. The model uses R to drive a NetLogo individual-based model together with microclimate and energy- and mass-budget modelling functions from the R package *NicheMapR*. The model comprises three coupled sub-models that operate simultaneously: 1) a metabolic model of an animal's energy and mass balance, including direct movement costs, based on a general theory of resource uptake and use by organisms (DEB theory; Kooijman 2010), 2) a transient heat budget model for calculating changes in individual thermal state in response to varying habitat microclimates, and 3) a decision-making model driving movement in space and time. The model generates spatial movement patterns, activity budgets of foraging and shade-seeking, home range behaviour, and life history consequences, including metabolic outputs of wet mass properties, under user-defined configurations of food and microclimates. To illustrate the model, we run simulations of *Tiliqua rugosa* under two different movement strategies in two contrasting resource densities of varying food and shade. The two movement strategies either emulate an active animal that incorporates social movement (optimising) or a passive animal that limits its movement to when its energy levels are below a given gut threshold (satisficing). The contrasting densities of sparse and dense resources represent how changes in external physical constraints to movement and habitat change influence home range emergence. We then compare the results with real, fine-scale movement data of a wild population throughout the breeding season.

Finally, Chapter 4 builds on the IDEBM model findings in Chapter 3 to explore further physical components of the individual that influence movement potential, activity state, and response rates to environmental change. I use different body sizes of the individual to represent the juvenile and adult life stages; this aims to show how movement strategy and habitat requirements shift throughout the animal life cycle. By incorporating the juvenile and adult metabolic states in the IDEBM model, we can use two extremes in structural body size and their associated maturation levels to explore how the interacting biophysical and metabolic effects of size influence movement and home range patterns. I simulate juvenile and adult animals under similar movement strategies (optimising and satisficing) and resource densities (dense and sparse) outlined in the previous chapter. The IDEBM model calculates how different sized animals make movement decisions when exposed to similar physical constraints in their habitat. The model also aims to show how activity patterns and movement decisions of animals throughout their life cycle influences their metabolic properties, such as growth and reproductive potential. This allows us to parse how differences in body size and response rates, such as mass-specific responses to environmental extremes, influence movement potential and home range patterns under the varying metabolic demands of the animal life cycle.

1

Individual-based energy budgets as next-generation extensions for modelling animal movement across scales

Matthew Malishev[1*] & Stephanie Kramer-Schadt[2]

[1] *Centre of Excellence for Biosecurity Risk Analysis, School of BioSciences, University of Melbourne, Parkville, Melbourne, 3010, Australia*

[2] *IZW, Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Strasse 17, D-10315 Berlin, Germany*

This chapter appears in 'Malishev, M. & Kramer-Schadt, S. Individual-based energy budgets as next-generation extensions for modelling animal movement across scales. In revision'.

[*]Corresponding author: matthew.malishev@gmail.com

I truly believe there exists some combination of words.

There must exist certain words in a certain specific order that can explain all of this.

I just can't ever seem to find them.

Heisenberg

Table of Contents

Abstract 12
Introduction 13
1.1. Small-scale displacement: Foraging and local habitat selection 16
1.1.1. Process-based models of small-scale movement reveal the importance of connecting movement to fitness consequences 16
1.1.2. Foraging IBMs incorporating energetics are useful for predicting movement across scales 18
1.1.3. Energetics IBMs suggest foraging and habitat selection involve fine scale time trade-offs 27
1.2. Cognitive processes 29
1.2.1. Spatial awareness alleviates movement challenges under environmental change 29
1.2.2. Cognition and energy use are complementary mechanisms to animal movement 29
1.2.3. Energy use is a useful mechanism informing prescient movement decisions . 30
1.3. Home range occupancy and dispersal potential 30
1.3.1. Explicitly modelling home range occupancy and dispersal potential with IBMs 30
1.3.2. General individual traits link resource use to home range behaviour in space and time 31
1.3.3. Energetics IBMs are useful frameworks for modelling complex home range behaviour 32
1.4. Migration and geographic distribution 32
1.4.1. Migrants use both internal and external cues at different scales 32
1.4.2. Animals assess energy reserves to make better migration decisions 33
1.4.3. Energetics links the equally important small- and large-scale movement behaviour of migration in space 34
Conclusions 36
Acknowledgements 37
Funding 37
Authors' contributions 37

Data accessibility 37
Competing interests 37
Ethics approval and consent to participate..... 37

Abstract

Animal movement is universal, spanning all time and space scales in nature. Resources, predators, and habitat change are all common drivers and constraints to movement absorbed by the individual, creating opportunities to predict movement from the direct links between them and their environment.

To progress, movement ecology needs an explicit focus on common mechanisms, such as energetics, linking behaviour to fitness consequences across scales, but simplified by process-based approaches, such as individual-based models (IBMs). We review the animal movement literature, from fine scale patch foraging to large-scale geographic migration, focussing on IBMs incorporating the individual energy budget.

The literature shows IBMs on movement ecology are mainly defined by the following four categories nested across different space and time scales: (1.1) small-scale displacement, i.e. foraging and local habitat selection by animals under different resource availabilities, including (1.2) cognitive processes, such as memory and learning, (1.3) home range occupancy and dispersal potential, and (1.4) migration and biogeographic distribution. Our review shows movement becomes more difficult to predict with increasing time and space scales, but the individual energy budget provides a unifying mechanism underpinning behaviour with general physical principles linking internal individual traits with external environmental cues, thereby directly addressing the challenge of modelling movement across different scales, species, and constraints.

We propose integrating the individual energy budget as a movement engine across scales into a practical process-based primer (i_{DEB}) as a next-gen extension for modelling the complexities of animal movement. This primer links individual energetics to the external environment in a unifying, individual-based movement framework based on general metabolic theory, sophisticated enough to capture the complexity of movement simply across different scales, but flexible to other complementary mechanisms dictating individual movement potential.

Keywords: Dynamic energy budget, energy reserves, environmental change, external cues, individual traits, mechanistic movement models, movement costs, physiology, resource use, trade-offs

Introduction

Animals move to survive and reproduce. They move by will or coercion, shifting within and dispersing to new habitats or migrating to other regions, constantly assessing their internal state against their changing environment. Movement is an essential element of individual life cycles and, consequently, of higher levels of organization, such as populations, communities, and ecosystems (Jeltsch et al. 2013; Bauer & Hoye 2014; Ayllón et al. 2016). Owing to improved detail from emerging technologies allowing tracking of fine-scale movement (Holyoak et al. 2008) and new statistics and models enhancing analyses (Giuggioli & Bartumeus 2010), 'movement ecology' has become a new, coherent branch of ecology (Nathan et al. 2008).

Movement extends from fractions of seconds to years, encompassing patches, habitats, and landscapes (Kokko & López-Sepulcre 2006). This spectrum of scales contributes to its complexity. General frameworks attempting to disentangle this complexity (Nathan et al. 2008; Van Moorter et al. 2013) may analyse physiological traits such as energetics fluxes (Louzao et al. 2014) together with cognitive states such as perception (Pe'er & Kramer-Schadt 2008), memory, and learning (Fagan et al. 2013), and thus (collective) decision-making (Sueur et al. 2011), including group movement (Dumont & Hill 2004; Bonnell et al. 2013), and external cues (Wilson et al. 2012). However, when these models are descriptive, e.g. using correlated random walks, Levy flight, or state-space models (Turchin 1998; Patterson et al. 2008; Delgado et al. 2014; Langrock et al. 2014), they often fail to capture adaptive decisions by individuals, such as risk-taking, in response to their fluid internal and external conditions (Bowler & Benton 2005; Schick et al. 2008; Pyke 2015). Therefore, they often focus on only single elements of movement, integrate only the cognitive state (see Table 1 for IBMs on perception, memory, and learning), or neglect key mechanisms (Holyoak et al. 2008), including physiology and principles relating to energy use. Recent advances link physiology and ecology to understand emerging processes in populations (Ellis et al. 2012; Ayllón et al. 2016) and communities (Buchmann et al. 2011), or to project range shifts under climate change (Gustafson 2013), as there is an urgency to understand how changing environments drive movement, especially migration (Börger et al. 2011; Bauer & Hoye 2014). As movement also varies among individuals, using realistic model constraints on individual traits and behaviour is essential before scaling to the population level (Louzao et al. 2014). Indeed, as our estimates of relationships between individual-level traits and ecosystem-level processes like climate change improve, trait-based approaches to modelling movement at different scales become less heuristic and more valuable (Purves et al. 2013). Therefore, understanding animal movement with constraints on physiology across appropriate time and space scales under a general framework (Giuggioli & Bartumeus 2010; Benhamou 2014) provides a useful tool to capture natural movement processes and behavior (Shepard et al. 2013; Wilson et al. 2013).

Animals use energy to move, incurring energetic costs linked to metabolism supporting survival, growth, and reproduction, as well as time, risk, and opportunity costs (Bonte et al. 2012). Basic principles of physiological ecology are important for understanding

animal movement that evolutionary theory predicts will maximise Darwinian fitness in context with resource allocation (Sibly et al. 2013). These principles suggest animals trade off movement against fitness outcomes either directly, i.e. direct energy costs of movement, or indirectly, i.e. mortality from predation or losses in reproductive output (Shepard et al. 2013). We can summarise energy costs and gains with energy and mass balances, generating an energy budget to connect the individual and the environment in a mechanistic way using first principles (Sibly et al. 2013). We propose Dynamic Energy Budget (DEB) theory (Kooijman 2010) offers a practical, general, metabolic theory capturing energy uptake and use by individuals. That animals use energy to move across different time and space scales suggests an individual's lifetime energy budget serves as a movement roadmap.

We reviewed the animal movement literature, focussing on IBMs incorporating individual energetics in various ways, from abstract to experimental case studies. We omitted review manuscripts that consider energetics in movement IBMs in this cohort because references to energetics were less heuristic and more descriptive. Of the 59 IBM movement papers, 39 claimed energetics were explicitly needed either for their respective time and space scale or movement ecology in general. Within, a common issue emerges: individual traits like energetics are sometimes species- and problem-specific. Indeed, IBM has been criticised of this is the past (Railsback 2001; Grimm et al. 2005). We tackle the inherent issues raised by these authors using the (i_{DEB}) primer to illustrate how the basic, unifying principles of energetics usefully capture the movement challenges animals face across the diverse time and space scales of nature. Individual-based models (IBMs) can integrate individual energy budgets with movement behaviour, where individual traits and the environment interact to drive behaviour and higher-level patterns over time and space. IBMs are useful tools for distilling complex processes from the environment within the constraints of individual behaviour and thus directly translating individual fitness responses against the environment in a tractable way (Railsback & Harvey 2002; Stillman et al. 2015; Ayllón et al. 2016; Malishev et al. in press). From this, individual behaviour can be scaled to population and community levels (Travis & Dytham 1998; Wilson 1998; Travis et al. 2005; Mueller & Fagan 2008; Singer et al. 2016), while maintaining a process-based relationship between animals and the environment by exploring movement from individual-level variations in behavior (Hawkes 2009; Cote et al. 2016). Movement at the individual level is based on adaptive decision-making (Zollner & Lima 2005; Grimm & Railsback 2005; Grimm et al. 2005; DeAngelis & Mooij 2005; Tang & Bennett 2010; Grimm & Railsback 2011). However, many individual-based models still mix imposed and emergent behaviour. Encouraging efforts (Bauer & Klaassen 2013 and therein) identify IBMs to progress mechanistic modelling of animal movement. By marrying the predictive capabilities of IBM with energetics frameworks (Sibly et al. 2013; Malishev et al. in press), we can model movement patterns of individuals over time and space with universal, internal mechanisms using biologically relevant rules for movement.

One mutual drawback of current energetics-based movement frameworks is movement behaviour is governed by ad hoc estimates of energy use and doesn't consider how potential movement costs may emerge from formal metabolic rules for energy and mass exchange that depend on mass and temperature relationships common across taxa. A

formalised metabolic theory built on energy and mass conservation rules, i.e. DEB theory (Kooijman 2010), integrated with IBM could generate an individual-based, internal movement engine that validates movement costs with metabolic rules for the individual in space and time, as shown when predicting population cycles (Bacher & Gangnery 2006; Martin et al. 2013). Further, recent advances in biologging are improving how we calculate energy expenditure of animals from fine to coarse scales (Gleiss et al. 2011; Nathan et al. 2012; Louzao et al. 2014; Scharf et al. 2016), reducing model development costs and advancing movement theory using direct energetic feedback between animals and their environment (Louzao et al. 2014), i.e. energy landscapes (Hawkes et al. 2013; Sachs et al. 2013; Shepard et al. 2013; Wilson et al. 2013). Therefore, our current state of knowledge combining energy budgets, movement theory, and data from advanced animal tracking technology, is timely for developing a general, theory-based energetics IBM framework to predict movement behaviour with the individual at its core (Malishev et al. in press).

Here, we review IBMs in movement ecology incorporating fine to coarse time scales from the local patch to the landscape scale published between 1991 and 2016 (Table 1) to isolate which models use basic principles, in particular how decision-making from the individual energy budget translates to fitness outcomes. When looking at common, higher taxa, we discovered that IBMs focus little on energetics. This was surprising; animals use energy as a direct currency for movement. Our review is motivated by this mechanistic basis from the individual level (i_{DEB}; cf. Fig. 1). The literature shows IBMs on movement ecology are mainly defined by the following four categories nested across different space and time scales that we define by their hierarchical movement process and resulting space use patterns: (1.1) small-scale displacement, i.e. foraging and local habitat selection under different resource availabilities (Fig. 1, section 1), including (1.2) cognitive processes, such as memory and learning; (1.3) home range occupancy and dispersal potential (Fig. 1, section 2); and (1.4) migration and biogeographic distribution (Fig. 1, section 3). These themes emerged as the most common studies and scales from the movement ecology literature focusing on IBMs and energetics. Further cognitive processes uniting the entire movement continuum include perception, learning, memory (see segment 1.2), species interactions, and adaptive behaviour (Fig. 1).

We review the strength of current, working IBMs to tackle key questions in movement ecology, namely how animals choose habitats under a changing environment, using resources in space to define their home ranges, and balance energy reserves over time to make foresighted migratory decisions. For each theme, we (a) review what existing IBMs teach us about movement challenges, (b) investigate whether IBMs incorporate energetics within the model design or process, including energy gain, use, and costs of movement, and (c) use landmark examples of IBMs to identify whether energetics models are well designed and how energetics and fitness seeking are linked in any way to model outcomes, ultimately advocating energy use as a unifying mechanism to movement across scales. We begin with fine scale movement such as foraging because this is the minimum level of hierarchy nested within all larger movement scales and from where energy and mass balance equations linked to resource availability and other adaptive decisions (predator avoidance, species interactions) translate to larger time and space scales. Finally, we conclude by introducing a primer based on energetics (DEB

theory) that uses the internal, metabolic engine to drive current and future movement decisions incorporating direct and indirect movement costs based on individual physiological responses to the environment.

1.1. Small-scale displacement: Foraging and local habitat selection

1.1.1. Process-based models of small-scale movement reveal the importance of connecting movement to fitness consequences

Animals adapt their movement for fitness-seeking activities like foraging, mating, and escaping predators that transpire on fine time and space scales (Fig. 1, section 1). Randomly walking (RW) animals, for example, can increase foraging success under uncertainty (Duffy 2011), but underperform in changing habitats where more advanced Correlated Random Walk (CRW) strategies may dominate (Morales et al. 2004; Duffy 2011). However, assuming CRW can be naïve, especially with complex vertebrate behaviour. Theory can help define movement strategy across taxa, such as classic foraging theory (Optimal Foraging Theory [OFT]; (Pyke et al. 1977; Charnov 1976; Wajnberg et al. 2013)) that argues animals uniformly optimise their space use in response to resources. However, it neglects key behaviour, such as movement capacity and habitat-dependent movement, and movement drivers, such as energy use and predator presence. Recent trait-based approaches, such as IBMs, can integrate these key behaviours and drivers and thus represent more ecologically real scenarios, shifting the OFT paradigm to the ecological stone age (Börger et al. 2008; Holyoak et al. 2008; Mueller & Fagan 2008; Giuggioli & Bartumeus 2010; Bauer & Klaassen 2013; Fagan et al. 2013).

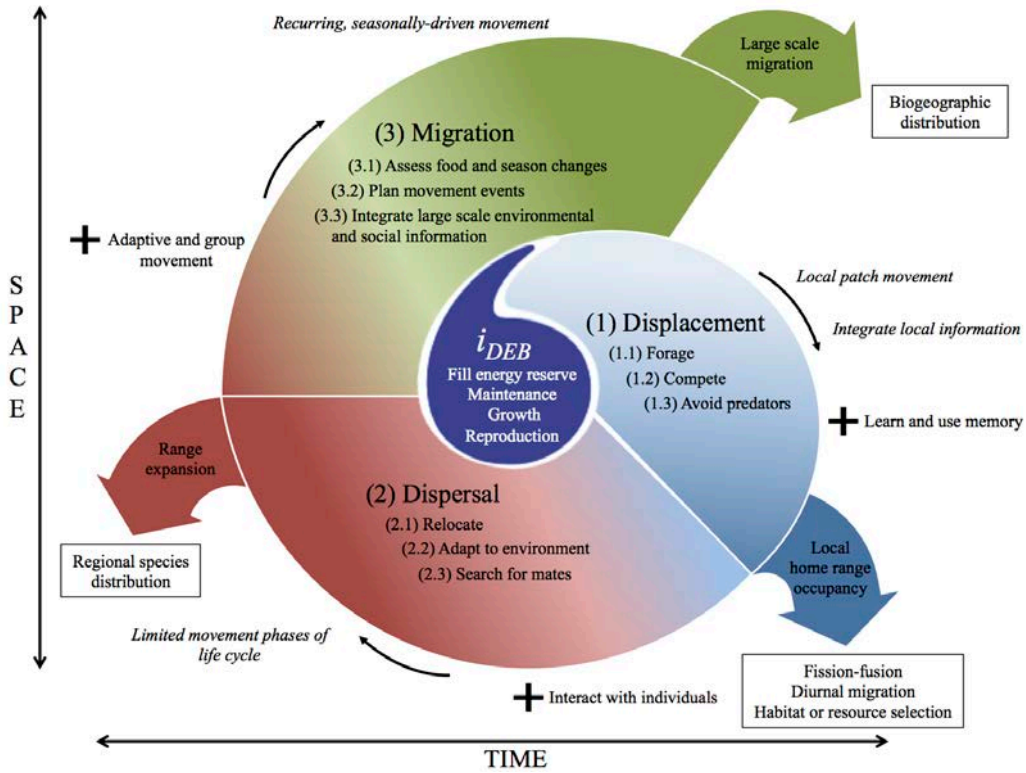

Figure 1. Conceptual hierarchy of individual movement spanning (1) fine, (2) intermediate, and (3) coarse time and space scales. Each section (Displacement, Dispersal, Migration) represents the common processes at each scale and the width and height represent the time and space scale, respectively. The central individual unit i with its internal state and dynamic energy budget DEB fluctuates with basic energy requirements, costs, and gains (i_{DEB}), ultimately linked to individual fitness. At each scale, thicker, coloured arrows represent emerging processes, boxes represent the end processes from movement, and plus signs denote dominant complementary behaviours or processes.

Fronhofer, Hovestadt & Poethke (Fronhofer et al. 2013) claim small-scale movement ought to be based on behaviour and physiology of the individual, not random. Foraging IBMs often involve multiple, interacting traits, i.e. turning angle relative to resources, habitat type (Buchmann et al. 2011; Earl & Zollner 2014; Kanagaraj et al. 2013), or predators in space (Morales et al. 2004; Duffy 2011; Kranstauber et al. 2012; Bode & Delcourt 2013; Wajnberg et al. 2013; Wilson et al. 2013; Latombe et al. 2014), step length (Leising 2001; Morales et al. 2004; Kranstauber et al. 2012), and behavioural states or rules (Railsback et al. 1999; Morales et al. 2004; Giske et al. 2013; Pauli et al. 2013; Ringelman 2014), as well as physiology, i.e. biomass (Roese et al. 1991; Buchmann et al. 2011) and energy reserves, including metabolism and gut capacity (Roese et al. 1991; Guensch et al. 2001; Peck & Daewel 2007; Giske et al. 2013; Pauli et al. 2013; Wood et al. 2013) that together define the movement process. These direct links between individual and environment suggest, for animals, the environment becomes a sandbox for combined traits to persist, dominate, or adapt (Roese et al. 1991; Railsback et al. 1999; Guensch et al. 2001; Mueller et al. 2011; Pauli et al. 2013; Shepard et al. 2013; Wood et al. 2013; Ringelman 2014). As a consequence, we can assess movement under different conditions, such as patchy landscapes and within populations, using a common

framework, particularly for conservation (Fahrig 2003). Estimating foraging success in space also involves multiple, cooperating behaviours like individual responses to food and group members (Giske et al. 2013; Bonnell et al. 2013), resource attractiveness (Dumont & Hill 2004; Bode & Delcourt 2013; Kułakowska et al. 2014; Earl & Zollner 2014), and individual to group movement (Dumont & Hill 2004; Couzin et al. 2005; Bonnell et al. 2013). Spatial IBMs also help bridge the gap between model and real movement patterns (Guensch et al. 2001; Bonnell et al. 2013; Mooij & DeAngelis 2003) under environmental change (Roese et al. 1991; Börger et al. 2011) and highlight traits often overlooked in classic foraging models, such as handling time and food size (Roese et al. 1991; Guensch et al. 2001; Pauli et al. 2013).

Process-based approaches, such as foraging IBMs, ought to emphasise not only movement detail at the immediate scale of survival (Roese et al. 1991), but also evolutionary processes such as fitness-seeking (Giske et al. 2013; Ayllón et al. 2016), including risky decision-making (Railsback & Harvey 2002; Laundré et al. 2014). Animals trade off activities like searching and sheltering against energy reserves, where wrong decisions inherently cost energy, or life; however, the movement trade-off against immediate mortality from a predator must consider future risks such as starvation (risk allocation hypothesis; (Lima et al. 1999)). Thus, physiology and behaviour adapted to mediate energy costs of maintenance, growth, and fitness, i.e. reproduction, may impose further, more vital constraints than simply optimising short-term foraging gain, emphasising how the individual energy budget can be pragmatic in predicting fitness outcomes from movement behaviour.

1.1.2. Foraging IBMs incorporating energetics are useful for predicting movement across scales

Despite their usefulness as foraging models, IBMs are surprisingly unfamiliar with the core underlying principle of feeding and movement, i.e. energetics. Movement capacity is often imposed, e.g. through a maximum number of steps, but not emerging directly from energetic principles (see Table 1 for overview). These limitations probably exist because energetics models can be species specific, data hungry, and parameter heavy (Sibly et al. 2013). However, incorporating energy reserves allow models to conveniently assess basic movement costs sensitive to behaviour (Roese et al. 1991; Guensch et al. 2001; Pauli et al. 2013; Bonnell et al. 2013). For example, combinations of turning angle and step length (Wilson et al. 2013), as well as movement speed (Shepard & Lambertucci 2013; Wilson et al. 2015), can generate diverse movement patterns that accumulate different costs depending on the scale of movement. Movement speed can also include additional detail, such as step frequency and length, when estimating movement costs. Miwa et al. (Miwa et al. 2015) suggest speed shares a stronger relationship with heart rate than step length alone as a proxy for energy costs (overall dynamic body acceleration, (Gleiss et al. 2011)); however, this method still only indirectly approximates energy costs from this relationship using previous data (Miwa et al. 2015). Animals trade-off energy costs against their physiology, motor control, and manoeuvre capabilities, where speed choice can play a key role when negotiating the movement task at hand, e.g. foraging versus escaping predators, and the current environmental conditions, e.g. open habitat versus proximity to refuge, which ultimately determines fitness (Wilson et al. 2015).

Table 1. Literature synthesised for the review showing the relationship between the time and space scales that current individual-based models on animal movement operate and the corresponding time and space scale referenced in Figure 1. The table also details the purpose of the model, the species considered, the time and space scale of the simulation/study site, and the extent each model considers energy use at the individual level.

Reference to Fig. 1	Purpose of the model	Species	Space and time scale	Energy modelled?	Reference
1.1	To demonstrate that energetic costs for turns in both terrestrial and aerial locomotion are substantial.	Generic: human (*Homo sapiens*), Andean condor (*Vultur gryphus*).	Generic	Direct and indirect: metabolic costs of turning mid-flight estimated from wind drag during change in flight path (condor); O_2 consumption via respirometer (human).	(Wilson et al. 2013)
1.1	To predict the optimal time foraging animals should decide to remain on patches of resources. Perception range included.	Generic	Generic; local.	None; patch depletion, no resource regrowth.	(Wajnberg et al. 2013)
1.1	To model the dispersal process with greater biological realism, e.g. including memory and perceptual range; this is likely to be critical for improving predictive capability regarding functional connectivity and population persistence.	Birds: Cabanis's greenbul (*Phyllastrephus cabanisi*); white-starred robin (*Pogonocichla stellate*).	Local; 5 × 5 m grid cells; in total ~ 1km².	None; movement costs estimated implicitly via cost-surface values assigned to different land use types.	(Aben et al. 2014)
1.1	To predict spatio-temporal distribution of foraging individuals; memory and a flocking mechanism is included to simulate group foraging. Can be used for pesticide risk assessment.	Birds: Woodpidgeon (*Columba palumbus*).	Local: 1–2 ha, Carlton Wood, Great Britain.	Explicit: energy content of food, food assimilation efficiency and body weight are modelled. Energy budget calculated for basal metabolism, activities, growth, reproduction, and energy reserves.	(Kułakowska et al. 2014)
1.1	To link the individual activity budget with an instantaneous energy budget of a free-range forager.	Wandering albatross (*Diomedea exulans*).	Landscape; short foraging trips (1000 km). Crozet Islands, Southern Indian Ocean.	Explicit; instantaneous energy budget calculated from daily energy intake directly measured from prey intake rate (including prey weight) from foraging trips. Also includes daily energy costs, daily net energy	(Louzao et al. 2014)

				gain, foraging efficiency, and individual mass.	
1.1	To simulate group movement patterns based on various hypotheses of environmental perception and memory and behavioural responses towards social interactions (leadership, food, competition).	Mammals (primates): red colobus monkeys (*Procolobus rufomitratus*).	Local: one single study group in Kibale National Park, Uganda; approx. 2000m².	Standardized units; patch depletion and resource regrowth.	(Bonnell et al. 2013)
1.1	To demonstrate how a habitat switch by a generalist herbivore is regulated by the seasonal change in the metabolic costs associated with foraging.	Birds: Mute swan (*Cygnus olor*).	Local: chalk river catchment of River Frome, Dorset, UK.	Explicit: Foraging intake rate based on energy metabolised from plants traded-off against energetic cost of aquatic foraging, calculated as the cost of swimming at a given water velocity.	(Wood et al. 2013)
1.1	To increase understanding of complex movement behaviour in response to resource landscapes on which individuals search and navigate. Memory and perception capacity included in oriented movement.	Generic	Generic	Standardized and implicit; resource uptake as fitness measure, no movement costs.	(Mueller et al. 2011)
1.1	To assess how animals use memory to reduce uncertainty in energy intake rate; inference on adaptive value of using information from past experience to forage more efficiently.	Mammals: Bison (*Bison bison*).	Local: south-western corner (ca. 1000 km^2) of Prince Albert National Park, Canada.	Uses fitness-based foraging currency: expected intake rate of digestible energy.	(Merkle et al. 2014)
1.1	To predict home range size; to show that by adding memory processes a biased random walker produces home-range behaviour as it gains experience, leading to more efficient resource use.	Generic	Generic	Standardized; resource gain discounted by travel costs similar to (Mitchell & Powell 2004)	(Van Moorter et al. 2009)
1.1	To assess carrying capacity of different landscape configurations by optimally distributed home ranges; these depend on optimal foraging on spatially distributed and	Generic	Generic; Landscape scale; simulated landscapes ranging from over-dispersed	Standardized units; costs of including a patch depending on its distance, i.e. travel costs traded-off vs. energy gain from depleted and	(Mitchell & Powell 2004)

	limited resources.		via clumped to highly continuous.	regrowing resource.	
1.1	Application of (Mitchell & Powell 2004) to field data.	Mammals: Non-territorial black bears (*Ursus americanus*).	Regional; Pisgah National Forest, North Carolina, USA.	See (Mitchell & Powell 2004).	(Mitchell & Powell 2007; Mitchell & Powell 2012)
1.1	To demonstrate the influence of structure and variable habitats on foraging efficiency in individual herbivores; non-regenerating resources are used to investigate short-term depletion effects.	Mammals: moose (*Alces alces*).	Regional; Denali National Park, Alaska, USA.	Physiology modelled explicitly: body size determines rumen capacity determines daily dry matter intake rate; trade-off between edible biomass and travel cost.	(Roese et al. 1991)
1.1	To show how a simple adaptive foraging strategy can lead to emergent home ranges and increased food intake; includes switching movement modes between memory-based area-concentrated food search or undirected random movements.	Mammals: harbour porpoise (*Phocoena phocoena*).	Regional (300 km); Kattegat, Belt Sea and western Baltic Sea (Europe).	Standardized; resource gain discounted by travel costs; builds on (Mitchell & Powell 2004) and (Van Moorter et al. 2009).	(Nabe-Nielsen et al. 2013)
1.1	To predict how foraging success varies with behavioural strategy, seabird densities, and prey swarm density and detectability; includes group movement, social interaction, and perception capacity.	Birds: Black-browed albatrosses (*Thalassarche melanophris*).	Regional: South Georgian waters.	None	(Grünbaum & Veit 2003)
1.1	To show under which conditions (changes in space and time) the efficiency of acquiring environmental information is highest. Includes memory and evolution of learning.	Generic	Generic	Standardized and implicit; energy gain per season through foraging used as fitness measure; patch depletion and resource regrowth.	(Eliassen et al. 2009)
1.1, 1.2, 1.3	To contribute to a unified perspective on the phenotype, by integrating effects of the environment, genetics, development, physiology, behaviour, life history, and evolution.	Planktivorous fish.	Local; Vertically stratified environment where prey performs diel vertical migration.	Standardized units. Ontogenetic stage represented by body mass; fear and hunger are modulated by neuronal responses to sensory input of remaining stomach capacity and	(Giske et al. 2013)

				food encountered.	
1.1, 1.3	To investigate how optimal diel and ontogenetic vertical migration might vary with season, individual state, and growth conditions, and the adaptive value of flexibility in migratory patterns. Trade-off in predator avoidance and food uptake included.	Copepods (*Calanus finmarchicus*).	Local; Vertical water column subdivided into three habitats; one year with daily steps.	Complete stage and state-based life history model including energy budget: ingestion and metabolism calculated; ingestion rate allometrically scaled with body mass.	(Fiksen & Carlotti 1998)
1.1, 1.3	To increase understanding of cognitive process underlying movement decisions; includes memory, perception range, and prioritising resource preference or predator avoidance.	Generic	Generic; discrete hexagonal grid; heterogeneous.	None	(Avgar et al. 2013)
1.1, 1.3, 2.1	To examine localized individual interactions coupled with long-range dispersal for all stages of predator and prey leading to system stability and spatial pattern formation.	Generic	An 8 × 1000 lattice with torus.	None, predator abundance depends on prey consumed, i.e. functional response.	(Wilson 1998)
1.1, 1.2, 2.1, 2.2	To explore using allometric relationships between body mass and resource use how animals optimise home ranges in variable environments and how this changes community structure, locomotion costs, resource depletion, and competition.	Terrestrial North American and Australian mammals	Landscapes of 257 × 257 grid cells (10m^2 cells); highly clumped to highly fragmented habitats.	Daily patch energy (dry biomass); energy requirements and costs per individual body mass; daily energy costs and gains.	(Buchman n et al. 2011; Buchmann et al. 2012; Buchmann et al. 2013)
1.1, 1.2, 1.3 2.1	To show how information can be transferred within groups both without signalling and when group members do not know which individuals, if any, have information; collective movement behaviour.	Generic	Generic	None	(Couzin et al. 2005)
1.1, 1.2, 1.3, 2.1,	To determine population density and class stability from evolutionary fitness costs under	Brown trout (*Salmo trutta L.*)	Patch to landscape: medium-sized stream,	Daily energy intake and individual biomass growth, including length,	(Ayllón et al. 2016)

2.2	future climate change.		River Belagua (Spain).	mass, age, and condition, and reproductive output of number of viable eggs. Used to estimate population classes and density.	
1.1, 1.2, 1.3, 2.1, 2.2	To test how competition, habitat type, and food availability influences habitat selection and ultimately growth and survival probability by simulated stream fish.	Rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta L.*).	Small–medium simualted stream reach (184 m) emulating Little Jones Creek California, USA.	Standardized; energy intake and growth calculated from food intake and standard metabolic and locomotion costs. Food per model spatial cell.	(Railsback & Harvey 2002)
1.1, 1.2, 1.3, 2.1, 2.3	Simulation platform to model animal dispersal through realistic, dynamic landscapes accounting for food, risk, home range suitability, and mate presence.	Generic; applied to mammals: raccoons (*Procyon lotor*), eastern chipmunks (*Tamias striatus*), American martens (*Martes americana*).	Generic	Standardized; energy gain from food layer.	(Pauli et al. 2013)
2.1	To investigate three questions about behavioural trade-offs that dispersing animals might face: (i) speed of movement against risk of predation, (ii) speed of movement against foraging, and (iii) perceptual range against risk of predation.	Generic	Generic; 100 suitable patches (10 cells in radius) embedded in hostile matrix of 1510 × 1510 grid cell landscape; different distributions (uniform, random, clumped).	Based on energy reserves representing maximum number of time intervals available for search before starvation; expenditure per step (grid cell); predation risk as per time interval probability of death; movement modelled as correlated random walk.	(Zollner & Lima 2005)
2.1	To increase our understanding of the processes that lead to animal movement decisions; a mechanistic model of an animal with a limited perceptual range and basic information storage capacities.	Generic; spatially informed forager.	Generic; hexagonal cells.	None; implicit via resource content of cells; no regrowth of resources.	(Fronhofer et al. 2013)
2.1	To explore how movement strategy and patterns of mortality risk affect the spatial distribution of living (consumer subsidies) and dead individuals (nutrient/energy subsidies).	Generic	Generic	Implicitly: movement costs represented by mortality risk.	(Earl & Zollner 2014)

2.1	To demonstrate that spatially explicit dispersal models, which take advantage of information on landscape details, suffer less from uncertainly than do simpler models.	Generic; applied to birds: Mexican Spotted Owls (*Strix occidentalis lucida)*	Generic; 120 × 120 grid cells with randomly distributed 4 × 4 cell patches of suitable habitat	None; costs of movement implicitly modelled in per step mortality probability.	(Mooij & DeAngelis 2003)
2.1	To establish how density-dependent emigration and settlement rules interact with landscape characteristics to determine spread rates.	Generic	Generic: 300 × 50 grid cells with different proportions of matrix cells.	Implicit; based on costs of moving to a neighbouring cell. Costs are based on landscape suitability, distance, and directional bias depending on animal's directional persistence. Mortality depends on habitat type.	(Bocedi, Zurell, et al. 2014) [based on RangeShifter (Bocedi, Palmer, et al. 2014)]
2.1	To infer dispersal behaviour of juvenile steelhead with a suite of IBMs to test different behavioural rules.	Fish: Steelhead (*Oncorhynchus mykiss*).	Local: Stream lengths of up to 2 km; heterogeneous habitat.	None	(Hayes & Thompson 2013)
2.1, 2.2	To determine how subpopulation equilibrium density, reproductive rate, and forms of competition affect the rate of dispersal that is selected for.	Generic	Generic	None	(Travis & Dytham 1998)
2.1, 2.2	To demonstrate that inter-annual variability in environmental conditions can influence the evolution of dispersal during range shifts.	Generic	Generic	None; prey encounter rate based on predator-prey population model.	(Henry et al. 2014) [based on RangeShifter (Bocedi, Palmer, et al. 2014)]
2.1 (2.3)	To assess connectivity, population dynamics, or invasion success of rare or endangered species; includes memory and perception range.	Mammals: Lynx (*Lynx lynx*) and tiger (*Panthera tigris*).	Regional: Germany, Terai Arc Landscape in India; heterogeneous habitat.	Implicit; dispersal capacity inversely fitted to field data for step length and mortality.	(Pe'er & Kramer-Schadt 2008; Kanagaraj

					et al. 2013; Kramer-Schadt et al. 2004; Kramer-Schadt et al. 2005; Kramer-Schadt et al. 2011)
2.1, 2.2, 2.3	To assess how different constraints to individual movement, such as resource and mate availability in time and space, influence home range patterns, dispersal potential, and ultimately population structure.	Common shrew (Sorex araneus).	Landscape of 10,000 5m cells. Agricultural habitat matrix (grasslands, hedges, and cereal fields).	Food per cell for different habitat types across season. Values are g dry weight m^2 (from previous field work by other authors).	(Wang & Grimm 2007)
3.1	To test the effect of removing wintering habitat on population development.	Birds: barnacle goose (*Branta leucopsis*) and brent goose (*Branta bernicla bernicla*); annual cycle.	Large scale: Central to Northern Europe (however, space indirectly modelled); annual cycle.	Daily intake rate; energy reserve classes based on abdominal profile index; intake rate calculated according to empirically derived relationships between feeding parameters, flock size, and food availability.	(Pettifor et al. 2000)
3.1	To study spatial movement of fish navigating in a variable and seasonal environment; super-individual approach; evolutionary modelling.	Artificial fish, e.g. capelin.	Large scale, e.g., Barents Sea; annual cycles; 300 years.	Bioenergetics model and stomach capacity; movement costs: mortality depends on body weight and water temperature.	(Huse & Giske 1998)
3.1, 3.2, 3.3	To investigate which decision rules geese use to time their spring migration. Based on energetics (sufficient body stores to fuel flight), time-related cues (internal clock under photoperiodic control), or external cues (temperature, food resources).	Birds: Pink-footed geese (*Anser brachyrhynchus*); but modelled as super-individual.	Large scale: Denmark to Spitzbergen.	Based on energy reserves stored in the body, body size, intake rate and metabolic rates, including expenditure for different behavioural states.	(Duriez et al. 2009)

3.1, 3.2, 3.3	To investigate what ultimate factors generally drive animal migration in seasonal environments and different modes of information use; evolutionary modelling; information use (resources, memory, social).	Generic	Generic: resources described by a gradient; space as 1024 × 1024 pixel square.	Modelled as fitness functions; cumulative (sum of values of resources digested at every time step over the course of a generation, e.g. ungulates), end-point (e.g. spawning migration of fish), and minimum (e.g. song bird surviving harsh conditions).	(Shaw & Couzin 2013)
3.1, 3.3	To model innate migratory pathways of wildebeest in the Serengeti Mara Ecosystem under hypotheses of vegetation primary productivity and rainfall.	Mammals: Wildebeest (*Connochaetes taurinus*); annual time step.	Large scale: Serengeti ecosystem, Tanzania and Kenya, Africa, annual cycle.	None	(Boone et al. 2006)
3.1, 3.3	To identify general features in migration pattern and trophic interactions, the movement, competition, foraging, growth, and mortality was modelled; super-individual approach.	Fish: Capelin (*Mallotus villosus* Mueller 1776) and cod (*Gadus morhua* L.).	Large scale: Barents Sea; 90 (x-axis) by 100 (y-axis) grid of 20 km^2 squares.	Bioenergetics model based on growth; balanced energy budget based on consumption, respiration, egestion, excretion, and action.	(Huse et al. 2004)
3.2	To show how maximum migration distance is constrained by body size for each mode of travel (walking, swimming, flying).	Generic for walking, swimming, and flying migrants.	Generic	Based on biomechanics, metabolic scaling, and allometry; body mass-dependence of the cost of locomotion, dynamic changes in the body masses of migrants as they utilise stored fuel and scaling of morphological characteristics and maintenance metabolism among migrants of different body masses.	(Hein et al. 2012)
3.3	To understand changes in migratory behaviour, a model including fish schooling behaviour based on individual decisions and orientation towards group members.	Fish: Norwegian Sea spawning herring (*Clupea harengus*).	Small scale model of fish schooling behaviour for large scale of Norwegian sea.	None	(Huse et al. 2002)

Food size, bite size, and intake rate are also key, but often-overlooked, energetics traits influencing movement (Roese et al. 1991; Guensch et al. 2001; Peck & Daewel 2007; Pauli et al. 2013). These detailed measures help estimate important functions such as feeding rates and digestive capacity (Peck & Daewel 2007; Giske et al. 2013) for growing animals (Roese et al. 1991; Peck & Daewel 2007) that in turn contribute to different activity states (Pauli et al. 2013; Louzao et al. 2014) and the overall time budget (Bergman, Carita et al. 2001; Merkle et al. 2014). Ultimately, this detail helps reveal functional movement limits via the ways animals adapt to changing habitat quality (Guensch et al. 2001; Pauli et al. 2013), different temperatures (Peck & Daewel 2007; Ayllón et al. 2016), or to paths of least physical resistance (Shepard et al. 2013; Wilson et al. 2012), as shown for soaring birds and costs of high-altitude migration (Hawkes et al. 2013; Sachs et al. 2013).

Energetics IBMs suggest animals use energy to connect habitat choice with survival probability under different risks in space. Guensch et al. (2001) show stream fish prefer habitats of higher energy gain and low movement costs. Railsback et al. (1999) use body condition to show stream fish trade off energy intake against habitat type and choose patches of low energy gain that maximise survival to escape fast-flowing water currents, while Pauli et al. (2013) use energetics to capture individual growth changes in response to changing resources and habitat type, and different predation and starvation risks. Energy reserves are a useful reference for animals to assess trade-offs in behaviour, such as negotiating predator and foraging risks within a landscape of fear vs. food (Laundré et al. 2014) or complementing perception ranges when resource density changes (Zollner & Lima 2005). As spatial models, energetics IBMs connect individuals with habitat and social information by using energy as a currency against direct risks, such as predators (Railsback et al. 1999; Giske et al. 2013; Pauli et al. 2013) and competing for food (Bode & Delcourt 2013; Bonnell et al. 2013). Energetics models also connect movement with time. Intake rate and bite size are intrinsically linked, suggesting handling time budgets help animals trade off energy costs and gains (Guensch et al. 2001) and shape foraging success (Roese et al. 1991). Energy drives metabolic functions on longer time scales like starvation (Railsback et al. 1999) and reproduction (Railsback et al. 1999; Guensch et al. 2001), as well as intake and growth rates (Guensch et al. 2001) as they vary under temperature and prey constraints (Peck & Daewel 2007). These trade-offs become amenable on longer time scales by affecting size classes within populations, thus influencing evolutionary adaptation to future environmental change (Ayllón et al. 2016). Models, such as IBMs, capable of capturing these vital interacting processes are thus useful frameworks using general mechanisms like energetics to link local actions, such as how animals absorb information and assess risk, with evolutionary ones, such as balancing fitness outcomes.

1.1.3. Energetics IBMs suggest foraging and habitat selection involve fine scale time trade-offs

Energetics IBMs teach us foraging is a complex relationship between costs and gains sensitive to the scale of movement, ranging from basic step length and turning angles (Wilson et al. 2013) to complex social behaviour (Bode & Delcourt 2013; Bonnell et al. 2013). Wilson et al. (Wilson et al. 2013) measured turn costs as individual energy output

depending on turn angle across distance travelled, which increases at finer scales; models assuming the environment absorb these costs thus should be treated with caution. By building from the individual level, IBMs help us understand movement constraints in space and time with changing environments (Giske et al. 2013; Pauli et al. 2013) and body size (Roese et al. 1991; Railsback et al. 1999; Peck & Daewel 2007; Fiksen & Carlotti 1998), identify the subtle interface between resource availability and movement in space (Earl & Zollner 2014; Bode & Delcourt 2013), and generate sensible outcomes at the population level (Roese et al. 1991; Ayllón et al. 2016). Individual rates of food intake provide clues on how behaviour reflects energy gain as resources vary across space (Bode & Delcourt 2013). Similarly, interpreting energy gain from physiology, such as stomach capacity, connects individual traits directly to how animals perceive individual risk and thus modify movement decisions (Giske et al. 2013). The type of system also determines how to appropriately interpret energy exchange between individuals and the environment, where energy uptake is either from surfaces or volumes in terrestrial versus aquatic habitats. That is, calculating metabolic rates becomes more uniform in oceans because prey is measured in biomass. This argument also suggests energetics models are sensitive to species and scale; here, static parameters, such as maximum feeding rate, may underestimate intake rates as prey density varies in space and time (Peck & Daewel 2007). The stability of an ecosystem depends on its individual parts, so connecting crucial individual behaviour like foraging to movement should translate across scales, particularly in space (Hosseini 2006). Behaviour and ecology at the population and ecosystem levels thus relies on real estimates of cues driving individual behavior (Buchmann et al. 2011; Buchmann et al. 2012; Buchmann et al. 2013; Earl & Zollner 2014), where basic and general individual mechanisms like energy use are useful and translate to appropriate scales.

Models concerned with predicting only single outcomes, such as growth, may suffer by ignoring cooperating constraints to movement in space, such as trade-offs to predation (Railsback et al. 1999; Fiksen & Carlotti 1998) and risk-taking in landscapes of food vs. fear (Giske et al. 2013; Laundré et al. 2014). Energetics models should also consider metabolic processes other than simply energy intake (Louzao et al. 2014), such as maintenance costs (Kooijman 2010; Sibly et al. 2013) and the consequences of metabolism over longer time scales related to fitness consequences (Ayllón et al. 2016; Malishev et al. in press). Incorporating energetics in IBMs at small scales creates opportunities to connect movement with time, specifically the activity budget of animals, such as food handling rates, as well as providing a mechanism directly linked to survival probability from which animals make their activity and habitat choices. Individual traits like physiology link time budgets directly to energy intake on fine movement scales, which translates simply to behaviour. Despite this straightforward relationship, movement models at this scale commonly make energetics subjective, probably because they are easier to develop and more convenient (Holyoak et al. 2008). Advanced technology, such as GPS units with accelerometers, can simplify how we estimate energy use for different behaviours when collecting data from the field (Gleiss et al. 2011; Louzao et al. 2014; Nams 2014; Wilson et al. 2014; Miwa et al. 2015; Kays et al. 2015; Scharf et al. 2016) . Using metabolic rules from energetics theory to formulate the individual energy budget provides a general approach to drive movement decisions and estimate movement costs, thus filling in the gaps from field data estimates of energy use

as well as escaping the demands and limitations of formulating species-specific models (Grimm et al. 2005; Louzao et al. 2014). Packaging a theory-driven energy budget into an individual-based model (Malishev et al. in press) thus supplies an underlying, unifying mechanism to individual movement across taxa and scales within a general movement framework.

1.2. Cognitive processes

1.2.1. Spatial awareness alleviates movement challenges under environmental change

Memory controls the ability to revisit previous patches (Nabe-Nielsen et al. 2013) to evolve movement strategies and yield more spatially aware animals for memorising previous gains or predicting new ones (Fagan et al. 2013). Movement may involve different types of memory, i.e. for remembering sites (reference memory) and assessing current gain from previous experience (working memory) (Van Moorter et al. 2009) to generate a localised understanding of habitats (Avgar et al. 2013; Fronhofer et al. 2013), so exploiting this ability is likely to expedite movement and probably infers selective advantages. Memory can also help predict seasonally-driven food availability across larger time and space scales, e.g. how mobile prey arranges itself in space may come from earlier decisions to settle or nest (Ringelman 2014). As food changes across scales, remembering previous food sites can outperform random foraging (Nabe-Nielsen et al. 2013); animals combining memory with habitat and social information (Huse et al. 2002; Couzin et al. 2005; Bonnell et al. 2013; Latombe et al. 2014), e.g. seabirds using fellows to find resources (Grünbaum & Veit 2003), use less space and improve foraging gain (Merkle et al. 2014), suggesting memory also depends on scale.

Memory can build more efficient movement paths, improving the ability to exploit landscapes as food becomes more predictable in space and time (Mueller et al. 2011; Avgar et al. 2013). However, remembering food location is more sustainable (and potentially improves fitness) with better quality food. Bison, for example, are better at remembering food location than quality (Merkle et al. 2014), but better food is a stronger incentive than location to re-visit profitable patches. For central place foragers or migrants, memory can become less effective in disturbed environments, i.e. when barriers are introduced (Mueller et al. 2011). Selection may then favour memory when high quality habitat translates simply to a location or under more stable environments. Therefore, cognitive-based IBMs sensitive to scale, spatially informed, and responsive to environmental change appear to be most sensible for predicting individual movement.

1.2.2. Cognition and energy use are complementary mechanisms to animal movement

Memory and energy reserves can concurrently drive movement, but both vary among individuals in how they define the movement process, suggesting other individual traits, such as movement strategy, may dominate. For example, predators modelled with a correlated random walk algorithm are more efficient at finding random prey and can exploit spatial memory to improve foraging success when prey is clustered (Ringelman 2014); however, being spatially aware can be less efficient when resources are random (Fronhofer et al. 2013). This relationship also tells us the benefits of memory vary with

how food is distributed in space. In changing environments, the turnover of remembering experiences should be rapid, as long-term memory can diminish the probability of gathering future, valuable information (Eliassen et al. 2009). The expected energy intake of animals over time can depend heavily on previous foraging experience to locate larger and closer food patches (Merkle et al. 2014). However, animals relying on estimates of future food yield from current working knowledge would probably benefit by combining traits and behaviours, such as assessing current energy reserves prior to revisiting food sites, particularly when food changes in time (Kułakowska et al. 2014) and against predator risk (Eliassen et al. 2007).

1.2.3. Energy use is a useful mechanism informing prescient movement decisions

Memory allows animals to be more spatially informed about resources without assuming food levels in their habitat (Nabe-Nielsen et al. 2013). However, can animals really know the yield of future, unpredictable food before departing? The ability to make prescient movement decisions based on internal, limiting cues, such as energy reserves, offers a useful mechanism for movement shared among taxa. We argue individual-based movement models tackling complex cognitive processes become more useful when standardized by a general, shared trait like energy use to improve predictive power under multiple behaviours. Cognitive-based models also need to forecast more than one movement step into the future, consider the value of long-term memory when information on habitat quality is low, especially over large spatial changes (Eliassen et al. 2009), and, for realism, incorporate restricted and imprecise memory (Fronhofer et al. 2013). Having some ability to forecast shares similar tenets with other mechanisms of movement. It is this. Mechanisms at the individual level tell us movement decisions ought to consider not only immediate benefits but be prescient. Memory infers movement evolves from internal traits using external feedback in the same way past energy use motivates future decisions. Finally, complementary individual traits tell us movement must be sensitive to changes in scale. Because exploiting memory creates more spatially aware consumers, linking resource use with individual mechanisms like energetics provides useful constraints upon which to base the memory and decision-making parts of movement.

1.3. Home range occupancy and dispersal potential

1.3.1. Explicitly modelling home range occupancy and dispersal potential with IBMs

We can define dispersal as fine scale movements of foraging, mating, or avoiding predators translated to larger scales, such as landscapes, linking these behaviours to habitat selection, range expansion, regional dispersal, and species distribution (Fig 1, section 2). Therefore, dispersal ability is useful for estimating how populations (Fahrig 2003; Latombe et al. 2014; Aben et al. 2014) and communities (Buchmann et al. 2011) respond to fragmented habitats; however, assessing dispersal ability and range expansion often involves species responses to resource availability and interacting individuals, such as avoiding predators, curbing mortality risk, and group social information, by using metrics to assess habitat suitability (Kramer-Schadt et al. 2004; Kramer-Schadt et al. 2005; Bocedi, Palmer, et al. 2014; Aben et al. 2014; Mooij & DeAngelis 2003; Bocedi,

Zurell, et al. 2014; Hayes & Thompson 2013; Henry et al. 2014). Therefore, habitat suitability indices to predict animal occupancy and range dynamics may ignore important behavioural detail, thereby diluting subtle, but decisive, movement mechanisms (Schurr et al. 2012; Kubisch et al. 2014; Mooij & DeAngelis 2003). For example, dispersal is a by-product of recurring, frequent movement linked to common behaviour connecting animals to space, such as resource use (van Dyck & Baguette 2005), competition (Moorcroft et al. 2006), mating opportunities (Wang & Grimm 2007), and mortality risk (Kramer-Schadt et al. 2005; Bocedi, Zurell, et al. 2014; Kramer-Schadt et al. 2004), in turn forming home ranges. Home range size and dispersal can then vary under combinations of these constraints, which influences future dispersal potential of individuals and thus population structure (Wang & Grimm 2007; Bocedi, Palmer, et al. 2014) over different time and space scales (Bocedi, Zurell, et al. 2014; Henry et al. 2014; Bowler & Benton 2005; Kramer-Schadt et al. 2011; Kanagaraj et al. 2013).

Home range behaviour is often complemented by individual traits such as cognition and thus directly related to memory, as animals occupy home ranges by revisiting previous sites. Animals can stabilise their home ranges by relying on memory over exploring new resources (Nabe-Nielsen et al. 2013) and using complementary types of memory e.g. reference and working (Van Moorter et al. 2009). However, because home range stability depends on scale (Lyons et al. 2013), home range models must balance the cost of animals requiring too much information (see (Börger et al. 2008)). Other key movement traits linked to home range behaviour, such as duration and frequency of patch visits, may include mechanisms that support biologically relevant movement rules and share direct trade-offs with the environment (Lyons et al. 2013; Van Moorter et al. 2015). Models that capture individual responses to resource, competitor, predator, or mate distribution, for example, are useful at predicting home range behaviour because they define the spatial limits of animal movement (Mitchell & Powell 2004; Moorcroft et al. 2006; Buchmann et al. 2011; Lyons et al. 2013; Bocedi, Zurell, et al. 2014; Bocedi, Palmer, et al. 2014). Therefore, future avenues where movement IBMs are well suited involve scenarios where home ranges are defined by individual preferences and how they change across different environments (Börger et al. 2008).

1.3.2. General individual traits link resource use to home range behaviour in space and time

Home range IBMs linked to energetics generally use resource intake as a proxy, i.e. resource sites visited (Mitchell & Powell 2004; Nabe-Nielsen et al. 2013) or patches consumed (Van Moorter et al. 2009; Buchmann et al. 2011), rather than individual energy reserves, highlighting a disparity in how we interpret individual-based energetics with home range models. These works propose that direct links animals share with their environment help animals form home ranges: selecting resource sites rather than simply movement to define home ranges (Mitchell & Powell 2004), using attraction rules to nearby, previously visited food (Nabe-Nielsen et al. 2013) or shelter (Moorcroft et al. 2006) to generate more stable home ranges. Because energy intake depends on patch residence time, visiting fewer patches but for longer can stabilise home range size (Nabe-Nielsen et al. 2013) depending on food renewal rates (Van Moorter et al. 2009). Home range models assuming animals optimise resource use based on their dispersal in the

landscape can accurately predict real home range size in black bears (Mitchell & Powell 2007) when animals use less area and fewer resources (Mitchell & Powell 2012), despite not strictly including individual energetics. Further, foraging strategy can shift with body mass, which can generate different home range sizes based on efficiency of resource use (Buchmann et al. 2012; Buchmann et al. 2011). Therefore, behavioural strategy can determine the potential movement costs required to optimise space use and generate stable home ranges. Mechanistic home range models based on movement rules (Van Moorter et al. 2009) could be more general and realistic by using mechanisms like energetics, rather than relying on random walks to drive movement in space.

1.3.3. Energetics IBMs are useful frameworks for modelling complex home range behaviour

A common, but abstract way to integrate energetics into movement is depicting decision-making surfaces based on resource availability or mortality risk (e.g. (Fronhofer et al. 2013; Pauli et al. 2013), which can translate small-scale movement models to the larger home range and regional scale by unifying energy uptake and use from the individual level (Fig. 1). Supplementing energetics with other traits like memory can make movement models more predictive and realistic (Latombe et al. 2014). For example, the restricted movement of individuals by energy costs may override the strength of reference memory, producing less sustainable home ranges. Energy intake changes in space; irrelevant patch use by animals visiting empty patches in a landscape can shape how we think animals forge home ranges (Mitchell & Powell 2012). This highlights the intimacy energetics share with other traits that models ought to balance depending on the species or system modelled. Home range behaviour and dispersal involve multiple cues (Pe'er & Kramer-Schadt 2008; Schick et al. 2008), so models assuming animals ignore time for other important activities in addition to finding resources (Mitchell & Powell 2004) can be misleading and inaccurate. Energy use that animals abide by across time and space thus represents useful logic when reasoning what general mechanism could usefully summarise complex movement, such as home range behaviour. This complexity teaches us exploring home range behaviour using mechanisms is simplified when movement decisions stem from cues directly reflecting the processes shaping home range behaviour, such as when internal energy reserves influence animals to compromise or exploit resources or mates in a landscape.

1.4. Migration and geographic distribution

1.4.1. Migrants use both internal and external cues at different scales

Individual-based movement models are less common at the large scale of dispersal and migration, where birds and fish dominate (see (Bauer et al. 2009)). The large time and space scale of dispersal and migration means migrants must adapt to long physical travel and uncertain habitat and resource availability at destination sites (Pettifor et al. 2000; Duriez et al. 2009). Because large-scale movement is often group-based (Merkle et al. 2015), social input can dilute the migration process (Shaw & Couzin 2013) that, together with large-scale environmental change (Boone et al. 2006), can make migration less predictable (Cote et al. 2016). Therefore, using both internal and external cues can help

animals make informed movement decisions, such as when to depart based on available food (McNamara et al. 2011) and climate (Boone et al. 2006) together with assessing energy reserve to forecast distances to future stopover sites (Duriez et al. 2009; Pettifor et al. 2000). Individual-based models typically use behaviour rules to model group movement during migration (Huse & Giske 1998; Pettifor et al. 2000; Duriez et al. 2009; Huse et al. 2004; Huse et al. 2002; Shaw & Couzin 2013). Dominant and experienced individuals can influence group behaviour through naïve or new migrants, but learning new migration paths depends on the demography of dominants and its timing with migration events (Huse et al. 2002).

Migration often involves two distinct movement phases: large scale to and small scale within a destination. External cues, such as season (Pettifor et al. 2000; Boone et al. 2006) and resource patterns (Duriez et al. 2009) regulate when animals move both between and within migration sites. Small-scale environmental change can help animals negotiate changing food availability or predation risk within foraging sites, e.g. geese navigating daily tidal cycles (Pettifor et al. 2000) or pelagic fish in diurnal migration (Giske et al. 2013). Over larger scales, migrants generally prefer seasonal cues between sites (Pettifor et al. 2000) but switch to favour localised cues, such as resources, within sites (Shaw & Couzin 2013).

1.4.2. Animals assess energy reserves to make better migration decisions

External cues, such as temperature, alter resources density and distribution in space and time, so adapting migration decisions to these cues may improve their success (Huse et al. 2004). However, adapting to short daily temperature profiles to assess habitat suitability can drive migrating birds such as geese to depart prematurely and risk starvation (Duriez et al. 2009), suggesting large-scale dispersal is sensitive to the rate and scale of change in external cues (Boone et al. 2006). Similarly, the immediate environment provides physical handicaps for animals to exploit, such as wind currents for migrating birds (Safi et al. 2013), e.g. dynamic soaring (Sachs et al. 2013; Shepard & Lambertucci 2013) that facilitates faster flying speeds and improves access to food sources, especially for individuals and species with greater wingspans (Shepard & Lambertucci 2013).

Conversely, internal cues, such as energy reserves, allow animals to make movement decisions from individual physical mechanisms. For example, given animals improve their energy use by exploiting different physical handicaps in their environment suggests energy use is a limiting mechanism across larger scales; however, it also constrains the potential frequency of small-scale repetitive movement within the larger, more steady migration path, which must be negotiated together with the total movement path across long time periods (Sachs et al. 2013). Categorising the migration path into distinct movement phases based on how migrating birds exploit their immediate environment, i.e. wind currents, identifies vital points in time and space animals ought to exploit to optimise energy usage (Sachs et al. 2013). However, migrants will not always capitalise paths of least resistance, such as bar-headed geese that, despite available tail winds, on average flew under conditions sub-optimal for reduced energy costs (Hawkes et al. 2013). The conclusions from these findings are twofold: 1) although migrating birds sometimes

utilise low altitude areas along migratory paths to fly faster and reduce movement costs, over longer time periods, this type of behaviour may not always be possible or sustainable (Hawkes et al. 2013; Sachs et al. 2013; Shepard & Lambertucci 2013); and 2) despite their availability, decisions to exploit physical handicaps vary among individuals, which is particularly evident in group-based migration (Cote et al. 2016), thus the general limiting constraint to movement in lieu of or dominant to the external physical environment is likely to be internal and individual-based, such as energy reserves.

Calculating food intake rate from gut capacity, feeding response to prey density (functional response), and food availability, as well as metabolic activities of respiration, egestion, and excretion, generates realistic metrics of how animal might behave in nature, linking large-scale dispersal to reasonable fitness outcomes, such as growth (Huse et al. 2004) and reproduction (Pettifor et al. 2000). Geese use external cues such as spring plant emergence to inform migration decisions, but combined with internal cues like energy reserves based on gut capacity, metabolic rates, and thermoregulatory costs allows individuals to select the best departure times (Duriez et al. 2009). Data on bite size, ingestion rate, and foraging efficiency allow models to specify when migrants depart based on energy levels (Pettifor et al. 2000). Because energy reserves at any given time vary among individuals, estimating movement from internal mechanisms retains individual-level responses to environmental change by assigning different movement rules among individuals. This has two advantages: it improves how we interpret movement costs in different ecosystems, i.e. terrestrial versus aquatic (Hein et al. 2012), particularly as energy use can become more abstract with increasing scales (Pauli et al. 2013; Wilson et al. 2015); and it addresses the common problem of such models neglecting key between-individual differences (Holyoak et al. 2008).

1.4.3. Energetics links the equally important small- and large-scale movement behaviour of migration in space

Energy reserves act as a movement engine to underpin movement across different migration phases, from small to large spatial scales, by a common physical mechanism. Because the costs of migration can be substantial and difficult to interpret across species and systems, using energetics, such as metabolic rules to interpret the relationship between body mass and movement costs (Hein et al. 2012) (see also (Buchmann et al. 2011; Buchmann et al. 2012; Buchmann et al. 2013; Fiksen & Carlotti 1998; Giske et al. 2013; Duriez et al. 2009; Roese et al. 1991)), unifies the migration process with general principles. Migration also often involves group movement, where the benefit of using general model traits such as energetics sorts individuals into common assemblages (see (Purves et al. 2013)); this satisfies the concept of the super-individual—one type of individual representing a suite of individuals with similar attributes—across large space and time scales (Huse et al. 2004), e.g. smaller juveniles with high metabolic rates than larger adults that require different handling times (time) and incur greater movement costs (space).

The ability for spatial models to more accurately reflect real movement patterns under large-scale habitat change (Pettifor et al. 2000; Shaw & Couzin 2013; Huse & Giske 1998), the importance of fine scale space on food encounter rates (Huse et al. 2004; Bode

& Delcourt 2013; Wajnberg et al. 2013), and the response of highly mobile prey to environmental change (Huse & Giske 1998) reinforce the need for explicitly modelling space at the migration scale. Habitat loss also increases the required travel distance to new sites, so spatial models need to also clearly define what makes habitats attractive for migrants (Pettifor et al. 2000). Due to the subtlety of spatial movement, however, IBMs should be vigilant when applying movement rules at large scales (Huse et al. 2004). For example, over long time periods, slow moving animals can incur greater movement costs across large scales compared to faster animals by accumulating more non-movement costs per distance travelled (Wilson et al. 2015). We suggest internal cues to estimate the success of large-scale movement are probably more reliable for animals because e.g. energy intake is the product of individual behaviour, which can be less fickle than external cues.

Conclusions

Individual-based models address animal movement across broad time and space scales, illuminating the interface between movement and constraints, such as resource density, to reveal universally complex patterns. Internal mechanisms, such as memory, assist animals in locating resources and structuring home ranges when movement decisions are complex. Cooperating internal and external cues facilitate movement, reinforcing the need for spatial models at different scales. The sensitivity of movement to different scales and constraints suggests general, simplified mechanisms can unify how we interpret movement. Our review suggests energetics models are useful candidates. At the individual level, their general physical principles drive movement including intake rate, prey handling, and growth across different scales. Movement research is beginning to embrace the principles outlined in this review by explicitly addressing energetic costs (Shepard et al. 2013; Bonte et al. 2012; Bonnell et al. 2013; Hawkes et al. 2013; Sachs et al. 2013; Pauli et al. 2013; Wilson et al. 2013; Wood et al. 2013). The field will progress from an explicit focus on mechanisms (Holyoak et al. 2008; Giuggioli & Bartumeus 2010) and scales (Benhamou 2014), simplified through process-based approaches such as IBMs (Bauer & Klaassen 2013).

Acknowledgements

We thank Volker Grimm, Mark Burgman, Michael Bode, Inka Veltheim, Lucy Rose, and two anonymous reviewers for helpful comments, discussion, and revisions.

Funding

MM was funded by an Australian Postgraduate Award (APA) and the Centre of Excellence for Biosecurity Risk Analysis.

1

Authors' contributions

MM conceived the idea and wrote the manuscript, figures, and tables. SKS wrote the manuscript, figures, and tables. All authors read and approved final versions.

Data accessibility

This manuscript does not use any data.

Competing interests

The authors declare they have no competing interests.

Ethics approval and consent to participate

Not applicable.

2

A primer for modelling movement from first principles

Matthew Malishev[1*]

[1] *Centre of Excellence for Biosecurity Risk Analysis, School of BioSciences, University of Melbourne, Parkville, Melbourne, 3010, Australia*

This chapter appears in 'Malishev, M. & Kramer-Schadt, S. Individual-based energy budgets as next-generation extensions for modelling animal movement across scales. In revision'.

[*]Corresponding author: matthew.malishev@gmail.com

Ich überlasse die Sorgen von morgen meinem morgigen Ich

Saitama

Table of Contents

Abstract 42
Introduction 43
Indirect movement costs as the primary constraint to movement 44
The *iDEB* primer for modelling individual movement 47
The primary metabolic pathways 47
Maintenance 48
Growth 48
Simulating individual movement behaviour using iDEB 49
Concluding thoughts and future directions 54
Acknowledgements 55
Funding 55
Authors' contributions 55
Competing interests 55
Ethics approval and consent to participate 55

Abstract

Movement ecology is a growing field, presenting opportunities for new tools to tackle its ecological challenges. We introduce a movement primer (i_{DEB}) based on the basic principles of energy and mass exchange following Dynamic Energy Budget (DEB) theory. The theory-based primer applies these common principles shared across taxa to update the individual, internal state, offering practical advantages over heuristic methods. This aims to directly address the need for a unified modelling approach to movement across scales, species, and different movement constraints. We present the opportunities, strengths, and limitations of the i_{DEB} primer through several aims: 1) to build the individual with a step-by-step approach using intuitive, behavioural building blocks. This generates more power to tackle the simplifying assumptions of movement models by redefining how the model process is reasoned. As a corollary, the primer identifies what current movement models might lack in their structure and assumptions; 2) to regain a systematic way of addressing the general and broad scope of movement ecology. Movement ecology has multiple origins and motives. Therefore, research approaches are often unsystematic with little congruence on the time and space spectrum being targeted. A theory-based primer aims to unify the many approaches dominated by case studies and specific individual-environment combinations; and 3) to redirect the way we approach movement models by constructing new scenarios of classic problems with hypothetical individuals. This encourages scientists to reason the motives behind their model assumptions.

Keywords: Dynamic energy budget, individual-based model, movement framework, metabolic processes, life stage, metabolic costs

Introduction

Models on animal movement incorporating energetics often habitually sum energy parameters as a measure of body condition with little thought to the theory behind energy use. Incorporating key concepts of energy use from theory into a working mechanistic framework extends models beyond *ad hoc* applications. We apply DEB theory to the i_{DEB} primer and introduce how the theory's assumptions can be integrated into an IBM. This aims to summarise the metabolic processes, including movement costs, driving movement decisions at the individual level. The working example of this model applying the i_{DEB} primer as a spatial IBM is outlined in Chapter 3.

In this chapter, I split movement costs into two domains, direct and indirect (see Fig. 2). In contrast to other theories (Metabolic Theory of Ecology; Brown et al. 2004) and frameworks (biomass budget models) on energy uptake and use by organisms, DEB theory presents several advantages. Firstly, it estimates the metabolic processes comprising the complete energy and mass budget of the individual throughout its life cycle, from egg to sexually mature adult. This allows us to partition the metabolic activity of the animal into different pathways. From here, we can then formulate these pathways into a modelling framework that explicitly considers how energy use contributes to other life history consequences of the animal, such as movement decisions and activity patterns. Secondly, DEB theory considers the overhead costs of metabolism [see (van der Meer 2006) for discussion], which is key to estimating direct movement costs. The body expels heat, water, and CO_2 as metabolic products on faster time scales than standard metabolic processes of maintenance and growth, for example, the overheads of processing and assimilating food, growing tissue, and consuming oxygen during movement (aerobic metabolism). In standard biomass budget models, these costs appear within the total loss of metabolic products (Nisbet et al. 2012); in DEB theory, they represent the direct costs of metabolism that over time accumulate to levels proportional to a fraction of somatic maintenance costs. Maintenance is paid per unit of structure, so it scales with volume. Therefore, movement costs, such as muscle use, are volume specific (Kooijman 2010), expressed as costs per structure of the individual to maintain generality across species (Nisbet et al. 2012). Up to 80% of an individual's structure is recycled (Kooijman 2010), the remainder is energy transported to meet metabolic demands, such as feeding and movement costs. Therefore, only by knowing the complete energy budget can we estimate these direct movement costs. Metabolism is expensive, paying enormous maintenance and growth taxes; this means under the entire energy budget, the direct costs of movement as a fraction of maintenance are negligible.

Indirect movement costs are reasoned differently. Animals moving between two adjacent patches experience little energy loss. Over time, however, the body's metabolic output represents the consequences of this movement. We apply this philosophy to individual animal movement using the i_{DEB} primer to estimate indirect costs of movement from the relationship between behaviour and the essential metabolic processes of the complete energy and mass budget.

Indirect movement costs change as the individual interacts with its environment over time due to increasing movement trade-offs associated with different behaviour, such as foraging, mating, and defending. The curve in Fig. 2 is a stylised example of how changes in behaviour and transitions among activity states perturbs the trajectory of these costs over the life cycle. The numbers represent common scenarios in which behaviour may influence indirect movement costs. For example, (1) may represent a peak in movement costs incurred by localised, vigorous patch movement, such as when escaping a predator. Finding food or capturing prey may follow two possible scenarios. Firstly, to minimise the average time it takes to find and handle food, which is mediated by ecological costs, such as predator presence (Weimerskirch et al. 2007; Basille et al. 2015). In the face of such costs, animals may compromise their original motivations to forage, such as their time dedicated to handling food (Werner & Anholt 1993; Zollner & Lima 2005; Ringelman 2014). Secondly, animals benefit from maximising energy return over time (Wilson et al. 2013; Louzao et al. 2014). When their ecological costs are low, increasing time spent finding food can maximise energy return (Huey 1974; Eliassen et al. 2009; Bonte et al. 2012; Mitchell & Powell 2012; Sears & Angilletta 2015). These trade-offs compare available activity time against energetic costs and gains, which can be interpreted at the individual level. In (2), a plateau at the intermediate time and space scale can represent an animal mediating its energy costs by considering how information from previous movement decisions may influence future movement potential and adaptive behaviour (Merkle et al. 2014). An example here would be an animal taking long rest periods to anticipate future periods of intensive movement or low energy gain, i.e. torpor (Walker et al. 1983). Finally, in (3), intense, localised foraging produces a spike in energy gain, presenting the animal with an opportunity to satisfy current energy demand with supply and thus balance out its energy budget; this ultimately leads to a drop in movement costs (Fig. 2). The next section elaborates upon how 1) indirect movement costs emerge as the primary constraint to movement and 2) IBMs, engrained with a similar, mechanistic philosophy of the individual as the central unit, are key to capturing these costs.

Indirect movement costs as the primary constraint to movement

In this section, I outline how trade-offs in behaviour as an animal negotiates its habitat generates the primary, indirect costs of movement. I apply DEB theory rules to summarise these costs at the individual level within the theory-based i_{DEB} primer for animal movement.

1) In DEB theory, energy reserves, proportional to incoming and outgoing energy, scale with individual body length. The individual pays maintenance and maturity costs using reserves at a rate equal to a proportion of body volume. Therefore, as the individual grows, the metabolic engine responds to changes in body size. Modellers using IBMs can define individual traits, e.g. mass, using parameters for body length, linking the DEB framework to the IBM platform with relative ease; Martin et al. (Martin et al. 2012; Martin et al. 2013) did this at the population level. For

individuals, this autonomy connects movement rules to metabolism. The energetic state of the individual thus changes over time and space as the animal interacts with its environment; here, indirect movement costs accrue as consequences of different movement decisions along a continuum of energy use linked to appropriate scales (Fig. 2).

2) Incoming food passes via surface areas from the external habitat to the internal body environment of the animal. In DEB theory, metabolism is independent of food intake, separating metabolic activity from the often variable outside environment. This partition allows for metabolic memory, where individual responses to changing food intake determine the severity of indirect movement costs. Reserve also buffers non-feeding periods with energy reserves to continue paying maintenance costs [see (Sousa et al. 2008)], allowing starving individuals to survive for short time periods.

3) Meeting the energetic demands of maturity and reproduction in later life stages depends on movement decisions in earlier ones. Therefore, life history is closely linked to movement. The internal state of the individual mediates future movement decisions, such as the probability of incurring future indirect movement costs and meeting the necessary energy demands in adulthood. Consequently, internal, individual traits can drive reproduction as a fitness measure over external, environmental cues. In DEB theory, energy allocated to maintenance and growth is fixed, allowing individuals to reproduce while growing (Sousa et al. 2010).

4) Finally, few strengths of IBM central to tackling key challenges in movement ecology are more relevant than the ability to discern individuals by behaviour. This is an essential criterion when attempting to generalise model forecasts at the population level (Louzao et al. 2014). Firstly, adults experience different energetic and thus movement costs to juveniles (Fig. 2). Physical obstacles are easier to overcome with growth, opening new movement options unavailable to juveniles (Rittenhouse & Semlitsch 2006). Therefore, the state of the individual, such as age, relaxes the limits imposed by natural processes like growth. This suggests energy use as the primary mechanism behind growth and other metabolic processes is the common currency connecting individuals. By establishing this currency as the central component defining the individual state, we can build flexible models that bridge the relationship between movement costs and individual behaviour. Secondly, this relationship assumes the indirect costs of movement are linear to growth; rarely do two animals face identical fitness challenges over their lifetime (perhaps the realistic exception is herds), as juvenile behaviour influences metabolic outcomes during the adult life stage. This relationship is directly related to energy intake during growth. For example, well-fed offspring benefit by growing bigger and faster, outcompeting siblings or conspecifics and more quickly reaching the more resilient adult size (Kilner 2001). Further, satiated adults also benefit from a rich energy supply for maturity, potentially maximizing offspring quantity. This trajectory suggests the ability to effectively meet the energetic demands of different life stages rests on performing well in activities like exploiting available resources. These activities primarily stem from individual movement behaviour, where

emphasis on the individual as the central unit is both well suited and tested in an IBM context.

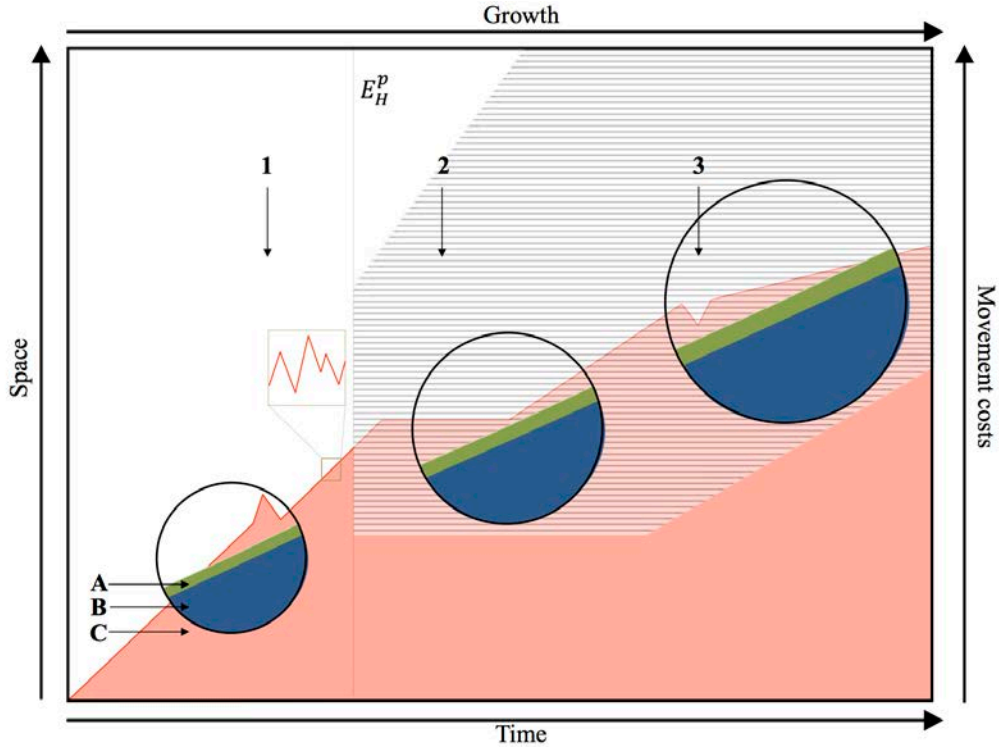

Figure 2. Stylised conceptual diagram of direct and indirect movement costs in time and space throughout the individual life cycle. Circles represent individual body mass of offspring, juvenile, and adult. Direct movement costs (A, green) form a proportion of somatic maintenance costs (B, blue) across growth. Indirect movement costs (C, pink) change as the individual interacts with its environment over time due to increasing movement trade-offs associated with different behaviour, such as foraging, mating, and defending. Hatched polygon represents points in time and space where the individual may anticipate how indirect movement costs influence performance, i.e. consciously change strategy in response to previous maladaptive behaviour, where E_H^p signifies the shift in maturity from offspring to juvenile and the onset of adaptive movement, e.g. dispersal events. Numbers represent different behavioural events (described in main text).

The i_{DEB} primer for modelling individual movement

The primary metabolic pathways

In DEB theory, flows of energy ($\dot{p}$) and mass ($\dot{J}$) from food are tracked through time to predict the individual state in terms of growth (structure, V, i.e. volume of body tissue built during growth and which requires maintenance), body condition (reserve, E, the chemical intermediary between the transformation of food and the growth and maintenance of structure), and maturity [E_H, the energy invested in increasing the maturation state, i.e. energetic costs of development, all of which is dissipated (Kooijman 2010)]. Temperature (T) influences all rates according to the Arrhenius model. Food (X) is eaten ($\dot{p_X}$) then converted ($\dot{p}_A$) to reserve, which is subsequently mobilized to fuel the rest of the metabolism. Reserve is readily available pools of generalised compounds, rather than simply energy or fat storage, contained within individual body cells and collectively, per structural volume, measured as reserve density, $[E]$. Food intake scales with food density following a functional response f (Table 1), whereby either searching or handling limits individuals as f increases from 0 to 1, respectively. Following an allocation rule (κ rule), reserves are mobilised ($\kappa\dot{p}_C$) to structure via the natural hierarchy of cell metabolism—first to somatic maintenance ($\dot{p}_M$) then to growth ($\dot{p}_G$). The remaining fixed fraction ($(1-\kappa)\dot{p}_C$) of mobilised energy ($\dot{p}_R$) then fuels maturation and reproduction. Animals switch between three maturity stages—embryo, juvenile, and adult—defined by maturity thresholds representing the cumulative energy invested in maturation. Energy is also invested in maintenance of a given level of maturity ($\dot{p}_J$) and, once reaching puberty, excess energy beyond maturity maintenance costs is invested in reproductive biomass ($\dot{p}_R$). See Fig. 4 in Kearney et al. (2013) for a schematic breakdown of the above processes.

In DEB theory, reserve dynamics drive metabolism. The rate of assimilated food into energy $\dot{p}_A$ follows the Holling Type II functional response (Holling 1959) f

$$[\dot{p}_A] = \frac{f\{\dot{p}_{Am}\}}{L} \tag{1}$$

where $\{\dot{p}_{Am}\}$ is the maximum assimilation rate and the volumetric body length $L \equiv V^{\frac{1}{3}}$. Parameters surrounded by square [*] and curly {*} parentheses are per volume and surface area, respectively. Energy is then mobilised from reserves with a constant fraction going to somatic maintenance and somatic growth

$$\kappa[\dot{p}_C] = \frac{\dot{v}[E]}{L} - \dot{r}[E] \tag{2}$$

where $\dot{v}$ is energy conductance of mobilised reserve and $\dot{r}$ is specific growth rate, i.e. change in structure V over time

$$\frac{\delta V}{\delta t} = V\dot{r} = V\frac{\frac{[E]\dot{v}}{L} - \frac{[\dot{p}_M]}{\kappa}}{[E] + \frac{[E_G]}{\kappa}} \tag{3}$$

with $[\dot{p}_M]$ the somatic maintenance cost (Eq. 5) and $[E_G]$ the cost of producing structural tissue (both biomass and overhead costs). This relationship means growth ($\dot{r}$) dilutes reserve levels, measured as reserve density per volume $[E]$, as it rises and falls with incoming energy $[\dot{p}_A]$ minus energy used for metabolic processes $[\dot{p}_C]$, giving the reserve dynamics equation

$$\frac{\delta[E]}{\delta t} = [\dot{p}_A] - [\dot{p}_C] \tag{4}$$

Maintenance

Heat, water, and CO_2 are expelled as products from the costs of maintaining the volume $[\dot{p}_M]$ and surface $\{\dot{p}_T\}$ of structure

$$[\dot{p}_M] = \left([\dot{p}_M] + \frac{\{\dot{p}_T\}}{L}\right) \tag{5}$$

Further costs include the overheads of reproduction, feeding (heat increment of f), and growth $\dot{p}_G$, including growth overhead costs and tissue biomass

$$[\dot{p}_G] = \kappa[\dot{p}_C] - V[\dot{p}_M] \tag{6}$$

while maturity maintenance $\dot{p}_J$ from $(1-\kappa)\dot{p}_C = \dot{p}_J + \dot{p}_R$, measured by energy dissipated as heat, contributes to maintaining the current and transitioning to the next maturity level

$$\dot{p}_J = \begin{cases} E_H\dot{k}_J, & E_H \leq E_H^p \\ E_H^p\dot{k}_J, & E_H > E_H^p \end{cases} \tag{7}$$

where $\dot{k}_J$ is a coefficient controlling the rate of maturity maintenance. The organism first pays maturity maintenance and, in an immature individual, the remaining flux feeds further increases in maturity

$$\dot{p}_R = (1-\kappa)\dot{p}_C - \dot{p}_J \tag{8}$$

Growth

Animals grow in structural length L (~ maximum L_m) with $\dot{r}$ (Eq. 3) only after paying maintenance $\dot{p}_M$; maintaining and growing cells incurs growth costs of new biovolume, calculated as an energy investment ratio g

$$g = \frac{[E_G]}{\kappa[E_m]} \tag{9}$$

where $[E_m]$ is maximum reserve density $[E]$ when $f = 1$. Reserve density $[E]$ is scaled to e to interpret changes in f as animals encounter food at different densities over time, giving

$$\frac{\delta e}{\delta t} = \frac{\delta \frac{[E]}{[E_m]}}{\delta t} = \frac{\dot{v}(f - e)}{L} \tag{10}$$

so under steady state, i.e. when food is constant, $f = e$. In the standard DEB model, body shape remains constant (isomorphic) during growth. Therefore, the body surface area is proportional to volume $V^{\frac{2}{3}}$. Following Eq. 3 so that $\frac{\delta L}{\delta V} = \frac{L\dot{r}}{3}$ given $L \equiv V^{\frac{1}{3}}$, an isomorphic animal increases in body length under constant food following

$$\frac{\delta L}{\delta t} = \frac{\dot{v}}{3} \cdot \frac{e - \frac{L}{L_m}}{e + g} \tag{11}$$

Simulating individual movement behaviour using i_{DEB}

This section details the step-by-step procedure of simulating an hypothetical animal in any habitat at any time and space scale. This includes the main energetic processes driving its movement as it interacts with its environment following DEB theory energy allocation rules, including direct and indirect movement costs. Figure 3 shows possible habitat arrangements seen in the field and associated spatial landscapes that the simulation model can emulate. Table 2 shows the related metabolic processes and equations for each simulation time step. Individuals do not respond directly to DEB variables; rather, the DEB dynamics fuel metabolism, which influences the overall movement strategy. At each time step, our hypothetical animal executes the following rules:

1. Pay somatic maintenance costs (Eq. 5) following the reserve dynamics (Eq. 4). By following the i_{DEB} framework, energy for paying maintenance costs retains its allocation rule across space and time. Maintenance costs scale with structural volume, so are faithful to changes in size as the individual grows. Direct movement costs (including feeding) are paid as a constant fraction of somatic maintenance (Fig. 2). These costs are volume specific and scale with movement in space because maximum movement (step length) depends on the size of the individual.

2. Find and eat food, then assimilate this into useable energy following Eq. 1 to fill reserves. Reserve is mobilised to supply the primary metabolic processes of the animal and also buffers starvation periods.

3. Grow structure (Eq. 3) and length (Eq. 11) from mobilised reserve. Growth competes with somatic maintenance for energy following the natural hierarchy of metabolic organisation.

4. Develop maturation E_H following the reserve dynamics (Eq. 8) according to Eq. 7. As a juvenile, maturity is stored as information and converted to a reproduction buffer when reaching adulthood. Because energetic costs change with growth, juveniles must build maturity before reaching adulthood after paying soma (somatic maintenance and growth). Paying maturity maintenance as a juvenile ensures the body uses energy to meet the complex and heavy demands of reproduction (Sousa et al. 2008). Maturation energy converts to a reproduction buffer of eggs and embryo reserve once mature. Low energy intake during growth means animals struggle to reach their maturity threshold and are unable to reproduce. Because paying somatic maintenance is sufficient for survival, malnourished animals alleviate the constraint of maintaining maturity. This trade-off means survival paves a different energetic landscape to reproduction. Producing offspring incurs the cost of maintaining somatic maintenance plus sufficient surplus energy to invest into reproduction buffer.

5. Produce offspring if mature and reproduction buffer meets energetic demands of the offspring yield.

The above sequence is a facultative example of integrating energy use simply as a mechanism driving animal movement into an accessible individual-based modelling platform. The i_{DEB} primer can apply user-defined individual behaviour, such as movement patterns, e.g. correlated random walk, alternative foraging strategies, memory of resource patches, different vigilance levels, and tolerance to microclimates. These contribute to individual fitness outcomes as different movement and home range patterns emerge. The metabolic engine operates as a secondary, unseen layer, but drives the individual internal state, including direct and indirect movement costs—the crucial component of the movement framework. By constructing a framework of metabolic theory-based movement, the i_{DEB} primer offers solutions to three common problems in animal movement models. Firstly, the primer is based on general theory, so escapes intensive data and time costs of empirical energetics models. Secondly, the primer applies only 12 parameters (the standard DEB model) to capture the full life cycle of the individual, where other empirical models are often parameter rich and, as with some IBMs in ecology, species- and problem-specific. Finally, a general primer underpinned by the unifying currency of energy use is plastic to different organisms and scenarios, allowing for greater predictive power in unpredictable environments, such as with changing climates.

Table 2. Primary metabolic processes occurring at each model time step of an hypothetical simulated animal moving in space and time as it interacts with its environment. The internal energetic state of the animal is governed by the DEB theory equations, which drives its movement decisions in response to direct and indirect movement costs.

Metabolic process at each model time step	**Reference to DEB theory equation**	**Energy use by individual**
Somatic maintenance	$[\dot{p}_M] = \left([\dot{p}_M] + \frac{\{\dot{p}_T\}}{L}\right)$ (5)	Pay maintenance following reserve dynamics Direct movement costs (including feeding) are constant fraction of maintenance (Fig. 2) Volume specific Scales in space because step length depends on size of animal
Reserve dynamics (E)	$\frac{\delta[E]}{\delta t} = [\dot{p}_A] - [\dot{p}_C]$ (4)	Energy reserve driving maintenance, growth, and reproduction Reserve buffers starvation periods
Assimilation (feeding)	$[\dot{p}_A] = \frac{f\{\dot{p}_{Am}\}}{L}$ (1)	Convert food into energy

Growth (structure, *V*)	$$\frac{\delta V}{\delta t} = V\dot{r} = V\frac{\frac{[E]\dot{v}}{L} - \frac{[\dot{p}_M]}{\kappa}}{[E] + \frac{[E_G]}{\kappa}}$$ (3)	Grow structure (*V*) following reserve dynamics Growth competes with somatic maintenance for energy following the natural hierarchy of metabolic organisation
Growth (length)	$$\frac{\delta L}{\delta t} = \frac{\dot{v}}{3} \cdot \frac{e - \frac{L}{L_m}}{e + g}$$ (11)	Grow body length following reserve dynamics
Maturation	$$\dot{p}_J = \begin{cases} E_H \dot{k}_J, & E_H \leq E_H^p \\ E_H^p \dot{k}_J, & E_H > E_H^p \end{cases}$$ (7)	Maturity is stored as energy information as a juvenile and converted to reproductive buffer as an adult
Reproduction	$$\dot{p}_R = (1 - \kappa)\dot{p}_C - \dot{p}_J$$ (8)	Develop maturation according to life stage Produce offspring when reproduction buffer meets energetics demands of offspring yield

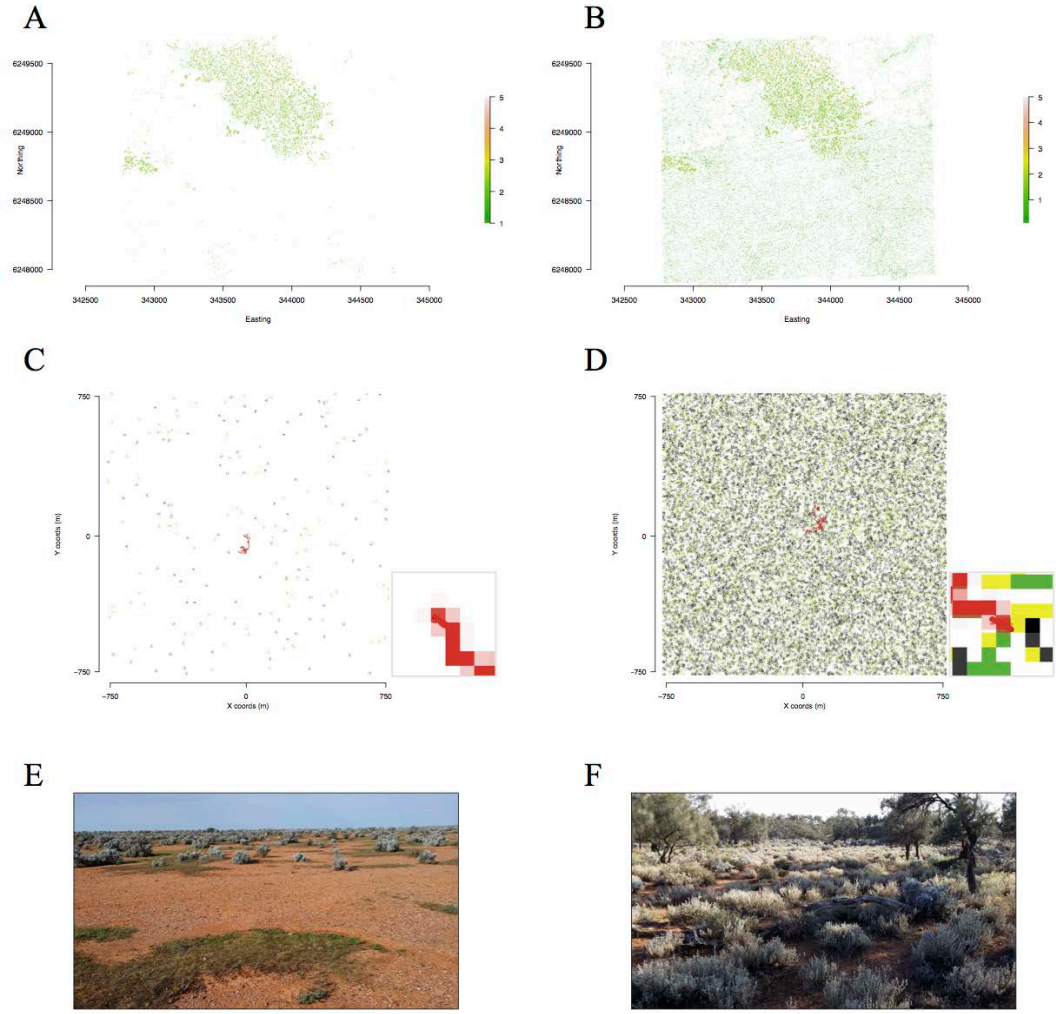

Figure 3. Examples of contrasting landscape and habitat structures that animals must negotiate in space and time. Top: Light Detection and Ranging (LIDAR) data of an arid, terrestrial environment in South Australia (139°21'E, 33°55'S) highlighting A) large vegetation in contrast to B) available small vegetation for the same site that acts as available refuges for animals throughout the day. Middle: Examples of simulated model landscapes showing C) low and D) high resource (food and shade) density to emulate the conditions seen in A) and B). Insets show simulated animal movement paths using a spatial movement framework that incorporates the i_{DEB} primer. Bottom: Field images of the study site in A) and B) showing the visible differences between E) low and F) high resource density within a habitat.

Concluding thoughts and future directions

Incorporating energetics into movement models at the individual level underpins essential and direct processes driving movement, such as intake rate, prey handling, and growth across different scales. By integrating a simulation model with metabolic theory-based movement framework based on general, physiological principles, the i_{DEB} primer isolates these essential principles to build the internal engine shaping movement potential. Movement research is beginning to embrace these same principles by explicitly addressing energetic costs (Shepard et al. 2013; Bonte et al. 2012; Bonnell et al. 2013; Hawkes et al. 2013; Sachs et al. 2013; Pauli et al. 2013; Wilson et al. 2013; Wood et al. 2013). As a field, it has identified what it needs to progress: explicit focus on mechanisms (Holyoak et al. 2008; Giuggioli & Bartumeus 2010) and scales (Benhamou 2014) simplified by exploiting the strengths of process-based approaches such as IBMs (Bauer & Klaassen 2013). A major limitation when summarising energetics in movement models is supplying the detail to capture the system, but still linking behaviour to fitness. The foundations to address these areas are established (Nathan et al. 2008; Benhamou 2014), but have not yet been executed in a practical, theory-based movement framework; here, we provide a unifying, process-based energetics framework (i_{DEB}) underpinned by internal mechanisms linked to fitness consequences, sophisticated enough to capture the complexity of movement simply across scales, but potentially flexible to other complementary mechanisms that may also drive individual movement potential, such as memory to navigate unpredictable resources (Fig. 1). The i_{DEB} primer applies user-defined individual behaviour to establish the movement strategy, e.g. correlated random walk. This allows modellers to match the resolution and scale of the model to represent the ecological problem at hand. The metabolic engine operates as a secondary, hidden layer, but drives the individual internal state, including direct and indirect movement costs, as the crucial component of the movement framework. Consequently, the i_{DEB} primer directly addresses three critical areas in movement ecology: 1) offers a practical solution to the limitation of modelling movement from ad hoc energy estimates; 2) supplements our growing knowledge of energetic costs obtained from improved biologging technology that bolsters the direct feedback between individual movement and energetic landscapes; and 3) improves how we interpret movement costs across different ecosystems by unifying energy use by individuals using common principles. Thanks to modern computing power, we have surpassed previous limitations of intensive fine to coarse scale models. Faster, more powerful IBMs with multiple dynamic data input are now possible, pushing energetics IBMs (i_{DEB}) as a next-gen extension to the forefront of modelling complex movement behaviour.

Acknowledgements

We thank Volker Grimm, Mark Burgman, and Michael Bode for helpful comments, discussion, and revisions.

Funding

MM was funded by an Australian Postgraduate Award (APA) and the Centre of Excellence for Biosecurity Risk Analysis.

Authors' contributions

MM conceived the idea and wrote the manuscript, figures, and tables.

Competing interests

The authors declare they have no competing interests.

Ethics approval and consent to participate

Not applicable.

3

An individual-based model of ectotherm movement integrating metabolic and microclimatic constraints

Matthew Malishev[1,2*], C. Michael Bull[3], & Michael R. Kearney[2]

[1] *Centre of Excellence for Biosecurity Risk Analysis,* [2] *School of BioSciences, University of Melbourne, Parkville, Melbourne, 3010, Australia*

[3] *School of Biological Sciences, Flinders University, Adelaide, 5001, Australia*

This chapter appears as 'Malishev, M. Bull, C. M. & Kearney, M. R. Individual-based energy budgets as next-generation extensions for modelling animal movement across scales, *Methods in Ecology and Evolution*. In press'.

[*]Corresponding author: matthew.malishev@gmail.com

Waarom vind je niet Skuumkoppe op het vasteland?

Anonymous

Table of Contents

Abstract 61
Introduction 62
Overview 63
Purpose 63
Entities, state variables, and scales 65
Energy budget model 65
Heat budget model 68
Decision-making IBM 68
Habitat 69
Microclimate 73
Scales 73
Process overview and scheduling 73
Design concepts 74
Basic principles 74
Emergence 74
Adaptation 75
Fitness 75
Prediction 75
Sensing 75
Stochasticity 76
Observation 76
Details 76
Initialisation 76
Input data 78
Habitat 78
Microclimate 78
Submodels 78
Activity budget 78
Results 78
Does the model capture realistic home range area and behaviour? 78
How does movement strategy shape activity budgets? 81

How does movement potential affect individual metabolic outputs? 82
Does the individual heat budget model capture realistic thermal changes and costs? 82
Discussion 85
Limitations and future work 89
Conclusions 90
Acknowledgements 91
Funding 91
Authors' contributions 91
Data accessibility 91
Competing interests 91
Ethics approval and consent to participate 91

Abstract

An understanding of the direct links between animals and their environment can offer insights into the drivers and constraints to animal movement. Constraints on movement interact in complex ways with the physiology of the animal (metabolism) and physical environment (food and weather), but can be modelled using physical principles of energy and mass exchange. Here, we describe a general, spatially explicit individual-based movement model that couples a nutritional energy and mass budget model [Dynamic Energy Budget (DEB) theory] with a biophysical model of heat exchange. This provides a highly integrated method for constraining an ectothermic animal's movement in response to how food and microclimates vary in space and time.

The model uses R to drive a NetLogo individual-based model together with microclimate and energy- and mass-budget modelling functions from the R package *NicheMapR*. It explicitly incorporates physiological and morphological traits, behavioural thermoregulation, movement strategies, and movement costs. From this, the model generates activity budgets of foraging and shade-seeking, home range behaviour, spatial movement patterns, and life history consequences under user-defined configurations of food and microclimates. To illustrate the model, we run simulations of the Australian sleepy lizard Tiliqua rugosa under different movement strategies (optimising or satisficing) in two contrasting habitats of varying food and shade (sparse and dense). We then compare the results with real, fine-scale movement data of a wild population throughout the breeding season.

Our results show that 1) the extremes of movement behaviour observed in sleepy lizards are consistent with feeding requirements (passive movement) and thermal constraints (active movement), 2) the model realistically captures majority of the distribution of observed home range size, 3) both satisficing and optimising movement strategies appear to exist in the wild population, but home range size more closely approximates an optimising strategy, and 4) satisficing was more energetically efficient than optimising movement, which returned no additional benefit in metabolic fitness outputs.

This framework for predicting physical constraints to individual movement can be extended to individual-level interactions with the same or different species and provides new capabilities for forecasting future responses to novel resource and weather scenarios.

Keywords: Individual-based model; movement ecology; biophysical ecology; spatial; dynamic energy budget; microclimate; thermoregulation

Introduction

Forecasts of individual responses to current and future climates and habitat modification should ideally be based on an explicit understanding of the physiological limits of animals in their environments (Kearney & Porter 2009; Helmuth et al. 2005; Porter et al. 2006; Buckley 2008; Sears et al. 2016). Exploring how individual traits interact with habitat features and environmental drivers, such as resources and microclimates, offer useful insights into individual behaviour, activity periods, and range shifts (Stevenson 1985b; Crozier & Dwyer 2006; Buckley 2008; Vickers et al. 2011). On short time scales, foraging animals must minimise exposure to extreme environments by exploiting microclimatic variation in their habitats, thereby avoiding physiological hazards such as overheating, cold stress, and desiccation (Huey 1991; Helmuth & Hofmann 2001; Franklin et al. 2007; Sears et al. 2011). Potential behavioural responses to such physiological constraints depend on the spatial configuration of resources in relation to microclimates. For example, animals may adjust body temperature while foraging by utilising shade (Shelly 1982), select oviposition sites by substrate temperature (Davies et al. 2006), and switch between different activities, such as basking and foraging, to navigate microhabitats (McClure et al. 2011) and respond to seasonal changes in habitat suitability (Christian et al. 1983). The extent to which an animal risks exposure to extreme environments depends, in turn, on its nutritional and hydration state (Adolph & Porter 1993; Kearney et al. 2010; Clissold et al. 2013).

By estimating how resources and microclimates drive animal movement, we can build a more realistic picture of animal displacement, habitat use, and ecology. Individual-based models (IBMs) are useful tools for exploring how environmental constraints influence animal movement in space and time. For example, they have been used to predict how the spatial distribution of resources drives home range behaviour (Mitchell & Powell 2012) and how habitat features motivate patch selection (Railsback et al. 1999). In doing so, IBMs can lead to a predictive understanding of the environmental conditions that allow species to invade new habitats and their subsequent shift in distribution (e.g. climate change; Pearson et al. 2006; Randin et al. 2006; see Sears & Angilletta 2015).

Owing to the multiple constraints imposed on animals, movement models can be complex. Interacting drivers, e.g. resources and cognition (Müller et al. 2011), are often estimated with empirically derived functions (Schurr et al. 2012). Such empirical models are necessarily limited in their generality. We can be more general by capturing and bounding these interactions according to basic physical principles. The fields of metabolic theory and biophysical ecology provide this basis for understanding environmental constraints on animal movement. Metabolic theory (Nisbet et al. 2000; Brown et al. 2004) aims to understand how organisms take up energy and matter from their environment and allocate them to the processes of growth, development, maintenance, and reproduction. Similarly, the principles of biophysical ecology (Porter et al. 1973; Gates 1980) can categorise how these processes are constrained by the thermal and hydration state of an individual. Together, metabolic theory and biophysical ecology provide a complementary understanding of how internal metabolic requirements and

external patterns in resources and microclimates constrain movement options (Kearney et al. 2009; Kearney et al. 2013).

Our approach builds on previous work integrating biophysical ecology and Dynamic Energy Budget (DEB) theory (Kearney et al. 2010; Kearney 2013) by being explicit about space and movement costs. As such, we aim to link the physical environment and physiological traits with movement-related phenomena, such as home range behaviour and displacement. We outline an energy and mass budget-driven individual-based model (Individual Dynamic Energy Budget Movement model; IDEBM) of an ectothermic animal moving in space and time using the individual-based modelling (IBM) protocol (Grimm et al. 2006). We explore how two contrasting movement strategies driven by physiological constraints generate different movement and home range patterns: optimising, where animals move during all thermally available activity times, and satisficing, where animals move only when sufficiently hungry based on their metabolism. We do this under two contrasting densities of food and shade.

The model comprises three coupled sub-models that operate simultaneously: 1) a metabolic model of an animal's energy and mass balance, including direct movement costs, based on a general theory of resource uptake and use by organisms (DEB theory; Kooijman 2010), 2) a transient heat budget model for calculating changes in individual thermal state in response to varying habitat microclimates, and 3) a decision-making model driving movement in space and time. We compare simulated movements to real movement data of 60 adult sleepy lizards for the 2009 breeding season with two major aims: 1) to test whether the IDEBM model can predict movement and home range patterns based on individual physical limits under different food and microclimate constraints; and 2) to interpret the movement strategy that real individuals in the population use to navigate these movement constraints.

Overview

Purpose

The focal species is *Tiliqua rugosa* (Scincidae), a medium-sized herbivorous lizard from Australia, for which we have detailed field movement data [see 'Data collection' in Appendix A and (Kerr & Bull 2006) for information on data collection and study site]. In the model, the metabolic and thermal state of individuals updates on 2-minute time steps to match observed data (see 'Data collection' in Appendix A and Kerr et al. 2004) as they switch among different activity states of searching (including socialising), feeding (including handling), and sheltering (resting in shade, basking, and 'sleeping') depending on whether in sun, food, or shade patches. These behavioural categories define their activity budget in space and time over a continuous time scale of the entire breeding season (Sep to Dec; 117 days). Individuals follow a correlated random walk (CRW) movement within a 2D model landscape of randomly distributed and clumped food and shade patches interspersed throughout open sun patches. We estimate distributions of shade patches from LIDAR data of the study site by combining a digital surface model (DSM) and digital terrain model (DTM) to reflect the spatial arrangement of habitat

features, thus providing a realistic picture of the thermal landscape. Hourly microclimates are computed with the *NicheMapR* microclimate model based on daily weather inputs from Australian historic weather data queried from continent wide 0.05º gridded products [Australian Water Availability Project, AWAP (Jones et al. 2009) and a daily wind database (McVicar et al. 2008). See 'NicheMapR microclimate model overview' in Appendix A and model overview in supporting material from (Kearney 2013)]. These hourly predictions are then splined to 2-minute intervals and used to update the landscape microclimate at each time step. See Fig. 4 for input pathways of microclimate data. Functions for the energy and mass budget calculations are part of the *R* (R Development Core Team 2015) package *NicheMapR* (https://github.com/mrke/NicheMapR). Metabolism is modelled using the function 'DEB.R' and a transient heat budget 'onelump_varenv.R' driven by the environmental output from the 'microclimate' function updates the individual thermal state (https://github.com/darwinanddavis/MalishevBullKearney).

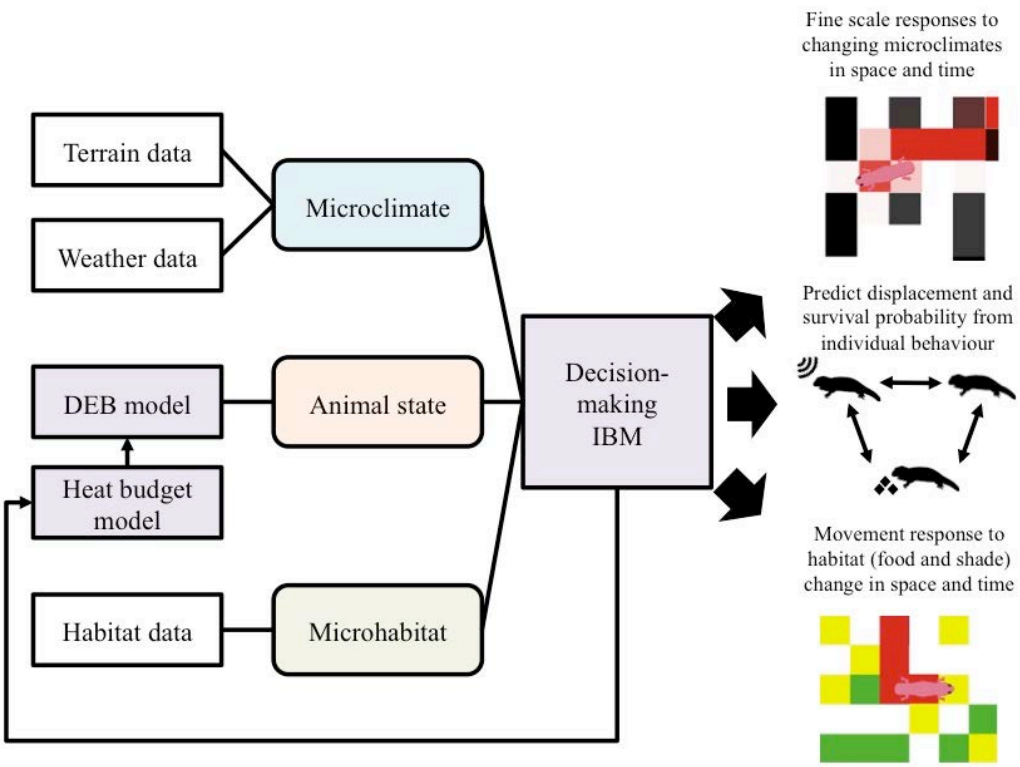

Figure 4. Schematic of data and model inputs of the IDEBM model. Examples of weather data: monthly to annual temperatures microclimate; Microclimate: local solar and infrared radiation temperature, ground and air temperature (Table 4); DEB model: See Tables 3 and 6; Heat budget model: See Table 4; Habitat data: food and shade patches (Table 5). The DEB and heat budget models update with the time steps of the decision-making IBM to form feedback loops. All weather and habitat data are modeled on the sleepy lizard habitat (139º21'E, 33º55'S). Animal data are for the adult sleepy lizard.

The decision-making IBM (Appendix A1) is implemented in Netlogo (Wilensky 1999) and simulated from *R*. The energy and heat budget models (Appendix A2) described

above are first implemented in *R*, then integrated with the IBM simulations using the *RNetlogo* package (Thiele et al. 2012). The detailed breakdown of the energy and mass budget is presented in Chapter 2. Italicised text denotes DEB and *NicheMapR* variables and parameters, e.g. *E*.

Entities, state variables, and scales

The model has three entities—individuals, habitat, and microclimate—simultaneously driven by the energy budget (DEB), the heat budget (*NicheMapR*), and the decision-making model (IBM).

Energy budget model

The energy budget model uses individual morphology and physiology data with theory-driven principles of energy and mass balances to update the internal metabolic state of the animal, including food processing and intake rates, somatic maintenance and movement costs, and growth and reproductive rates. We incorporate the core assumptions and basic rules of DEB theory (see Chapter 2) as a coupled energy and mass budget model (see Fig. 3 in Kearney & Porter 2009) into an IBM that updates the individual internal state on 2-minute time steps. This then drives movement and changes in metabolism (including direct movement costs) to generate changes among activity states and the overall activity budget, home range emergence, and habitat use. It thus provides a way to compute the animal's motivational state for movement (hunger, reproduction) and predict fitness consequences (growth, reproduction, condition) of different movement strategies. Table 3 shows the DEB parameters estimated using the 'covariation method' (Lika et al. 2011) from animal data and Chapter 2 shows a summary of DEB procedures.

Table 3. Individual variables and parameters of the DEB model (Kooijman 2010) parameterised for the sleepy lizard, *Tiliqua rugosa*. Parameters are estimated from available animal data (Table 4). Dimensions: — dimensionless; *J* Joules; *L* structural length; *t* time. Units: *d* days; *cm* centimetres. Square [*] and curly {*} parentheses denote parameters per volume and surface area, respectively; dot accents denote rates.

Parameter	Value	Dimension	Unit	Description
$\dot{p}_X$	330.04	$J\,t^{-1}$	d	flux for food uptake from environment to individual
$\dot{p}_A$	280.53	$J\,t^{-1}$	d	flux for food assimilated to energy, where $\{\dot{p}_{Am}\}$ is the maximum assimilation rate ($f = 1$).
κ	0.84	—	—	kappa rule of energy allocation
$\dot{p}_C$	232.51	$J\,t^{-1}$	d	energy flux mobilised from reserve. $\kappa\dot{p}_C$, energy allocated to soma; $(1-\kappa)\dot{p}_C$, energy allocated to maturity
$\dot{p}_M$	117.56	$J\,t^{-1}$	d	flux for somatic maintenance
$\dot{p}_G$	78.71	$J\,t^{-1}$	d	flux for growth
g	1.95	—	—	energy invested into growth (per maximum reserve $[E_m]$)
$\dot{p}_J$	12.49	$J\,t^{-1}$	d	flux for maturity maintenance
$\dot{p}_R$	23.75	$J\,t^{-1}$	d	flux for maturation or, once fully matured, for reproduction
v	0.03	$L\,t^{-1}$	$cm\,d^{-1}$	energy conductance
r	0.00017	t^{-1}	d	specific growth rate (of structure)
$[E_G]$	7772	$J\,L^{-3}$	cm^{-3}	cost of structural tissue
$\{F_m\}$	6.5	$L^{-2}\,t^{-1}$	$cm^{-2}\,d^{-1}$	maximum surface-specific searching rate of food
κ_X	0.85	—	—	energy assimilation efficiency

κ_R	0.95	—	—	reproduction efficiency
$\{\dot{p}_T\}$	0	$J\,L^{-2}\,t^{-1}$	$cm^{-2}\,d^{-1}$	flux for surface-area specific somatic maintenance
$\dot{k}J$	0.002	t^{-1}	d	coefficient for rate of maturity maintenance
E_H^b	102980	J	—	maturity threshold at birth
E_H^p	249580	J	—	maturity threshold at puberty
E_R	0	J	—	reproduction buffer

Heat budget model

The heat budget model computes heat exchange between animal and environment based on morphology (e.g. body mass, length, surface area, and solar reflectance), physiology (e.g. metabolic rate, rates of food intake and processing), behaviour (e.g. foraging temperature thresholds), and environmental conditions (e.g. ground and air temperature, wind speed, solar radiation, and infra-red radiation) (Kearney & Porter 2004). Following Porter et al. (1973), we compute body temperature T_b as the sum of the steady y_s and transient y_t thermal state, $T_b = y_s + y_t$

$$T_b = \frac{j}{k} + \left(T_b - \frac{j}{k}\right) e^{-kt} \text{ and } \frac{\delta T}{\delta t} = j - kT_b$$

where

$$j = \left(\frac{Q_{sol} + h_c A_{conv} T_{air} + h_r A_{rad} T_{rad}}{C}\right)$$

$$kT_b = T_b \left(\frac{h_c A_{conv} + h_r A_{rad}}{C}\right)$$

k is a time constant, Q_{sol} is the total solar radiation absorbed, A_{conv} and A_{rad} are the surface areas for convective and radiative heat transfer, respectively, C is the thermal capacitance (specific heat capacity × mass), h_c is the convection coefficient, h_r is the radiation coefficient (approximated in our model by a Taylor series expansion $4\epsilon\sigma\left(\frac{T_b+T_{rad}}{2}\right)^3$ with emissivity ϵ and Stefan-Boltzmann constant σ). Note, for simplicity, we here neglect metabolism, evaporation, and conduction, but they can be incorporated if required (Porter et al. 1973). The time constant $\frac{1}{k}$ accounts for the response time of T_b between steady and transient states that influences heat transfer through the animal depending on individual thermal mass. See Table 4 for individual parameters and variables, Appendix A2 for detailed heat budget *R* code, Kearney et al. (2010) for complementary ways to integrate biophysics with energetics (DEB theory), and Kearney et al. (2013) for applying the combined framework in a spatially implicit manner with a steady-state heat budget model to the Cunningham's skink, *Egernia cunninghami*.

Decision-making IBM

The decision-making IBM simulates CRW movement in a 2D model landscape of randomly distributed food and shade, where environmental conditions update the coupled energy and heat budget to define the individual internal state and thus inform future behaviour and movement potential. Individuals follow either an optimising or satisficing movement strategy and move only when within their physiological limits (T_{lower} and T_{upper}, Table 4): optimising animals move during all available activity hours, whereas satisficing animals move only when hungry [gut fullness level is < 75% (Kearney et al. 2013)] and thus avoid socially-motivated movement. We choose these strategies for their relationship with decision-making and animal behaviour studies, i.e. foraging under

environmental extremes is risk-taking and involves trade-offs. Individuals switch between three activity states depending on their current state and whether in food, sun, or shade: searching for food or shade (Searching), consuming food (Feeding), or sheltering in shade (Resting). For example, under either strategy, being in open sun while Searching or Feeding can push the animal outside its physiological limits (T_{lower} and T_{upper}), forcing it to seek refuge in shade.

Optimising animals have the additional socialising activity state, which involves the same CRW movement, but motivated by social and territorial requirements categorised within Searching. Socialising is included in this strategy as it can contribute to dispersal potential and behavioural adaptation within an animal's overall activity budget (Wang & Grimm 2007; Kays et al. 2015; Bateman et al. 2015; Spiegel et al. 2016). Additional traits include perception range for locating food and shade patches and activity counters for time spent searching, feeding, and sheltering. See Table 5 for individual-based parameters and variables.

Habitat

The habitat variables are food, shade, and sun patches distributed in the environment (Table 5). Food is either a small or large food item per open sun patch and is either sparsely or densely distributed under the two movement strategies. Food intake by individuals is determined by handling time (patch residence). Shade is single patches and estimated from vegetation inputs from Light Detection and Ranging (LIDAR) data of the study site.

Table 4. Individual variables and parameters of the transient heat budget model. Units: — dimensionless; *C* Celsius; *J* Joules; *kg* kilograms; *m* metres; *s* seconds; *t* time; *W* watts.

Parameter	Unit	Description
T_b	$°C$	core body temperature
T_{lower}	$°C$	lower body temperature bound of activity range
T_{upper}	$°C$	upper body temperature bound of activity range
σ	$°C$	Stefan-Boltzman coefficient
cp	$J kg^{-1}$	specific heat of flesh
$emis$	—	emissivity of skin
Fo_e	—	configuration factor of animal to absorb infrared radiation
ρ	$kg\ m^{-3}$	density of animal mass
abs	—	solar absorptivity of animal
Q	W	heat fluxes
y	$°C$	thermal state of animal: steady y_s and transient y_t
j	$°C$	temperature constant
k	$1/s$	time constant
C_1	—	dimensionless constant
e^{-kt}	—	dimensionless rate of T_b change

Table 5. State variables and parameters of model individuals, habitat, and microclimate. Units: — dimensionless; *C* Celsius; *J* Joules; *m* metres; *s* seconds; *t* time; *T* temperature; *W* watts. As in 2. Entities, state variables, and scales.

Entity	Variable/ parameter	Notation		Unit	Description
		DEB	IBM		
Individual	Reserve density	$[E]$	`reserve-level`	$J\ cm^3$	DEB individual state variable that relates to nutritional state and contributes to part of the biomass. Dynamics of reserve flux is determined by the kappa (κ) rule of energy allocation that controls energy allocation to essential metabolic processes, such maintenance, growth, maturity, and reproduction. $[Em]$ is maximum reserve density. See Eq. 4 in Appendix A.
	Structure	V	—	cm^3	A DEB state variable proportional to physical length that contributes part of the biomass. Structure increases (growth) based on flux of mobilised reserve. See Eq. 11 in Appendix A. Growth is modelled by the DEB growth equation, the parameters of which are estimated from individual traits, e.g. snout to vent length (SVL). See Table 6 for empirical data used to parameterise the DEB model.
	Maturity	E_H	—	J	A DEB individual variable that determines the maturity stage of animal. The case study model considers a mature adult, so $E_H = E_H^p$.

	Movement strategy	—	`Optimising`
			
			`Satisficing`
				—	An IBM parameter defining the movement strategy of the individual in space. Optimising animals include an additional socialising activity state.

	Gut level	E_{sm}	`Gutfull`	$J\ cm^3$	A DEB variable representing stomach capacity that determines the level of food in the animal gut. Parameterised on the Cunningham's skink (Kearney 2012).
	Vision	—	`min-vision`	*Patch* (m^2)	An IBM parameter defining the visual scope of the individual and its encounter probability of food and shade patches in space. `Min-vision` refers to the normal visual scope (10 m) (Auburn et al. 2009).

	Functional feeding response	f	`energy-gain`	—	A DEB individual parameter that defines food (X) intake per encounter rate with food patches. $f(X) = \frac{X}{X+K}$, where $K = \frac{\{\dot{p}_{Am}\}}{\kappa_X\{F_m\}}$ the half saturation coefficient, following (Holling 1959) (see Table 1 for K).
Habitat	Food	X	Yellow patch: small food Green patch: large food	*Patch* (m^2)	Food items vary in size (bites) per food patch. Small and large food items take one (2 mins) or two (4 mins) time steps, respectively (handling time). Food and sun patches represent similar microclimates.
	Shade	—	Black patch	Patch (m^2)	Shade patches are distributed randomly in the model landscape, reflecting typical spatial arrangement in nature.
Microclimate	Solar radiation	*SOLR*	—	$W\ m^{-2}$	A NicheMapR variable. The model environment is loaded with these data prior to simulation runs, updated hourly within NicheMapR, and splined to 2-minute time steps.
	Local air temperature	*TALOC*	—	T (°C)	A NicheMapR variable. Input as per solar radiation.
	Infrared radiation	*IR*	—	$W\ m^{-2}$	A NicheMapR variable. Input as per solar radiation.
	Relative humidity	*RHLOC*	—	%	A NicheMapR variable. Input as per solar radiation.
	Soil temperature	*TS*	—	T (°C)	A NicheMapR variable. Input as per solar radiation.
	Local wind speed	*VLOC*	—	$m\ s^{-1}$	A NicheMapR variable. Input as per solar radiation.

Microclimate

Patches are either shade or open sun (including food) determined by microclimate inputs of air temperature, relative humidity, ground temperature, wind velocity, solar zenith angle, and solar and infrared radiation from microclimate input data of the study site. We calculated microclimates from Australian historic weather data using the *NicheMapR* microclimate model [see model overview in supporting material from (Kearney 2013)], which we pre-computed hourly, then interpolated (splined) to 2-minute time steps during the simulation with the *R* function 'approxfun' from the *stats* package (Chambers et al. 1988).

Scales

One patch is one cell on the model spatial grid (2 m^2; Table 5). Simulations run on 2-minute time steps. Initial microclimate inputs are initialised hourly then projected (splined) to 2-minute time steps.

Process overview and scheduling

Individuals are motivated both to find food (*X*) and to avoid environmental extremes. Food may be small (3 kJ) or large (6 kJ) items with one (2 mins) or two (4 mins) handling time steps, respectively. These energy values reflect the stomach-emptying rate specified by DEB theory following the Holling Type II functional response (Holling 1959). Energy reserves change on each time step as dictated by the reserve (*E*) dynamics of the DEB model relative to body temperature (T_b) (influenced by microhabitat/microclimate) and by whether or not it is feeding in that time step. Movement incurs a direct movement cost estimated from O_2 consumption rates for a similar-sized ectotherm (John-Alder et al. 1986) and converted to maintenance costs per unit of body mass generated by the DEB model (ml O_2 g^{-1} converted to Joules per hour). The reserve level then influences the dynamics of fitness outputs, such as growth, development, and reproduction (see Chapter 2 for summary of DEB parameters and primary metabolic pathways). Individuals also regulate their body temperature within their thermal constraints (Table 4) on each 2-minute time step according to their current location in space, i.e. shade vs. sun patch and the time of day/month. See Figure 4 for data inputs, Figure 5 for schematic of simulation runs, and Appendix A1 for IBM simulation code.

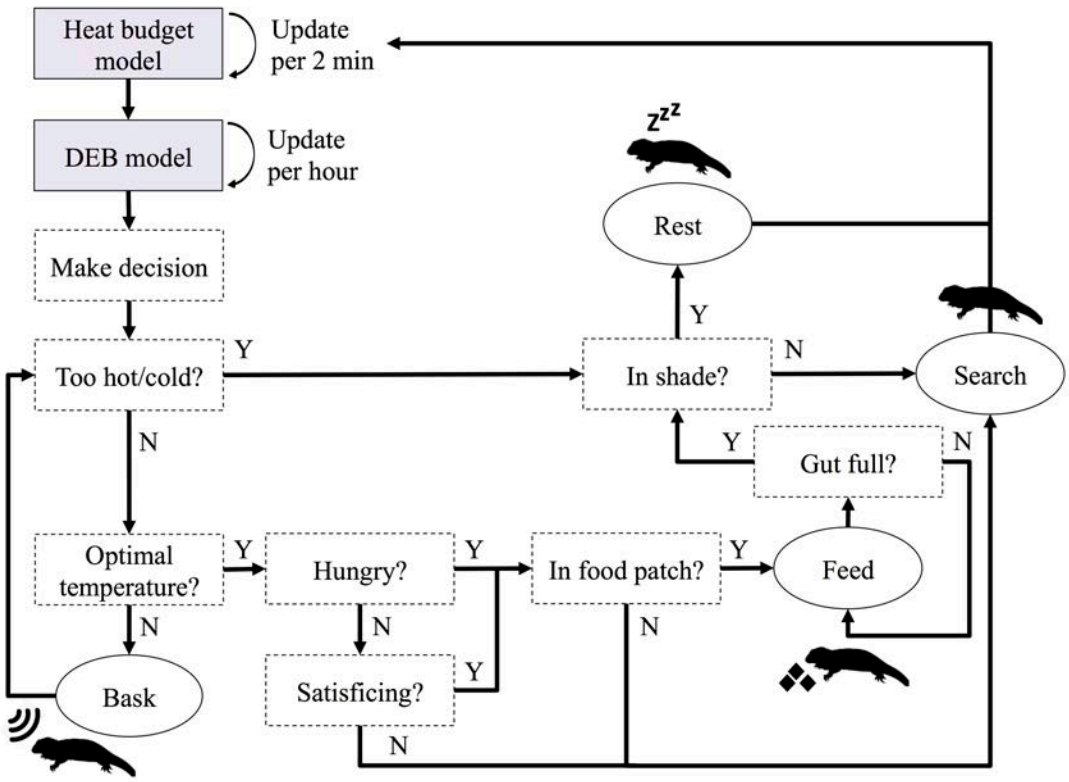

Figure 5. Schematic of decision-making IBM simulation runs. Solid boxes are processes, dashed boxes are individual decisions, and ellipses are individual actions. Searching refers to either searching for food, shade, or socialising, depending on the current thermal or metabolic state or movement strategy of the animal. Hungry refers to whether the gut fullness threshold is < 75%.

Design concepts

Basic principles

The environmental conditions (microclimatic values in the extremes of available shade), animal traits (DEB and the heat budget model), and resource densities (food and shade) are the three model inputs. The individual executes its movement decisions—searching for food or shade (Searching), consuming food (Feeding), or sheltering in shade (Resting) under either an optimising or satisficing movement strategy—in response to changes in these types of input, generating spatial movement patterns and fine-scale behavioural responses to changing constraints (see Fig. 4).

Emergence

Activity and home range patterns emerge from the two movement strategies in space and time in response to microclimate and food constraints. We interpret individual activity states and home range emergence in space using the 95% kernel utilisation (UD) distribution

$$UD'(x, y|t_i) = \frac{UD(x, y, t_i)}{\int_{x',y'} U\,D(x', y', t_i)}$$

where x, y, and t_i are x coordinates, y coordinates, and time for the ith coordinate relocation, respectively. Individual T_b, including the rate of T_b change, and current metabolic state of the animal updates the individual internal state per model time step to drive future movement decisions and thus home range emergence. For example, the individual will seek shade or forage depending on the external environmental temperature and whether within its activity temperature range (T_{lower} and T_{upper}). Based on how the external environment influences the internal individual state, this leads the individual to either displace from its current location in search of shade or food or remain in a resting state in shade to avoid environmental extremes, thus expanding or contracting its home range area.

Adaptation

The internal metabolic and thermal state drives individual responses to environmental change. For example, if environmental conditions are outside the specified range for emergence or activity, the animal will remain in its shelter. Within these limits, animals can bask by actively seeking sun patches when attempting to reach a preferred basking temperature, or search for food, feed, or socialise when within their T_{lower} and T_{upper} activity range limits. Individuals must regulate their T_b in response to changing microclimates by adapting their movement on fine scales to their current physiological state (mass, energy reserve), the level and availability of shade, and photoperiod. For simplicity, we assume no burrowing behaviour.

Fitness

The DEB model computes the trajectory of the life history at any stage in the life-cycle and thus defines potential fitness components, such as growth or fecundity for a given simulation.

Prediction

By simultaneously computing individual movement from thermal and resource limits of the habitat and the metabolic drive to move based on temperature and hunger levels, the model predicts movement constraints from purely individual physiological limits.

Sensing

Individuals are aware of their habitat (food and shade) in space and time within a defined visual range (min-vision; Table 5), allowing them to gravitate toward food or shade patches that lie within this range depending on their current activity state.

Stochasticity

Individual decisions are to some extent random (e.g. which direction to turn) following correlated random walks (CRW), which assume the least about any preferences for habitat features. This stochasticity generates different activity budgets under different movement strategies and resource distributions. When food or shade patches fall within the vision range, the individual will orientate and move itself directly toward the appropriate patch given the current activity state, i.e. Searching or Resting.

Observation

The model produces individual outputs for body temperature (T_b), rate of change in T_b, activity budget in time and space (time spent and spatial coordinates of different activity states), accumulated direct movement costs, accumulated wet mass (structure, storage, food, and reproductive mass), gut fullness, and home range polygons for both movement strategies.

Details

Initialisation

All animal data are based on the adult sleepy lizard, *Tiliqua rugosa*. Activity temperature range for Searching is 26ºC and 35ºC for the lower and upper bounds, respectively (Table 4) and basking temperature is 14ºC (Pamula 1997). Vision range (min-vision) is 10 m (Table 5) (Auburn et al. 2009). Table 6 details the parameters for initialising the DEB model for *Tiliqua rugosa*. We set up the IDEBM model to simulate real movement data of location tags every 10 minutes and movement steps, body temperature (T_b), and energy reserves recorded every 2 minutes of 60 adult sleepy lizards in the 2009 breeding season (September to December).

Individuals are initialised as adults at the onset of maturity and begin in a shade patch (Resting) in the centre of the landscape with maximum reserve (Maximum-reserve). Initial body temperature (T_b) depends on the user-defined location in space and time of year. Minimum and maximum activity temperature range (ºC), basking temperature (ºC), body mass (g), and vision range (m) are user-defined. We simulated an individual in a habitat of randomly distributed food and shade patches for 117 days from September 5, 2009. Simulations were repeated 100 times using a seeded habitat arrangement for 1) the optimising vs. satisficing strategies and 2) sparse (1000) vs. dense (100,000) food and shade distributions. We then compared movement pattern simulations with home ranges of sleepy lizard GPS data for this time period.

Table 6. Organism data for parameterising the standard Dynamic Energy Budget model of *Tiliqua rugosa*. Unit: *d* days; *g* grams; *K* Kelvin. All data are from Kearney, M. R., Munns, S. L., Moore, D., Malishev, M. and Bull, C. M., unpublished data, (http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Tiliqua_rugosa_res.html), except life span, which is from (Snider & Bowler 1992).

Parameter	Value	Unit	Description
a_b	150	*d*	age at birth at *f* (age 0 is at onset of embryo development)
T_{ab}	302.25	*K*	temperature for a_b
a_p	1642.5	*d*	time since birth at puberty at *f*
T_{ap}	302.25	*K*	temperature for a_p
a_m	7628.5	*d*	life span at *f* (accounting for ageing only)
T_{am}	296.35	*K*	temperature for a_m
L_b	16.5	*cm*	snout to vent length at birth at *f*
L_p	23	*cm*	snout to vent at puberty at *f*
L_i	32.8	*cm*	ultimate snout to vent length at *f*
W_b	29.7	*g*	dry weight at birth at *f*
W_p	54	*g*	dry weight at puberty at *f*
W_i	215.1	*g*	ultimate dry weight at *f*
R_i	0.0024	d^{-1}	maximum reproduction rate at *f* (for individual of max length)
T_{Ri}	296.35	*K*	temperature for R_i

Input data

Habitat

The habitat represents an arid, terrestrial environment in South Australia (139º21'E, 33º55'S), 1.5 × 1.5 km. Grid cells in the model landscape are 2 m wide.

Microclimate

The habitat is a mosaic of sun and shade patches (sparse or dense) that animals, when simulated to enter either patch type, are exposed to the respective sun or shade microclimate for the study site throughout the breeding season (September to December, 2009). We estimated distributions of shade patches from the LIDAR data of the study site and calculate hourly microclimates from the *NicheMapR* microclimate model using continent-wide weather data.

Submodels

Activity budget

Individuals switch between three separate activity states that encompass the fundamental behavioural repertoire: Searching for food, Feeding (including handling), and Resting (sheltering, seeking shade, and basking). For example, less time spent sheltering relative to feeding could imply that the animal is malnourished or lives around patchy resources. Emergent individual behaviour generates transition probabilities between activity states and thus a global state space model. Optimising animals have the extra activity state of socialising.

Results

Does the model capture realistic home range area and behaviour?

We used a metabolic theory-based movement model defining the internal energy and mass budget to drive movement decisions and generate activity budgets and home range emergence in response to external environmental constraints of food and microclimates explicitly defined in space and time. Using satisficing and optimising strategies as proxies for minimum and maximum potential movement, the IDEBM model produced distributions of home range size which overlap with that of the wild population (Fig. 6). Mean home range area for real animals (0.038 km^2) was significantly greater than simulated satisficing animals (0.0126 km^2, $t_{54.6} = 7.0376, p < 0.001$), but not different from simulated optimising animals (0.0397 km^2, $t_{69.5} = 0.39715, p = 0.6925$) (Fig. 6). This implies that actual lizard movement extends beyond basic behaviours of feeding, searching, and resting to include extra movement relating to socialising (Fig. 7B). Some

home ranges of real animals were larger than those from any of the two simulated movement strategies, but this portion of the total number of observed animals was only 10% (n = 6).

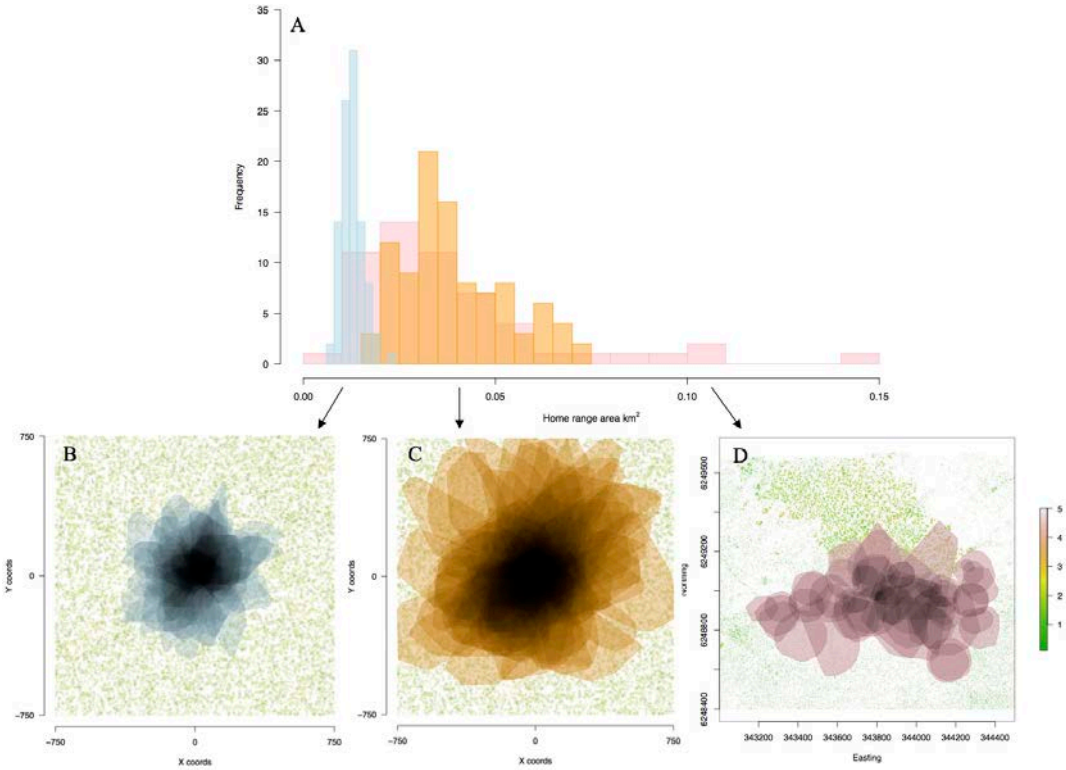

Figure 6. (A) Distributions of home range area (km^2) of real (pink) and seeded simulated optimising (orange) and satisficing (blue) movement strategies under dense resource distribution (food and shade). Home range polygons in space showing overlap of seeded simulated (B) satisficing and (C) optimising individuals and (D) real individuals. Home ranges in (D) appear more scattered due to different starting locations of real animals, whereas (B) and (C) have seeded starting locations in the centre of the landscape. The vegetation layer in (D) is generated from LIDAR data of the habitat site, showing the thermal mosaic of the landscape.

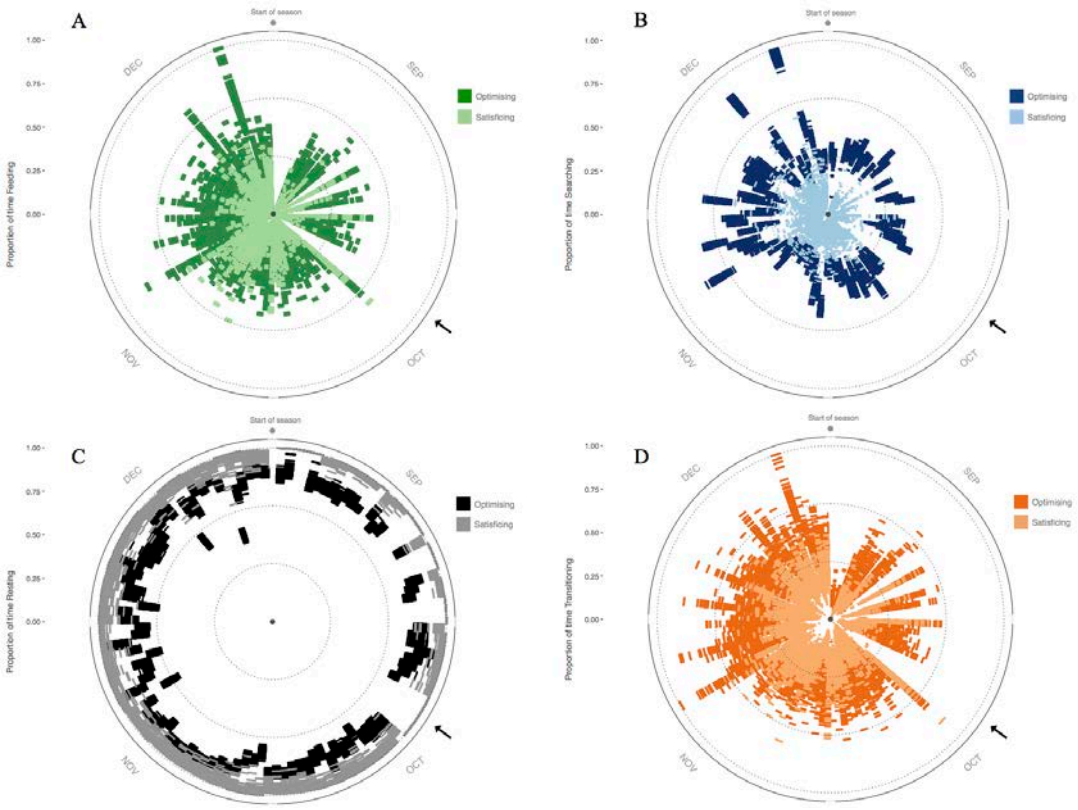

Figure 7. Activity budget for all optimising and satisficing animals throughout the breeding season showing proportion of time spent (A) feeding, (B) searching, and (C) resting, as well as (D) proportion of number of transitions between activity states. Radius = time spent in activity state; circumference = days throughout the breeding season. Black arrows indicate a 5-day period where environmental conditions were not conducive to activity, so animals spent this time resting in shade.

Further, the mean home range area of observed animals is closer to that of either simulated movement strategy than the maximum observed home range area. Under an optimising strategy that allows socially-motivated movement, individuals covered more ground and thus explored more food and shade patches within a similar time period compared to satisficing ones (Fig. 8C–D). Animals were also able to successfully negotiate different habitat arrangements, as shown by similar home range sizes between sparse and dense resource distributions (Fig. A1 in Appendix A).

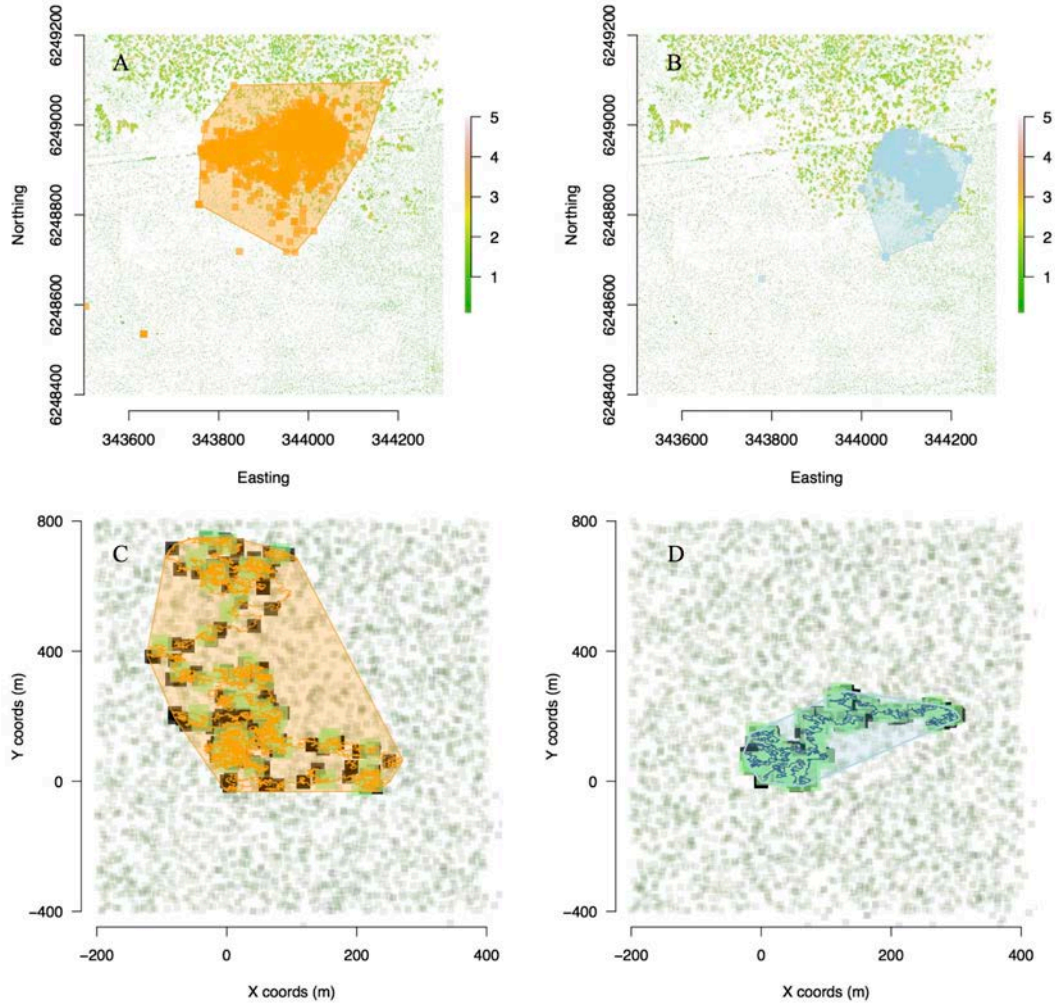

Figure 8. Movement path and home ranges of real versus simulated sleepy lizards. (A) Individual #11885, a real sleepy lizard showing active movement and (B) individual #11533, a real sleepy lizard showing passive movement, throughout the breeding season. (C) A random simulated optimising individual representing the maximum potential movement and (D) a random simulated satisficing individual representing the minimum movement necessary throughout the breeding season based on its physiological limits. (C–D) green = food patches, black = shade patches, and polygons represent home ranges. Patch size in simulations represents time elapsed on patch.

How does movement strategy shape activity budgets?

From individual-based decisions based on the internal energetic and thermal state of the animal in response to a spatial resource landscape, home range vertices show that optimising individuals under high resource distribution covered 1.2-fold more area (km^2) feeding than either searching or resting. Optimising animals spent on average 4.1-fold more time searching, 2.7-fold more time feeding, and 1.8-fold more time transitioning between activity states than did satisficing animals (Fig. 7). As expected, the largest difference in activity between movement strategies was for resting; satisficing animals, who spent 1.2-fold more time resting than optimising animals, were restricted from any

non-feeding activities, i.e. socialising. Optimising animals spent 10.5-fold more time searching and 48-fold more time resting than feeding. Conversely, satisficing animals spent 6.9-fold more time searching and 149-fold more time resting than feeding.

How does movement potential affect individual metabolic outputs?

Movement was, on average, 1.4-fold more costly for maximum (optimising) over minimum (satisficing) movement potential due to extra overall time engaging in non-feeding movement (Fig. 9A). The IDEBM model predicted relatively minor impacts on the energy budget of the two movement strategies: structure, wet mass storage, converted food mass, and reproductive organ wet mass of optimising animals were, on average, 0.0004%, 0.0008%, 0.0009%, and 0.0023% (g) lighter after the breeding season than in satisficing animals, respectively (Fig. 9B).

Does the individual heat budget model capture realistic thermal changes and costs?

We found the upper and lower T_b limits per hour of the day for the different simulated movement strategies encompassed those of the wild population throughout the breeding season, while average hourly simulated T_b varied from observed by ±5ºC (cf. Fig. 10A–B). An example of the fine scale changes in T_b as the individual enters and exits shade patches across the day is shown in Figure 10. Rates of T_b change for simulated minimum and maximum movement potential showed a similar range to those of the real animals (Fig. A2).

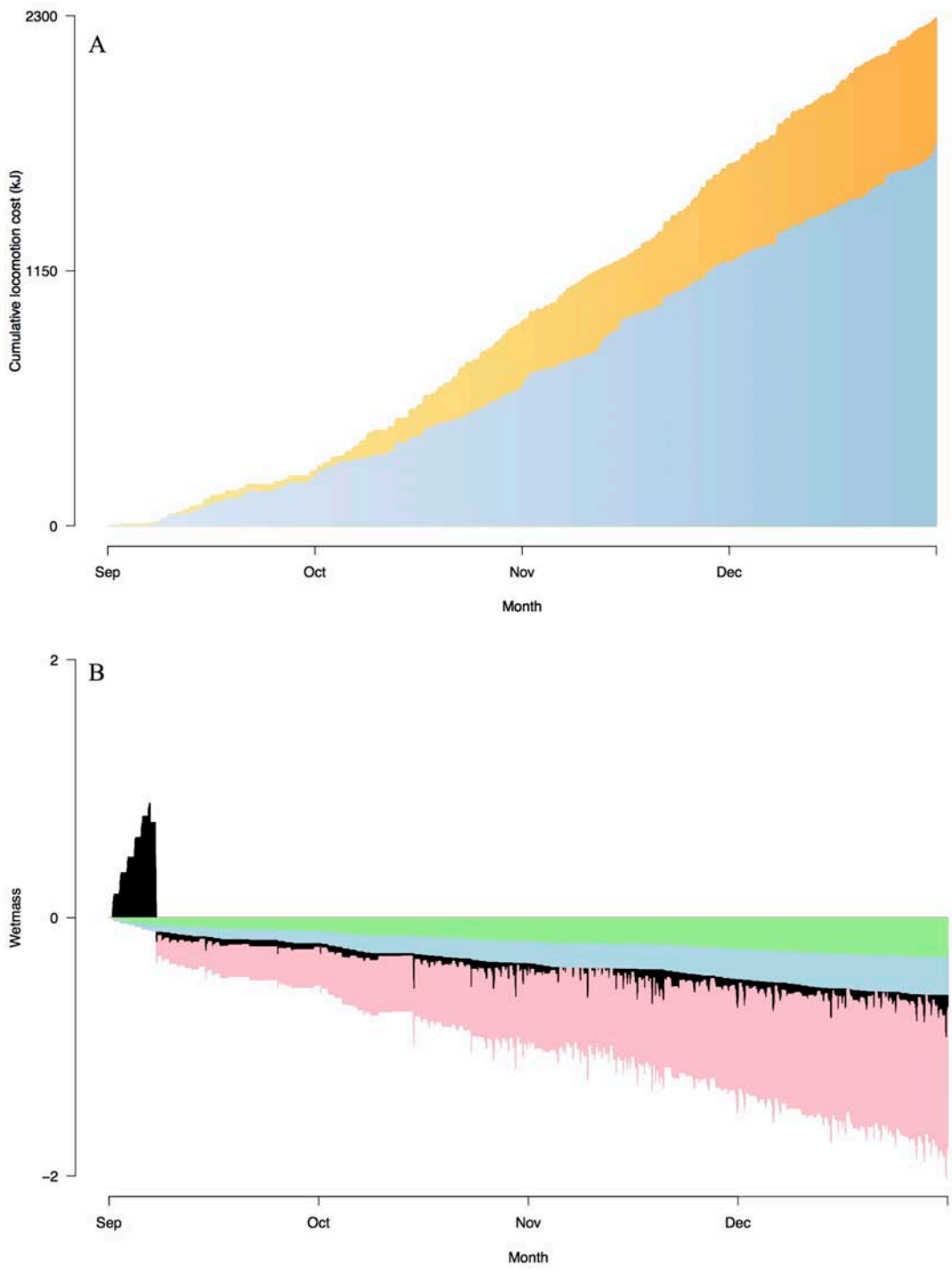

Figure 9. Energetic outputs showing differences in maximum (optimising) and minimum (satisficing) potential movement. (A) Cumulative movement costs (kJ) for a random simulated optimising (orange) and satisficing (blue) individual throughout the breeding season. (B) Difference in mean structural volume (g^{-1} cm^3; green), wet mass storage (g; blue), converted food mass (g; black), and reproductive organ wet mass (g; pink) between optimising and satisficing movement strategies throughout the breeding season.

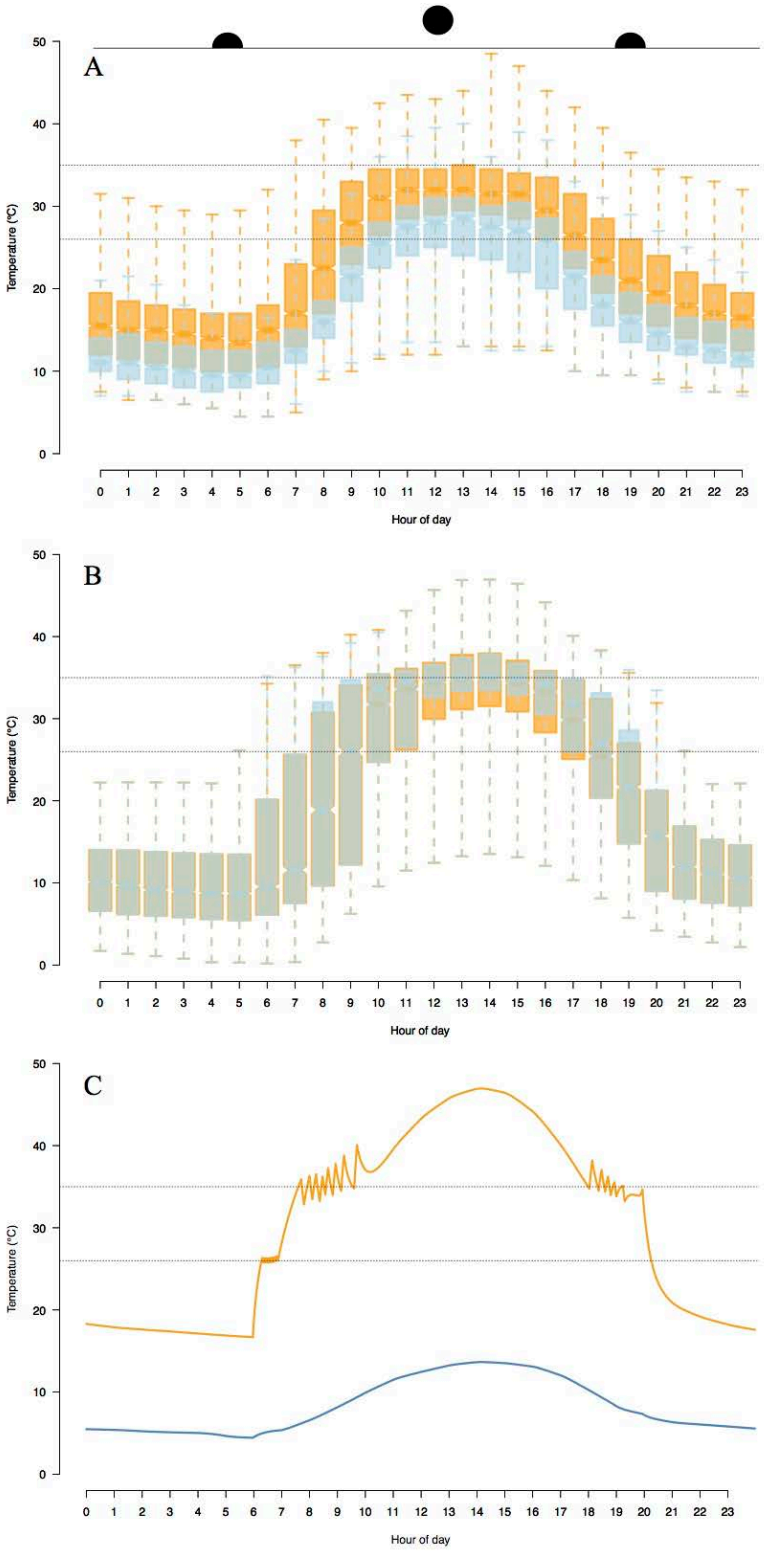

Figure 10. (A) Hourly T_b for individual #11885 (orange), a real sleepy lizard showing active movement and individual #11533 (blue), a real sleepy lizard showing passive movement, throughout the breeding season. (B) Hourly T_b for a simulated optimising animal (orange) and satisficing animal (blue). (C) Example of daily T_b profile for the same optimising animal during the hottest (orange curve) and coldest (blue curve) day of the breeding season. Dashed horizontal lines show thermal limits of activity period (26ºC–35ºC) and black graphics atop (A) represents the sun cycle.

Discussion

We built an individual-based spatial movement model driven by mechanistic models of heat exchange and metabolism to predict movement and home range patterns under different food and microclimate constraints. Our aim was to interpret how animals navigate these movement constraints from interacting internal (physiology and metabolism) and external (resource and weather) cues under different movement strategies to capture habitat use of the wild population.

Simulated average home ranges under the optimising strategy closely approximated real home ranges throughout the breeding season (Fig. 6). Therefore, our movement model driven from bottom-up physiological and metabolic consequences was able to provide biologically realistic predictions. Given that real animals move significantly more than predicted by the simulated satisficing strategy, our results imply that sleepy lizards are exploiting available thermally suitable time for activities above and beyond what is needed for feeding (Fig. 6). This is consistent with field studies of sleepy lizards showing that males in particular engage in extensive movements associated with mating and social behaviour (Kerr & Bull 2006).

The motivations of animals to trade-off available time for different activities are diverse e.g. growing versus mortality risk (Werner & Anholt 1993; Stamps 2007), rapid habitat change (Fahrig 2007), and the interplay between the internal state and external environmental cues (Schick et al. 2008; Clobert et al. 2009; Shaw & Couzin 2013). Animals face movement trade-offs depending on how food and microclimates change in space and time on fine scales (Porter et al. 1973; Stevenson 1985b; McClure et al. 2011). By adjusting behaviour and activity windows to exploit different thermal landscapes, animals can better regulate their body temperature (Sears et al. 2011; Vickers et al. 2011; Villén-Pérez et al. 2013) and better adapt to fine scale environmental change. The 95% home range vertices we computed for each activity state showed that simulated patch use from searching for food and feeding covered the most ground because when food is abundant, i.e. under high resource distribution, animals can easily find and move to nearby food patches. Animals can then use food patches as stepping-stones to find more food; in contrast, more patchy food distribution lowers the chance of finding and thus moving to food patches. Therefore, space use by simulated animals when feeding required more directional movement and was less random than when searching, including socialising. More time spent feeding suggests that, under physiological constraints, foraging drives movement over socialising.

Simulated shade-seeking behaviour, including retreating to shade, covered less area because resting animals are more stationary and displace less than foraging ones. This result is likely due to the time costs of different activities. For example, animals heat up and cool down over much shorter time intervals than those involved in searching for and handling food. That is, they may have to continually leave a food patch to cool down in a shade patch in hot weather. Therefore, thermal extremes can impose significant overhead costs to foraging time. For example, active lizards in open patches can spend up to 20-fold more time in foraging than non-foraging behaviour (Wilson & Lee 1974). We found

simulated animals spent more time exposed to thermal extremes when foraging than when retreating to refuges. Our modelling framework directly links these time costs to food availability in the model landscape and to metabolism via satiation, i.e. a gut fullness threshold imposing hunger. Therefore, we can naturally capture how changes in T_b affect gut emptying rates via metabolic rate to drive foraging opportunities and thus movement decisions. By connecting the web of metabolic and heat pathways of the animal [Fig. 4; see Fig. 2 in (Kearney et al. 2010)], the IDEBM model shows the feedbacks in time and space between the internal energetics of the animal and external environmental change of the habitat form inescapable, interacting constraints. From these interacting constraints arises complex conditional movement behaviour from simple rules.

We used theory-based estimates of direct movement costs to represent the metabolic investment of movement between different strategies of the sleepy lizard to further interpret differences in minimum (satisficing) and maximum (optimising) movement potential. On average, movement for satisficing animals cost less (Fig. 9A), allowing for more metabolic input into structural volume, storage, converted food mass, and subsequently reproductive mass (Fig. 9B). Despite affording increased space use and more freedom when finding resources, non-essential movement, i.e. socialising, for optimising animals yielded a lower, albeit marginal, metabolic return than satisficing ones after the breeding season across all mass properties. Coupled with the home range overlap of optimising and wild animals (Fig. 6), this suggests real sleepy lizards may indeed invest substantial amounts energy into movement with little nutritional return. This is supported by field observations that male sleepy lizards in particular spend large amounts of time mate guarding in addition to foraging (Kerr & Bull 2006; Godfrey et al. 2012).

Movement is a costly process (Wilson et al. 2013; Wilson et al. 2014; Wilson et al. 2015) and difficult to generalise across models due to the complexity of how metabolic pathways allocate energy and mass to different metabolic functions. This complexity means movement models often apply *ad hoc* or field-based movement costs (Buchmann et al. 2011; Kułakowska et al. 2014; Louzao et al. 2014; Ayllón et al. 2016) and thus can overlook or ignore key physical processes essential to energy budget estimates, such as how metabolic rates depend on temperature. We can gain a more structured approach to the problem of integrating movement costs with energy budgets by incorporating these costs into formal metabolic theory. DEB theory applies a metabolic hierarchy to energy allocation via the κ rule (Table 3), where energy diverges to the κ branch to supply somatic maintenance and growth (Eq. 2 in Chapter 2) and the remainder to the $1-\kappa$ branch for reproduction (Eq. 7 and Eq. 8 in Chapter 2). Movement costs could indeed be added to either of these branches, but they are most often considered part of somatic maintenance costs (Kooijman 2010), as per our simulations. In this case, movement costs compete directly with growth. Because we modelled animals that were near to maximum size, and thus very little energy was being allocated to growth, the costs were mostly manifested as minor reductions in body condition. For juveniles, where a greater proportion of this energy flow is allocated to growth, the fitness costs of movement would be manifested as reduced growth rate. An alternative would be to impose locomotion costs on the $1-\kappa$ branch. Here, costs for adults would manifest as reduced

size-specific reproductive output, while costs for juveniles would be an increased time to sexual maturity. A mixed strategy is also possible, where a portion of movement costs come from the κ branch and some from the $1 - \kappa$ branch. Indeed, the extra movement costs of male sleepy lizards (Kerr & Bull 2006) could equate to the energy females allocate to offspring. Exploring these various ways of imposing movement costs, and thus movement decisions in space and time, under the IDEBM framework is an interesting avenue for future research.

Rapidly changing thermal environments from climate change may reduce activity time and consequently increase localised extinction risk (Sinervo et al. 2010). However, animals experience microclimates that vary substantially within and between habitats, on daily cycles (Fig. 10), in their spatial patterns (Sears et al. 2011), and in proximity to resources (Kearney 2013). We found rates of T_b change of simulated satisficing and optimising strategies were similar to observed passive and active movement between the morning (06:00–12:00) and afternoon (12:00–18:00) hours of the day (Fig. A2), suggesting that animals incur similar thermoregulatory time costs when exposed to morning and afternoon thermal extremes. For animals to tolerate these costs and exploit available activity time depends on basic individual differences, such as body mass, food requirements, and movement strategy (Huey & Pianka 1981; Stevenson 1985a; Kearney & Porter 2004). For example, small, opportunistic foragers, such as *Sceloporus serrifer*, require more time exposed to thermal extremes to satisfy foraging needs than larger and hardier omnivorous foragers, such as *Tiliqua rugosa*. Therefore, a smaller body mass runs a higher risk of overheating and thus restricted dispersal ability (Kearney & Porter 2004; Sinervo et al. 2010). Indeed, high rates of T_b change on fine scales impose direct physical limits to animals in space due to the trade-offs between choosing to move and the distance required to escape environmental extremes (Sears et al. 2011; Sears et al. 2016); this in turn can restrict movement patterns to localised areas in space, thus limiting available activity time (Grant & Dunham 1990). Therefore, the challenge for the animal is to balance its movement trade-offs, i.e. the frequency at which they emerge and retreat from and to shelter and use different movement strategies (Fig. 7), against available and actual activity time as changing weather shifts activity windows throughout the day and year (Stevenson 1985b; Kearney et al. 2009; Vickers et al. 2011).

Ideally, a model capturing these detailed individual responses to varying environmental processes ought to be general and applied to biologically relevant scales (Sears & Angilletta 2015). The IDEBM model achieves these ideals using general principles of energy and mass exchange, realistic microclimatic inputs, and basic movement rules in a spatially explicit context (Fig. 4), addressing the need for more detailed physiology-based movement models in space (Sears et al. 2016). This provides a general, bottom-up framework to capture different movement motivations and highlights the importance of attributing individual-based physiological constraints to movement when exploring fine scale patch to home range behaviour (Martin et al. 2008; Kearney & Porter 2009; Sears & Angilletta 2015; Sears et al. 2016). Populating the model landscape with realistic fine-scale microclimate inputs generates detailed and varied environmental scenarios. In our simulations, changing resource distribution had no effect on home range size between simulated movement strategies (Fig. A1). However, by using LIDAR data of the study site to configure resource (food and shade) distribution in space (see insets of Fig. A1),

the model landscape can simulate realistic changes in habitat structure expected in nature, such as the boom and bust of shady vegetation following rainfall and fire events. This captures movement and behavioural responses to habitat change by allowing users to simulate how environmental disturbances (external cues) influence individual decisions (internal cues).

By combining both internal and external movement drivers, the IDEBM model highlights how food and shade patterns determine suitable movement corridors and the frequency at which activity windows occur and persist based on physiology-driven movement limits. Simulations of home range behaviour from physiology-based estimates shows that the relationship between potential home range patterns and spatial distances among food and refuge sites is subtle, but crucial (Leu et al. 2010). We need a solid, bottom-up understanding of this relationship to interpret shade-seeking behaviour in specific habitat contexts (Belliure et al. 1996; Kearney et al. 2009) or predict home ranges when resources vary in time and space (Fig. 6; Tracy & Christian 1986; Mitchell & Powell 2004; Moorcroft et al. 2006; Börger et al. 2008). The time animals spend within various activity states (e.g. Searching, Feeding, or Resting) can shift their activity patterns as habitat conditions change. For example, a switch in the frequency of time spent in different states depends on food availability and temperature; after depleting local food sources, animals can increase their searching effort (measured as space use) assuming that suitable conditions, such as more foraging hours in the later and warmer breeding season, permit further foraging (Sinervo et al. 2010; Sears et al. 2016).

We show optimising animals searched and foraged more in the later and warmer breeding season (Fig. 7A–B). Further, despite a similar gut fullness threshold for foraging, satisficing animals in our simulations still only fed less than half as much as optimising animals. Therefore, optimising animals more often transitioned and spent more time overall transitioning among activities, suggesting habitat conditions during this time of year permitted increased searching and foraging (Fig. 7A–B), but still induced movement trade-offs by forcing them to regulate their internal state, i.e. shuttling in and out of shade whilst trying to forage (Fig. 7D). Optimising animals, however, displaced further throughout the landscape when feeding, despite spending more time resting and searching than feeding. This implies that, in the short term, the surplus time for optimising animals to move freely during available activity hours meant locating food patches or at least settling in areas where food was more abundant, such as shade adjacent to lots of food, was easier (Fig. 8). In the long term, however, this benefit yielded little energetic return (Fig. 9B). These results also suggest that directional (gravitating toward food) over correlated random movement is more useful for negotiating landscapes when animals are constrained by physiological limits to movement (Fronhofer et al. 2013), such as thermal limits and movement costs, including turn costs (Wilson et al. 2013). Building movement models around different behavioural states fills necessary biological gaps in model development and addresses inherent model fitting issues across varying time scales (Morales et al. 2004). The IDEBM model adds to these important modelling criteria by incorporating a theoretical basis to the mechanisms driving movement, thereby providing a generic framework to address movement costs and motivations across scales.

Limitations and future work

Feedback delays between the rate at which activity states update and the scale of the decision-making model time steps could influence overall activity budgets and thus space use over time for each activity state. This is a potential artefact of the model update procedures that requires further fine-tuning. The similar home range sizes of animals under sparse and dense resource distributions was surprising (Fig. A1). Future work could consider simulating habitats with larger thermal extremes (Christian & Weavers 1996; Blouin-Demers & Nadeau 2005), different topography (Sears et al. 2011) and ecoclines (Sunday et al. 2014), or similar resource distributions, but under increased warming scenarios. Our aim here is to deconstruct how the subtlety of habitat arrangement influences displacement and home range behaviour.

Because the model assumes 50% shade levels and no burrowing, some simulated animals reached unnaturally high T_b on the hottest day of the season (Fig. 10C). Future model configurations incorporating varying shade levels and perhaps burrowing behaviour would refine T_b outputs during resting and shade-seeking behaviour. Further work dissecting how the consequences of direct movement costs, including turn costs (Wilson et al. 2013), change throughout the animal lifecycle is also needed. Our study species is long-lived and slow to mature. By simulating longer time periods, the life-history consequences of movement costs will become more apparent for this species, including how energy allocated among maintenance, growth, and movement shapes juvenile dispersal periods and gender differences in movement for females encumbered by the heavy metabolic demands of reproductive egg investment. We can also use the interacting internal and external drivers of the model to summarise basal metabolic rates of endotherms and thus use a similar approach to how internal energy and water costs constrain their movement decisions (Porter et al. 1994; Kearney & Porter 2009). Finally, the physiology-driven mechanics of the model opens opportunities to explore within-species behaviour differences, including territoriality and interacting individuals (Spiegel et al. 2016; Leu et al. 2016; Spiegel et al. 2017), as well as scaling to population-level responses, such as using GPS data of movement rates to forecast range expansion of invasive species fronts, e.g. cane toad dispersal (Phillips et al. 2007).

Conclusions

Here, we presented an individual-based movement model built on general biophysical and metabolic principles of the individual animal and its direct relationship with food and weather in space and time. By explicitly capturing the physical limits driving movement, the IDEBM model presents a realistic and flexible approach for predicting current and future movement and home range activity under changing food and weather. This flexibility also makes the model robust to different time and space scales, so animals can experience different weather and habitats throughout the year. That is, we can refine how we interpret behavioural limits necessary for survival across scales and the physiological and ecological limits under which animals persist over their lifetime. The theory-driven estimates of movement costs in the model represents a reliable physiological understanding of movement and bottom-up forecasting of fine scale environmental change on habitat use and interpreting the ecological niche. Using a general, first principles approach to animal movement, the IDEBM model is thus suitable for tackling a wide range of questions in ecology and behaviour to improve our understanding of how spatial patterns of resources and microclimates influence complex behaviour, especially in the context of environmental change.

Acknowledgements

We thank Mark Burgman, Michael Bode, Stephan Leu, Roger Nisbet, and Mike Sears for constructive discussion and Daniel Ayllón, Pascal Fust, Eduardo Arraut, Hugo Thierry, and Ben Martin for input on early model development. We also thank two reviewers and Luca Börger for helpful comments that improved this manuscript. We dedicate this work to the memory of Prof. Mike Bull who passed away before the work was completed.

Funding

This research was funded by an APA, Holsworth Research Grant, and CEBRA to MM, ARC Discovery grants DP140101240 and DP110102813 to MRK and DP0877384 to CMB, a resource allocation grant from Victorian Life Sciences Computation Initiative to MRK, and Flinders Animal Welfare Permit E232 and South Australian Dept. of Environment Water and Natural Resources Research Permit A23436.

Authors' contributions

MM conceived and wrote the manuscript, developed the simulations and parameterised the energy budget model, CMB collected field data and contributed to revisions, and MRK co-conceived and wrote the manuscript and developed the microclimate model, the *NicheMapR* package, and parameterised the energy budget model.

Data accessibility

Full code for the microclimate model ('onelump_varenv.R'), energy budget model ('DEB.R'), Netlogo code for the decision-making model (Appendix A1), *R* code for the simulation model (Appendix A2), and microclimate data for sun ('metout.csv' and 'soil.csv') and shade ('shadmet.csv' and 'shadsoil.csv') conditions for the model landscape are available on Github at https://github.com/darwinanddavis/MalishevBullKearney.

Competing interests

The authors declare they have no competing interests.

Ethics approval and consent to participate

Not applicable.

4

How body mass influences activity and home range patterns across the individual life cycle

Matthew Malishev[1,2*] & Michael R. Kearney[2]

[1] *Centre of Excellence for Biosecurity Risk Analysis,* [2] *School of BioSciences, University of Melbourne, Parkville, Melbourne, 3010, Australia*

[*]Corresponding author: matthew.malishev@gmail.com

Es chevere ser grande, pero es más grande ser chevere

Erre

Table of Contents

Abstract 96
Introduction 97
Methods 99
Dynamic Energy Budget model 99
Microclimate data inputs 99
Life stage 99
Initial maturity 100
Structure 100
Mass 100
Simulations 100
Results 100
Home range area and body mass 100
Rate of Tb change and body mass 102
Activity budget and body mass 104
Metabolic properties 106
Discussion 110
Home range area and body mass 110
Rate of Tb change and body mass 112
Activity budget and body mass 112
Metabolic constraints on life stage and habitat requirements 113
Conclusions and future directions 115
Acknowledgements 117
Funding 117
Authors' contributions 117
Data accessibility 117
Competing interests 117
Ethics approval and consent to participate 117

Abstract

The motivations of animals to move and the constraints on how animals use habitats scale with individual body size, which changes among species and throughout the individual life cycle. We extend the work in Chapter 3 to explore how body mass of simulated animals influences home range size patterns, activity budgets, and available activity time through individual physiological responses associated with the heat budget and metabolic demands of the animal. We simulated juvenile (90 g) and adult (700 g) sleepy lizards, *Tiliqua rugosa*, under two contrasting movement strategies (optimising and satisficing) in low and high resource densities for the summer breeding season at a site in semi-arid southern Australia. By grounding the physical response rates of the individual on a metabolic theory-driven framework, we use differences in mass of juveniles and adults to represent the different life stages of the animal. This aims to explore how resource and climate constraints to movement shape home range area and patterns under varying metabolic demands of the animal life cycle, such as energy investment into growth and reproduction. We found adults have an advantage with their movement potential and ability to tolerate fine scale environmental change over juveniles under thermal extremes. However, access to resources, as determined by resource abundance, can be more important than physiological traits at the home range level. Further, movement strategy had no bearing on the relationship between differences in body mass and home range size. Low resources induced higher thermal stress in open patches. We show a smaller and thus more vulnerable body size is more at risk under multiple constraints and costs to movement, such as the physiological, i.e. heat stress and ecological, i.e. potential predation. A larger body size in later life stages enables the animal to mediate the metabolic investment of movement when these costs are inherently uncertain.

Keywords: Individual-based model, life stage, physiology, body mass, home range, energy budget, climate, activity budget

Introduction

As human-induced climate warming becomes an increasingly pertinent issue, adapting to the new challenges it brings requires applying practical and reproducible solutions (Wilson 1998; Anderson et al. 2009; Harley 2011). Due to their predictive ability and use at multiple scales, our attention is progressively shifting toward methods based on mechanisms and processes to forecast species responses to climate change at different time and space scales (Helmuth et al. 2005; Kearney & Porter 2009; Buckley 2010; Bauer & Klaassen 2013; Jeltsch et al. 2013; Fourcade et al. 2014; Cagnacci et al. 2015). In Chapter 3, we show how the direct mechanisms driving movement patterns and home range emergence in space and time can indeed be physiological (Angilletta et al. 2004; Helmuth et al. 2005; Kearney et al. 2009; Buckley 2010; Bauer & Klaassen 2013). For example, body size is closely tied to metabolic rates that depend on environmental temperature, which influences and constrains an animal's ability to exploit suitable habitat patches (Tracy & Christian 1986; Weiss et al. 1988; Diaz 1997; Torres-Contreras & Bozinovic 1997; Davies et al. 2006) and food sources at different times of the day (Vickers & Schwarzkopf 2016; Malishev et al. in review).

Adults with their larger mass have slower rates of heating and cooling than juveniles (Stevenson 1985; Ayers & Shine 1997; Martín & López 2003). For juveniles, a smaller body size means a thinner boundary layer between the animal and surrounding environment, which increases the way processes such as convection heat and cool the animal (Kearney & Porter 2009; Porter & Kearney 2009). We can attribute the different ways juveniles and adults respond to their surrounding habitat using physical mechanisms. For example, smaller animals are closer to the ground and thus experience lower wind speeds; coupled with their smaller size, this places the animal deeper in the boundary layer to the ground. Therefore, smaller individuals heat and cool faster than larger bodied ones and thus experience a different thermal environment. Further, smaller animals need to feed more frequently to meet higher metabolic demands. However, warmer climates restrict future available activity time (Sinervo et al. 2010; Kearney 2013). These biophysical effects may make animals of relatively smaller body size more vulnerable to environmental extremes, thus increasing thermal stress and metabolic requirements. Therefore, favourable access to resources becomes an important constraint to movement potential for different life stages of the animal.

By building the decision-making part of the IDEBM model on the physical attributes of the animal defining its internal state through time, we can use body mass to represent different life stages of the animal. Rates of T_b change and movement decisions occur on shorter time steps than changes in body mass. Therefore, smaller animals, such as juveniles, ought to make more judicious movement decisions than adults to ameliorate the physiological disadvantage of smaller body size in earlier life stages. Omitting the various life stages of the individual from our models could mean we overlook crucial aspects influencing the way animals respond to habitat change (Crouse et al. 1987; Radchuk et al. 2013). Using body mass to represent the early and late life stages aims to

show how movement strategy and habitat requirements shift throughout the animal life cycle.

Body size is a commonly used trait to observe direct impacts of environmental change on the individual (Schoener 1968; Damuth 1981; Nagy 1987; Cardillo et al. 2005; Genner et al. 2010; Ozgul et al. 2010; Gardner et al. 2011), including at the home range level (Mysterud et al. 2001; Haskell et al. 2002; Greenleaf et al. 2007). Incorporating body size in a process-based simulation model allows us to explore the impact of habitat change on the different life stages of the animal. We use differences in body size to tease apart the consequences of habitat change on individual activity budgets, space use, and how these interact to influence home range size. Here, body size has the potential to influence the metabolic demands of the individual and thus movement motives. By including the juvenile and adult metabolic states in the IDEBM model, we can use two extremes in structural body size and their associated maturation levels to explore how the interacting biophysical and metabolic effects of size influence movement and home range patterns.

We apply the IDEBM model to the same model landscape, resource densities (low and high) and movement strategies (optimising and satisficing) as described in Chapter 3 to simulate movement and home range patterns of juvenile and adult sleepy lizards, *Tiliqua rugosa*, with the addition of appropriate microclimate data inputs for both juveniles and adults. We predict that the adaptive advantage of a larger body size later in life presents more behavioural flexibility for controlling physiological responses and thus movement and home range potential than earlier life stages. Our aims are to determine 1) how differences in metabolic demands throughout the individual life cycle influence space use and activity budgets, 2) how habitat constraints, the activity budget, and home range size between juveniles and adults shift as body size varies across growth, and 3) whether changes in life stage infers any physiological or ecological advantage under different, interacting movement constraints.

Methods

Dynamic Energy Budget model

We estimated the parameters for the DEB model as described in Chapter 3 with the addition of changes in metabolic parameters for the juvenile life stage (Table 7).

Table 7. Individual variables and parameters of the DEB model (Kooijman 2010) for simulating juvenile and adult sleepy lizards, *Tiliqua rugosa*. Units: *J* Joules; *cm* centimetres; *g* grams.

Parameter	Adult	Juvenile	Unit	Description
E	7222.30	7222.30	J	initial reserve
E_H	159945	49188	J	initial maturity
V	354.80	45.80	cm^3	initial structure
mass	703.75	90.85	g	wet mass

4

Microclimate data inputs

We set microclimate inputs (local air temperature, local wind velocity, and local relative humidity) for sun and shade conditions for both juveniles and adults to update the model landscape and individual parameters prior to simulations. We set microclimate conditions for each life stage by specifying the mid-point heights of the animal above the ground; this defines the convective and radiative heat transfer between the body mass and the ground. See Table 4 for heat budget parameters and Figure 4 for input pathways of microclimate data. Energy and heat budget functions operate akin to those in Chapter 3. Environmental output from the 'microclimate' function updates the individual thermal state for either the juvenile or adult life stage (https://github.com/darwinanddavis/adultjuv).

Life stage

We simulated both juvenile (90 g) and adult (704 g) life stages of the sleepy lizard. Individual parameters for determining differences in body mass include reserve E, maturity E_H, structure V, and wet mass (Table 7). These parameters set the initial internal state of the animal before the beginning of the simulation. Habitat conditions (food and shade) were identical for both juveniles and adults, allowing changes in movement and home range patterns to emerge from differences in the physiological state (height above ground) and responses of the animal. We tracked changes in these metabolic properties throughout the breeding season simulation to determine how habitat (resource density)

and behaviour (movement strategy) drive home range patterns for different life stages of the animal. The optimising strategy includes additional socially motivated movement where individuals move during all available activity hours.

Initial maturity

$$E_H = \begin{cases} juvenile, & E_H = E_H^b + 5 \\ adult, & E_H = E_H^p + 5 \end{cases}$$

Structure

$$V = \begin{cases} juvenile, & V = L_b \\ adult, & V = L_i^3 \cdot 0.85 \end{cases}$$

where L_b and L_i are structural length at birth and maximum structural length, respectively.

Mass

$$mass = V + \frac{V \cdot E \cdot d_V \cdot 23.9}{\mu_E}$$

where d_V is the density of structure ($g\ cm^3$) and μ_E is the chemical potential of reserve E measured in molar Gibbs energy (J/mol).

Simulations

We ran 100 simulations for both life stages (juveniles and adults) in a model landscape of dense (100,000 patches) and sparse (1,000) resource (food and shade) densities under the two movement strategies (optimising and satisficing), giving a total of eight permutations:

Life stage (juvenile and adult) × resource density (high and low) × movement strategy (optimising and satisficing)

Simulations began with individuals in the centre of the landscape and ran for the entire 2009 breeding season (117 days).

Results

Home range area and body mass

Figure 11 shows the relationship between home range area and potential changes in physical properties of the animal under different resource densities. Adults and juveniles gained similar mean amounts of mass (~9 g difference) under high resource density throughout the breeding season, irrespective of movement strategy (Fig. 11A). When

resources were low, despite their initial larger size and potential to shed more weight, adults lost significantly more mean mass (135 g) than juveniles ($t_{103} = -56.61$, $p < 0.001$), even when scaled relative to initial starting masses ($t_{99} = 113.83$, $p < 0.001$) (Fig. 11C).

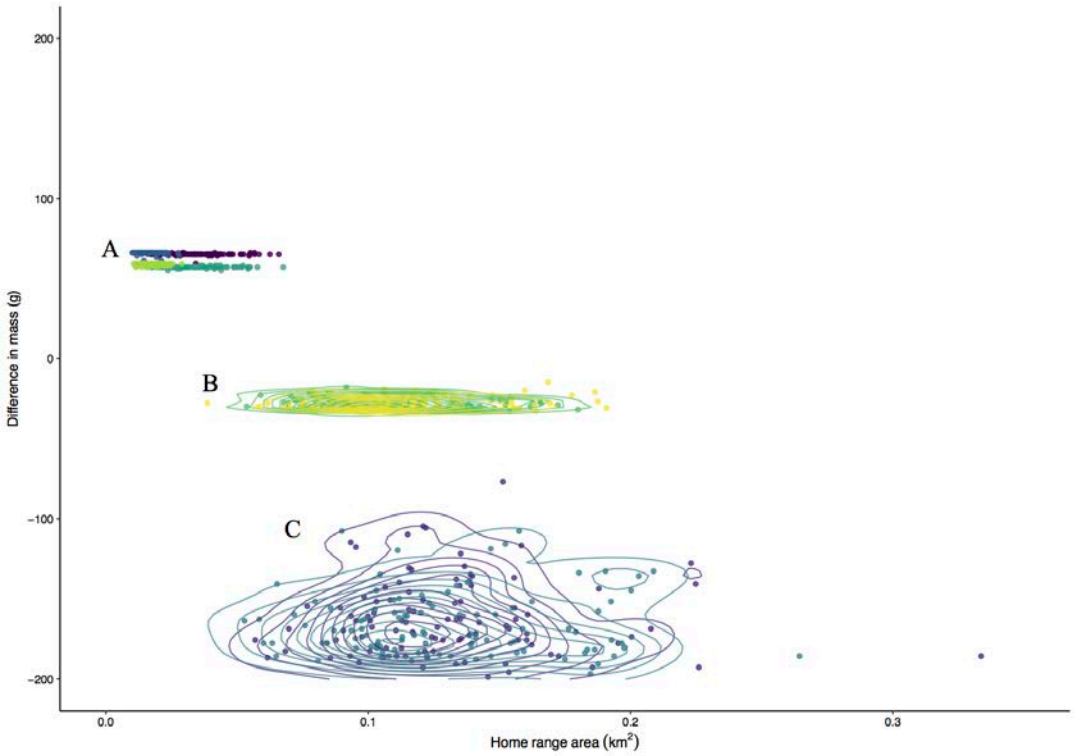

Figure 11. Distribution of home range area against differences in mass of simulated adults and juveniles. A) Adults and juveniles under high resource density; B) juveniles under low resource density; C) adults under low resource density.

Socially motivated adults and juveniles under an optimising strategy had similar range areas under high resources (Fig 11A and Fig 12A & C). However, under scarce resources, movement strategy and time spent searching for shade were primary drivers of home range patterns for both adults and juveniles. Adults were able to form the largest home ranges when resources were scarce (Fig 11C and Fig. 13A–B) and juveniles under both movement strategies generated smaller mean home ranges than adults (0.02 km^2, $t_{176} = 4.13$, $p < 0.001$) (cf. Figs 11B & C).

Examples of space use by simulated animals shows satisficing individuals used less space due to no social movement, where they spent more time resting as indicated by the higher peaks in Figures 12B & D and Figures 13B & D.

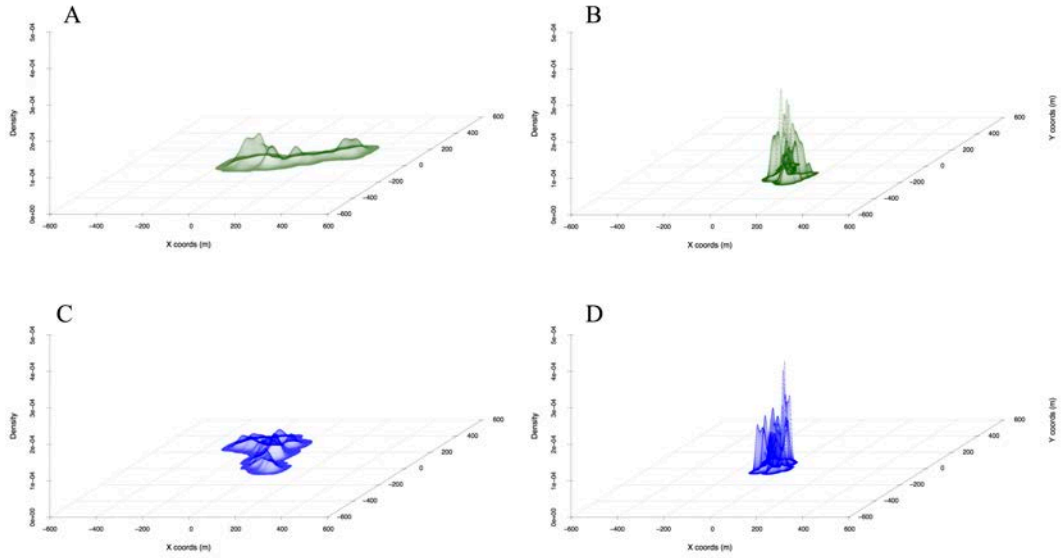

Figure 12. Kernel utilisation distribution of simulated home ranges from a random individual under high resource density. Top panel: A) Optimising and B) satisficing adults (green). Bottom panel: C) optimising and D) satisficing juveniles (blue).

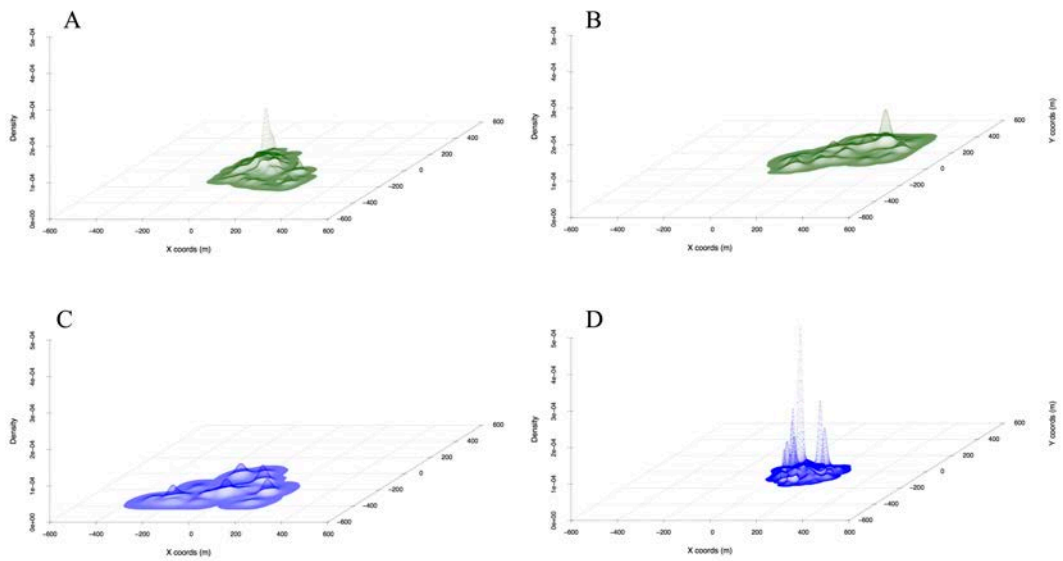

Figure 13. Kernel utilisation distribution of simulated home ranges from a random individual under low resource density. Top panel: A) Optimising and B) satisficing adults (green). Bottom panel: C) optimising and D) satisficing juveniles (blue).

Rate of Tb change and body mass

Compared to adults, juveniles experienced an almost twofold greater rate of T_b change when resources were scarce (cf. Figs 14C–D). Under high resource density, the rate of T_b

change for juveniles was 1.75-fold when compared to low resource density (cf. Figs 14A–B). This was consistent for both movement strategies.

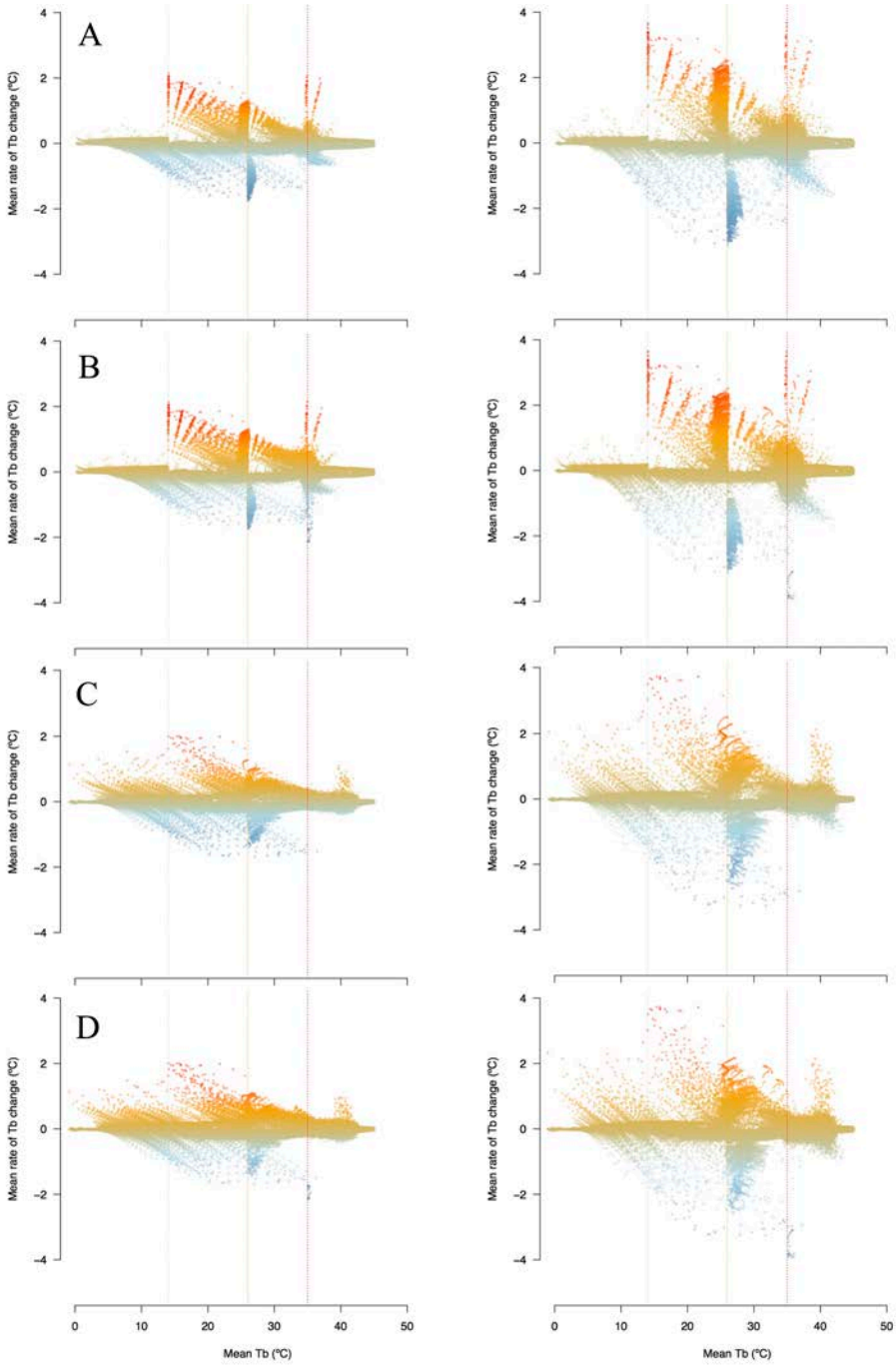

Figure 14. Mean rate of T_b (ºC) change against mean T_b (ºC) of simulated adults (left) and juveniles (right) for A) optimising and B) satisficing movement strategies under high resource density and C) optimising and D) satisficing movement strategies under low resource density. Vertical dashed blue, orange, and red lines represent basking temperature (14ºC), lower activity range temperature (T_{lower}, 26ºC), and upper activity range temperature (T_{upper}, 35ºC), respectively.

Activity budget and body mass

Adult and juvenile T_b at a given time of the day (09:00) showed an increasing trend throughout the season (Fig. 15). We chose this time of day as it represents the point in time when the T_b profile of the animal spans its activity range (both T_{lower} and T_{upper}). Under high resources, both adults and juveniles hovered around a mean 11ºC in the earlier, cooler season and 32ºC in the later, warmer season (Fig. 15); under low resources, this shifted to 19ºC and 36ºC, respectively (Fig. 16). This pattern was consistent for both life stages, showing body size had no effect on T_b at a given time of the day across the breeding season. However, having fewer resources in the environment amplified T_b at a given hour of the day to ~15ºC both early and late in the season (cf. Figs 15 & 16).

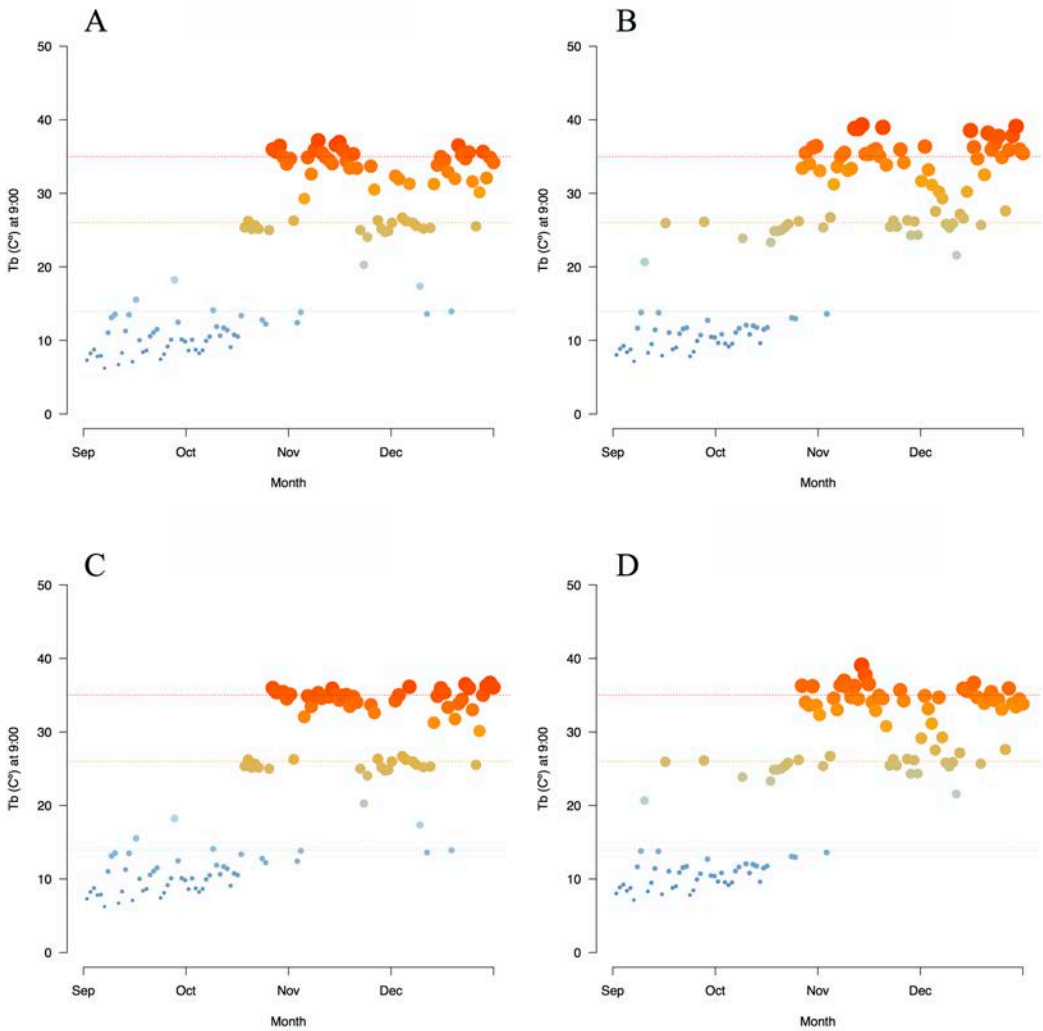

Figure 15. Example of T_b (ºC) in the morning (09:00 hours) throughout the breeding season comparing simulated adults and juveniles under high resource density. A) Optimising adult, B), optimising juvenile C), satisficing adult, and D), satisficing juvenile. Horizontal dashed blue, orange, and red lines represent basking temperature (14ºC), lower activity range temperature (T_{lower}, 26ºC), and upper activity range temperature (T_{upper}, 35ºC), respectively.

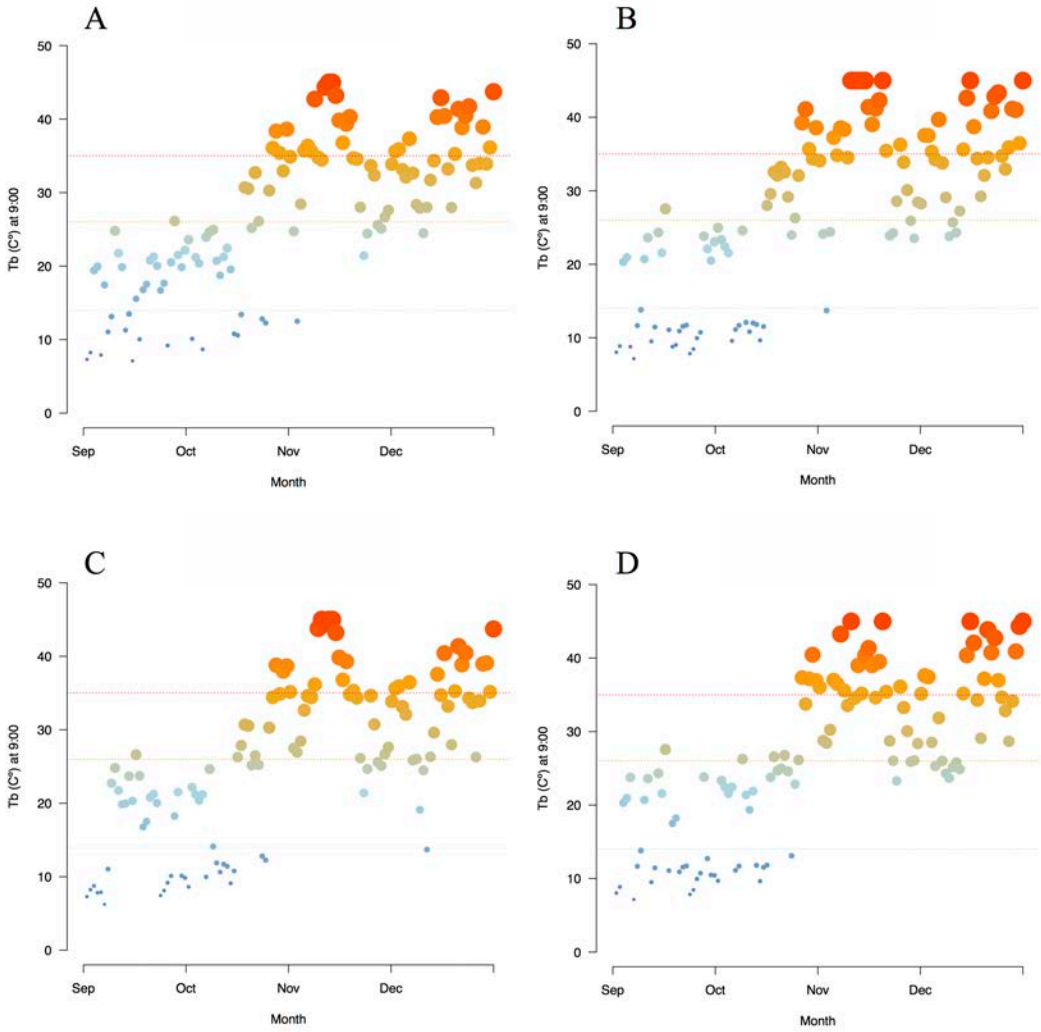

Figure 16. Example of T_b (ºC) in the morning (09:00 hours) throughout the breeding season comparing simulated adults and juveniles under low resource density. A) Optimising adult, B), optimising juvenile C), satisficing adult, and D), satisficing juvenile. Horizontal dashed blue, orange, and red lines represent basking temperature (14ºC), lower activity range temperature (T_{lower}, 26ºC), and upper activity range temperature (T_{upper}, 35ºC), respectively.

Adults and juveniles took the same amount of time throughout the breeding season to reach their activity range temperature (T_{lower}, 26ºC) from a given time in the morning (09:00; Fig. 17). The later, warmer half of the season allowed both juveniles and adults to reach their activity range temperature by 09:00 (Fig. 17, black arrows), a difference of 0.5 hours compared to the same time at the beginning of the season. From 6:00, both adults and juveniles needed half of the season (2 months) to reach the same T_b to that of 09:00 at the beginning of the season, but never reached their minimum activity range temperature (T_{lower}, 26ºC; cf. Figs 17A & B). This summed to 46 hours of activity time deficit across the entire breeding season.

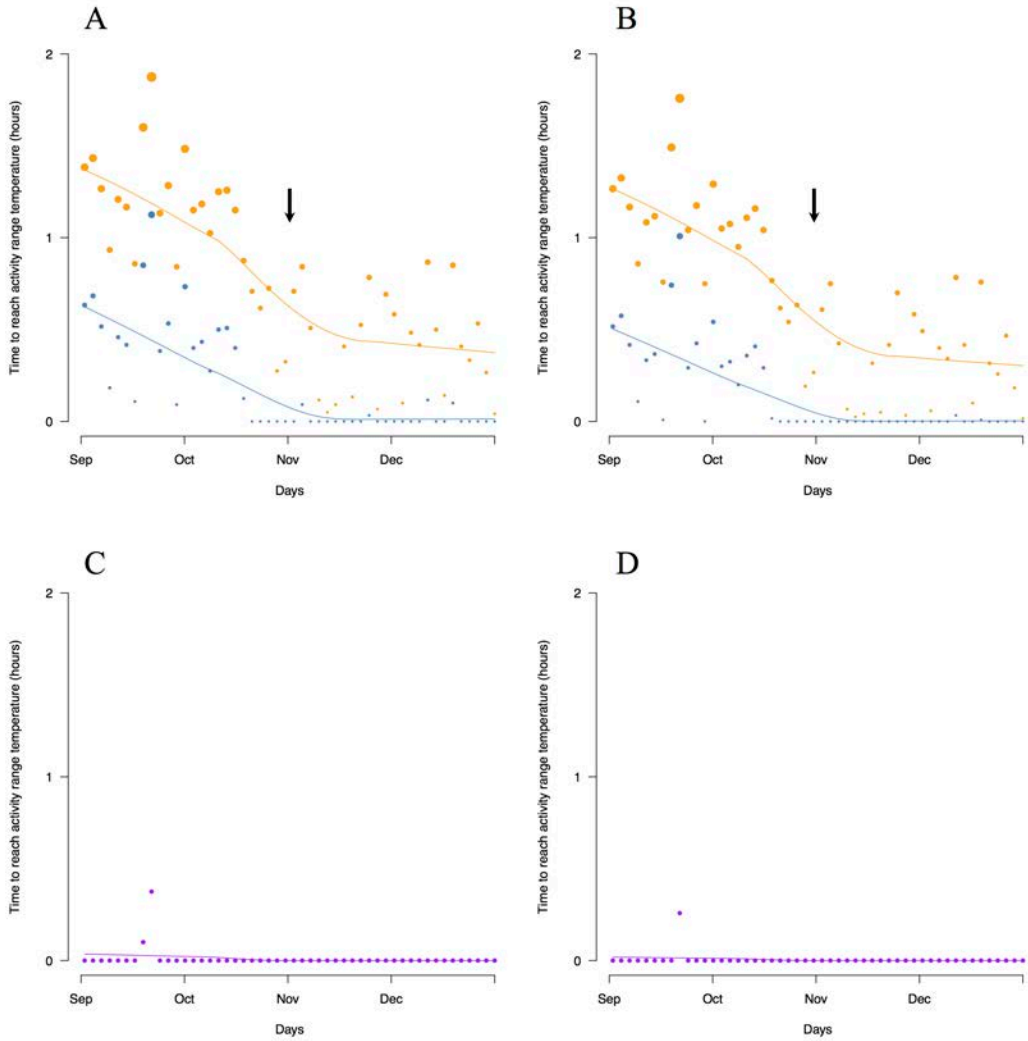

Figure 17. Time simulated optimising A) adults and B) juveniles take to reach their activity range (T_{lower}, 26ºC) from 06:00 AM (orange) and 09:00 AM (blue) throughout the breeding season. As a comparison, C) and D) show the time adults and juveniles, respectively, take to reach activity range throughout the breeding season when surrounding microclimate conditions are near optimal (12:00 PM; purple).

Metabolic properties

Juveniles under high resources showed the most growth potential, as indicated by growth of structure V compared to starting conditions at the beginning of the breeding season (Fig. 18). Juveniles under scarce food were also able to grow until halfway through the season when local food sources diminished.

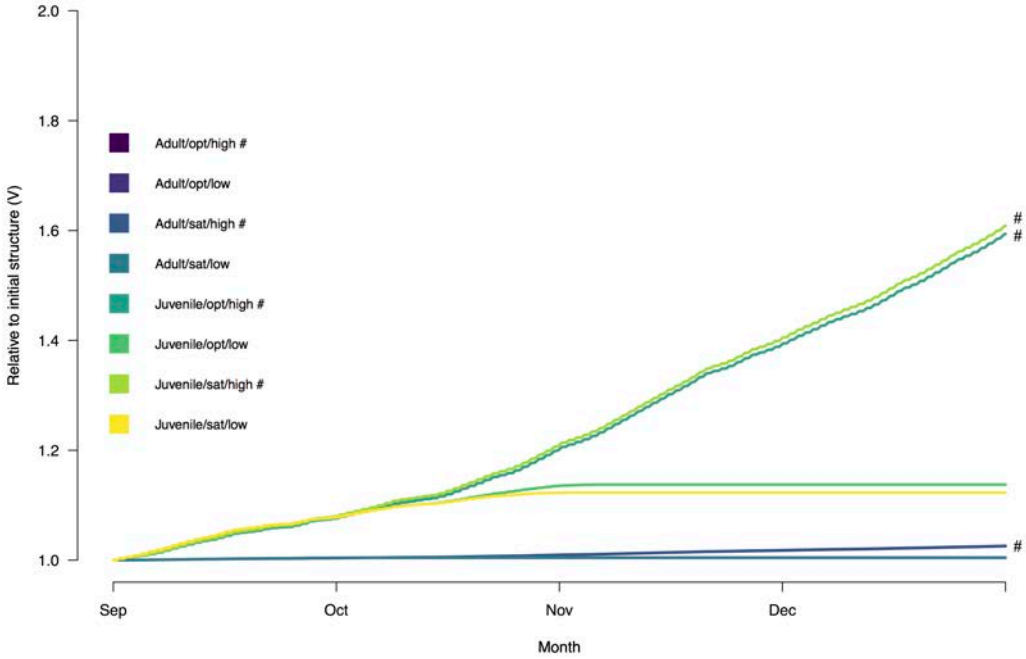

Figure 18. Relative structural volume to initial structural volume (*V*) of a random simulated adult (dark colours) and juvenile (light colours) under high (#) and low resources across the breeding season.

When resources were abundant, juveniles also showed the highest gain in wet mass (structural volume and energy reserve) relative to their initial starting mass for both movement strategies (Fig. 11 and Fig. 19). Adults under high resources that did not socialise (satisficing) were able to maintain a consistent body mass throughout the season. However, despite access to available resources, optimising adults lost the most relative mass. This was similar to satisficing juveniles and adults under low resources.

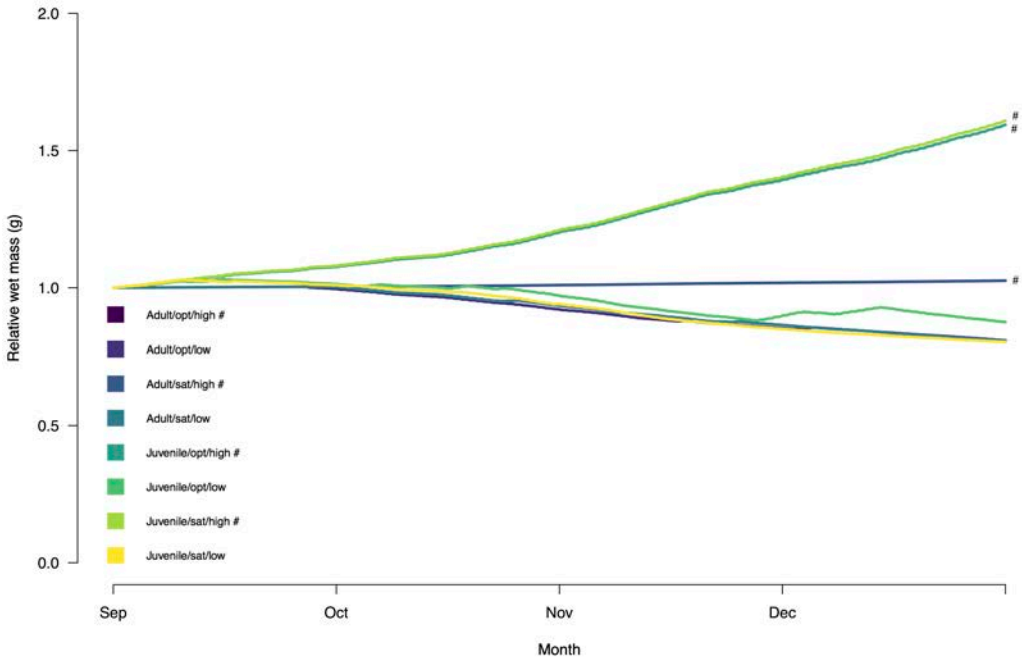

Figure 19. Total wet mass (structural volume *V* and reserve storage *E*) of a randomly simulated adult (dark colours) and juvenile (light colours) under high (#) and low resources across the breeding season.

Juveniles maintained a stable body condition (measured by the ratio of energy reserves to total wet mass) when resources were abundant and the individual avoided social movement (Fig. 20), thus reducing potential movement costs. In contrast, when resources were low, juveniles avoiding social movement suffered the greatest loss in body condition throughout the season. This suggests access to adjacent resources is more important than movement strategy for the early life stage susceptible to high thermal costs.

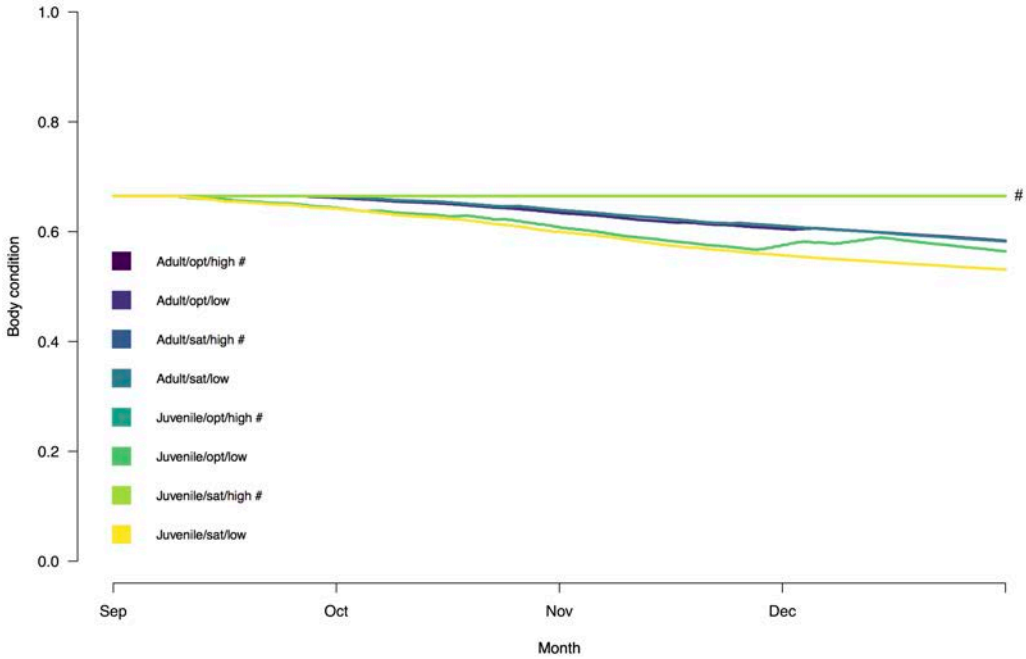

Figure 20. Body condition, measured as the ratio of reserve storage *E* to total wet mass (structural volume *V* and reserve storage *E*) of a random simulated adult (dark colours) and juvenile (light colours) under high (#) and low resources across the breeding season.

Discussion

We extend the IDEBM model in Chapter 3 to explore how body sizes and its relationship with the physiological responses of the animal throughout the day influences activity patterns and home range emergence within a varying resource and climate space. These responses include changes in T_b, heating and cooling rates, the time to reach their activity range, differences in activity budgets, and changes to metabolic properties throughout the individual life cycle. By simulating animals of different body size and their associated maturation state, we show how habitat requirements and movement strategies can depend on physiological mechanisms throughout the animal life cycle.

Home range area and body mass

Adults and juveniles gained similar amounts of mass and shared similar home range areas under high resource density throughout the breeding season. In contrast, this suggests having fewer accessible resources can shape home range area at different times in the animal's life cycle. Indeed, body mass influences home range size when resource type and abundance varies, which changes with season (Saunders & McLeod 1999; Mysterud et al. 2001; Haskell et al. 2002; Greenleaf et al. 2007). For example, larger ruminants can better retain necessary fat storage than smaller animals (Millar & Hickling 1990), inferring a metabolic advantage of larger body mass under low resources that correlates with different home range areas (Mysterud et al. 2001). Therefore, body mass offers a practical mechanism for interpreting potential differences in home range area when resources vary.

Further, there is an interesting relationship between the density of resources in the landscape and how environmental conditions influence the animal's physiological response when these resources change. A large body mass can be a physical advantage to improve how the animal navigates its habitat (Fig. 12; Mysterud et al. 2001), leading to differences in home range emergence. However, movement strategy also plays a crucial role. In other words, when an animal takes a minimising approach to its movement, e.g. satisficing, emergent home ranges become the product of basic and essential movement. Therefore, accessible resources in the landscape could be more important than body mass in facilitating additional movement behaviour, such as socialising, which leads to differences in home range area. For example, an active foraging mode compared to a more passive sit-and-wait strategy in snakes led more active individuals to grow and mature faster, which occurred during the juvenile life phase (Webb et al. 2003). Food intake under different temperatures also drives juvenile size in anurans, as animals experience higher metabolic rates with increasing temperatures that determines growth relationships under changes in resource quality (Atkinson 1994; Álvarez & Nicieza 2002). The mechanism influencing growth success under different food availabilities can also be hormonal (Crespi & Denver 2005). Combined, these results suggest access to resources can be more advantageous than simply having a larger body mass earlier in the life cycle.

With fewer resources, avoiding additional and costly movement can inherently favour a more minimising movement strategy that is risk-averse and would otherwise expose the animal to detrimental risks, such as predation. This trade-off has long-term metabolic benefits. For example, despite having less foraging time, tobacco hornworm caterpillars compensated for reduced food access under predation by maturing faster, thus mediating the metabolic cost of their movement against their energetic intake with a movement strategy that meant less resource access (Thaler et al. 2012). For the individual activity budget, this reaffirms food availability at different times of the year shapes foraging success (Kitaysky et al. 1999; Metcalfe et al. 1999; Naef-Daenzer et al. 2000; Walther & Gosler 2001; Crawford et al. 2006) and future foraging time (Fig. 17), but becomes less important when socialising behaviour is not an integral part of the daily activity budget. Scenarios where this occurs include starvation periods (Newton 2007), that is closely tied to season (Brown & Brown 2000) and individual energy reserves (McNamara & Houston 1990).

A landscape of low resources also presented riskier and more immediate costs to juveniles than adults, such as more extreme rates of T_b change (Fig. 14). Despite their initial larger size, adults lost more mass than juveniles, even when scaled to initial starting mass (Fig. 11). However, large animals are better at regulating physical response rates, such as evaporative water loss under acute thermal stress (McKechnie & Wolf 2010) and, more importantly, tolerating these on finer time scales (Wright et al. 2004). An adult with a large mass heats and cools at slower rates to that of a smaller juvenile (Ayers & Shine 1997; Martín & López 2003). The inherent advantage of a larger body mass under thermal extremes has immediate consequences on the essential time and space scales of feeding, searching, and socialising. For example, a large mass contains more reserves, such as water, to withstand temperature extremes during essential activity hours in the day, allowing a competitive foraging advantage (Hoyle & Keast 1987; Weimerskirch et al. 1994; Grieco 2002). This has flow-on effects for future energy intake by increasing the possible active hours in the day during poor habitat conditions, such as low food (Monaghan et al. 1994; Hurlbert 2004). Further, animals in these scenarios are still susceptible to inherent movement costs that scale with mass (Garland 1983). However, existing approaches to this problem are often heuristic and thus lack a common mechanism based on general interpretation. To our knowledge, our work using a process-based, individual simulation model is the first to show how differences in physiology as a common mechanism across life stages influences individual responses rates to varying habitat conditions at a home range level.

At the home range level, increased activity hours can promote greater resource and home range emergence. However, the costs of this movement vary with the individual. We show these costs have a physiological mechanism. For juveniles, increased activity time is only adaptive if mediated against the higher costs of exposure to open patches (Huey 1974; Huey et al. 2009). These direct costs and challenges for juveniles produced the functional differences in microclimate zones and thus home ranges compared to adults (Fig. 11). We also found when resources were low, animals used shade patches as stepping-stones to disperse further and reach unexplored resource patches in the model landscape; for juveniles, this allowed some individuals to form large home ranges (Figure 13C). However, as mentioned, the costs of this increased space use on fine time and

space scales can be detrimental. These costs are both physical, i.e. heat stress (Huey et al. 1989; Cooper 2000; Huey et al. 2012; Kingsolver et al. 2013) (Fig. 14) and ecological, i.e. reduced foraging time (Ricklefs & Hainsworth 1968; Ayers & Shine 1997), territorial constraints (Grant et al. 1992), and higher predation (Huey & Pianka 1981; Brown 1988; Wehner et al. 1992).

Rate of Tb change and body mass

Both juveniles and adults showed similar T_b when measured at a consistent time of the day, e.g. 09:00, throughout the breeding season (Figs 15 & 16). Low resources forced animals into more extreme microclimates and thus higher T_b at all times throughout the season (Fig. 16). This suggests the impact of increasingly warmer temperatures later in the season on juveniles and adults in similar on long time scales. However, the rate of T_b change juveniles experienced on shorter time scales compared to adults primarily influenced their activity state. Under low resources, this impact was greater due to the longer exposure time to thermal extremes. This suggests the response rate of the animal to environmental change is intrinsically driven by physical attributes, such as body size. Indeed, this relationship is well-known (Nagy 1987; Brown & Nicoletto 1991; Gillooly et al. 2001; Cardillo et al. 2005; Woodward et al. 2005; Gardner et al. 2011; Sheridan & Bickford 2011), including in birds (Schoener 1968; Crick 2004; Teplitsky et al. 2008), fish (Mittelbach 1981; Genner et al. 2010), and mammals (Damuth 1981; Brown & Nicoletto 1991; Nagy 1994; Pélabon 1997; Toïgo et al. 2006; Ozgul et al. 2010).

Interestingly, adults and juveniles took the same mean time to reach their minimum activity range temperature (Fig. 17) at any given time throughout the season. This outcome is most likely due to more stable rates of T_b change when resting in shade (Huey 1991). Once animals switch from resting to basking or searching, juveniles indeed experienced a more rapid increase in T_b than adults. However, the time scale of this is finer than what can be captured by analysis. Juveniles took the same time to reach their activity range T_b, but experienced higher rates of T_b change than adults once within their activity range (Fig. 14). There is an obvious advantage here to having a larger body size: slower heating and cooling rates enable more exposure time to thermal extremes. However, juveniles can also benefit. Given the time to reach their activity range matched that of adults infers an equal opportunity to exploit available resources. However, for juveniles to benefit from this requires more actively limiting their exposure time to thermal extremes than adults. High resource abundance affords this. Therefore, the potential for juveniles to regulate their overall indirect movement costs, i.e. the energetic costs of movement associated with switching activity states, over longer time periods relies heavily on timely access to shade patches and refuge sites.

Activity budget and body mass

There was a consistent difference of approximately 15ºC in T_b between both the cooler, earlier months and the warmer, later months, irrespective of life stage, between being in low and high resources (Figs 15 & 16). This suggests fewer resources later in the breeding season could be more detrimental than fewer resources in the cooler and thus more tolerable earlier months, as individuals still have not reached their activity range

(Fig. 17). Further, metabolic costs increase in warmer temperatures, so being unable to satisfy metabolic demands under more extreme environmental conditions becomes costly. Indeed, fewer resources earlier in the season (Fig. 16) pushes the animal closer to its operative activity range earlier in the day (Fig. 17). This was consistent for both juveniles and adults and suggests two possible outcomes.

1) In an environment of fewer resources, animals are more frequently forced to displace from their current patch and thus can more readily exploit their available climate and resource space earlier in the day. The challenge for the animal in navigating its available niche lies in the trade-off between the energy levels of the animal, its energetic demands relative to its life stage, including future movement costs, and the amount of resources left in the landscape for the remainder of the season.

2) Being active at 09:00 in the later, warmer season afforded an extra 28 hours of potential activity time compared to the start of the season. For the individual activity budget, this means surplus essential foraging and socialising time to access much-needed resources at critical times in the season (Fig 7). For the individual energy budget, this discrepancy could contribute to increasingly important energetic demands in later life stages, such as reproductive buffer.

Metabolic constraints on life stage and habitat requirements

Access to resources became important later in the season for juveniles, where low resource density limited smaller bodied animals in maximising growth potential (Fig. 18). The high thermal costs to the smaller and less robust juveniles reduced their movement potential and thus access to resources under these conditions. This highlights the trade-offs animals face in their earlier life stages in scenarios where habitat conditions are less suitable to meet essential metabolic demands. Essentially, smaller animals need to feed more frequently, but their smaller size under thermal extremes constrains available activity time and movement in space. Smaller animals are also more susceptible to predation (Werner 1986; Woodward & Hildrew 2002; Floeter & Temming 2003), so also need to minimise ecological risks. In addition to these constraints, juveniles need to grow quickly during these early and more vulnerable life stages. Meeting the high metabolic demands of growth requires ample energy reserves, a process that begins with access to sufficient resources that are likely to become less accessible under global warming scenarios (Sinervo et al. 2010). Further, animals must compensate any potential movement under extreme habitat conditions with sufficient incoming energy for metabolic and movement costs incurred. Therefore, habitat use, the associated risks to movement potential, and the energetic costs of activity times appear to shift with changing body size and life stage of the animal.

Measurements of relative wet mass loss among juveniles and adults showed both juveniles and adults lost relatively more mass than starting conditions when resources were scarce (Fig. 19). Animals that only foraged when hungry and did not socialise (satisficing) only performed well when resources were abundant. Despite their larger size, both optimising and satisficing adults lost the same amount of relative mass as

juveniles under low resources (Fig. 19). This was similar to the other end of the body size spectrum, where juveniles under low resources suffered the most irrespective of their movement strategy. A number of factors can explain this pattern.

Firstly, both the costs and benefits of having a larger body size at different times in the life cycle are indeed linked to resource use, where access to resources is imperative to maintaining or gaining weight. Secondly, the larger initial mass of adults means they have the most potential to lose weight, so total potential mass lost by smaller-bodied animals is restricted by their smaller structural size. It is possible habitat constraints appear to ease as the animal grows and becomes less susceptible to environmental extremes. However, growth performance and survival can depend on how well animals compensate for mass loss during times of depleted resources; this pattern shifts throughout year, where performance changes with the ability to acclimate and tolerate environmental extremes (Van Dijk et al. 2005). Under low resources, active adults were exposed to higher thermal extremes and thus needed to meet higher metabolic demands. Our results show that, even under high resources, meeting the metabolic demands of increased activity became more difficult in the later and warmer season. Finally, higher levels of activity are energetically expensive. Despite having access to resources, optimising adults in our simulations had additional behaviours that can potentially lead to losses in performance by markedly increasing movement and metabolic costs. For example, mate competition among males and parental care during the breeding season can incur high energetic costs, leading to weight loss at specific times of the year (Dietz et al. 1994; Achenbach & Snowdon 2002). Therefore, access to food throughout the year to ameliorate metabolic losses from increased activity may depend largely on efficient strategies for maximising energy return (Monaghan et al. 1994; Bergman, Carita et al. 2001; Guensch et al. 2001).

Compared to relative wet mass, we found animals were able to maintain their body condition (measured by the ratio of energy reserves to total wet mass) under high resources, but lost condition when resources became scarce (Fig. 20). This infers abundant resources are sufficient to fill energy reserves. A larger body mass allowed adults under low resources to withstand high environmental temperatures and better utilise energy reserves to offset the high metabolic costs of activity under environmental extremes. Despite less overall activity time, satisficing juveniles suffered the greatest loss in body condition when resources were scarce. It is likely increasingly warmer temperatures in the latter part of the season pushed juveniles into higher acute thermal stress and increased metabolic rates. Therefore, having a larger mass offers a physiological advantage when environmental conditions push the individual outside their operative temperature and when movement becomes more restricted in space.

Conclusions and future directions

Our previous results show the IDEBM model captures space and home range use of observed field data for an ectotherm model (Chapter 3). By simulating different activity states, we can use simulations to infer observed activity of real animals based on movement periods at different times of the day and breeding season. For this chapter, we extend the IDEBM model to incorporate body mass as a surrogate for the different life stages of the animal. Typically, body mass is a common metric for conveniently measuring many correlated individual traits that may otherwise be difficult or unnecessary to measure separately. While this approach may be useful and convenient (Yen et al. 2017), we argue the benefit of incorporating explicit physiological traits that capture individual response rates is a necessary step when estimating activity, movement, and home range patterns from a process-based perspective.

We show that such individual traits, such as physiology, mass, and energy reserves, are unifying mechanisms driving such patterns. We achieved this by integrating a complete individual energy and mass budget model that estimates the essential differences in physiology among life stages. By using a process-based model that considers how habitat constraints directly impact the changing metabolic state of the animal, we show the combination of individual metabolism and energy use, the physical environment, and constraints on different life stages offers essential insights into how individuals may adapt to changing environments throughout their life cycle. As a result, we show the individual energy budget and physiology are universal and scalable mechanisms among different-sized animals tenable within a variety of habitats and niches.

We applied an individual-based movement model to simulate how the different life stages of the animal respond to habitats of varying resources. Specifically, the IDEBM model simulates a mosaic of food and thermal patches to interpret the physiological response of the animal to fine scale environmental constraints. Juveniles and adults took the same mean time to reach their minimum activity range temperature (T_{lower}, 26ºC). However, this result is tricky to parse because of the very fine time scale at which this physiological response rate occurs. As we have shown, we can simulate and analyse the rate of T_b change. However, measuring the time difference it takes animals of different mass to reach a certain body temperature is less simple. This is partly due to the feedback between the model simulation time step and generating the results. It would be worth exploring this further by simulating movement paths of both juveniles and adults through precisely constructed, but realistic landscapes that force the animal to navigate identical paths. The movement paths of simulated animals from the IDEBM model are CRW. However, for the purposes of exploring the time to reach a certain T_b, enforcing a calibrated movement conduit through different microclimates would parse the difference in elapsed time at an appropriate time scale.

Our model emphasises the crucial role of physical mechanisms at the individual-level to interpret differences in movement outcomes and habitat use throughout the individual life cycle. By using two extremes in structural body size and associated maturation levels, we

show that habitat use by animals changes throughout the individual life cycle. Juveniles were under greater thermal stress than adults when resources abundance was low, suggesting timely access to resources is a key constraint to available activity time for different sized animals. Faster heating and cooling rates force juveniles into increasingly narrower activity windows as the season shifts climates to greater thermal extremes. Therefore, a larger body size infers an adaptive physiological and ecological advantage in scenarios that induce high metabolic costs to the individual. The combined results highlight the relationship between the physiology of the animal and how the metabolic requirements of different life stages influence expected activity times, space use, and home range patterns.

Acknowledgements

We thank Joanna Pelc for help with analysis and Michael Bull for early guidance on manuscript development.

Funding

This research was funded by an APA and Holsworth Research Grant to MM and ARC Discovery grants DP140101240 and DP110102813 to MRK. Simulations were possible from a resource allocation grant from the Victorian Life Sciences Computation Initiative to MRK. MM also acknowledges funding from the Centre of Excellence for Biosecurity Risk Analysis.

Authors' contributions

4

MM conceived and wrote the manuscript, developed the simulation models and parameterised the energy budget model and MRK co-conceived the manuscript, developed the microclimate model, the *NicheMapR* R package, and parameterised the energy budget model.

Data accessibility

Full code for the microclimate model (onelump_varenv.R), energy budget model (DEB.R), and Netlogo code for the individual-based decision-making model are available in Appendix A and https://doi.org/10.5281/zenodo.998145. Microclimate data for the study site and *R* simulation code for juveniles and adult simulations are available on Github at https://github.com/darwinanddavis/adultjuv.

Competing interests

The authors declare they have no competing interests.

Ethics approval and consent to participate

Not applicable.

Summary and further thoughts

Throughout this thesis, I have identified possible mechanisms linking the external environment with the individual. The main thrust of this thesis was to distil individual movement into a common mechanism shared across taxa, then build a framework based on this mechanism to forecast movement in future scenarios under environmental change. I showed that interpreting how changing environments will impact movement patterns in space and time depends on the direct, mechanistic link between the internal state of the animal and the constraints on the individual from the external environment. I identified energy uptake and use by the individual as a general and unifying mechanism among animals driving the internal, individual state and its outcomes in space and time. In space, these include movement patterns, patch use, habitat selection, dispersal potential, and home range use. Over time, such physical constraints on individual physiology and the energy budget manifest as direct and indirect movement costs that scale to fitness consequences on growth and reproduction, as well as costs and gains on the activity budget.

In Chapter 1, I discussed how individual-based models present useful and practical modelling platform to incorporate processes and mechanisms driving species responses to environmental change. I argue that energy use and the individual energy and mass budget of the animal connect individuals to their environment, other animals, and higher levels of biological complexity. This allows us to translate species' responses to change across scales. Further, we require appropriate theory to fill in missing parts of individual ecology when extrapolating beyond empirical work. The individual is the core unit of measurement for understanding how habitat constraints are expected to impact animal movement directly.

I reviewed the literature on how individual-based models at the patch, home range, I reviewed the literature on how individual-based models at the patch, home range, and landscape levels apply and deal with energy use by the individual. This incorporated fine scale movement, home range emergence, dispersal potential, and migration decisions. I also identified the complementary and common processes that influence movement across all time and space scales. These include learning and memory use, mating and sociality, predator avoidance, group movement, and seasonally-driven migration. Majority of the papers I reviewed support the idea that explicit treatment of energetics is a growing need in movement models. Future environments are variable and uncertain. Building movement models with the general and predictable principles of energy exchange at their core allows us to translate behavioural changes, activity budgets, and movement patterns across different space and time scales.

Chapter 2 introduced a general metabolic theory—Dynamic Energy Budget (DEB) theory—that bounds the principles of energy and mass exchange to the individual. I applied DEB theory to package the metabolic state of the animal into an individual-based modelling primer, i_{DEB}. The i_{DEB} primer links the internal state of the animal with

decision-making to estimate the trajectory of metabolic costs of movement. I summarised movement costs into direct and indirect to partition the way habitat constraints on the energy budget impact 1) the metabolic state of the animal and 2) future movement potential from activity and behaviour. The aim was to build a modelling framework that can connect the internal state with movement decisions in a general way. As a corollary, this aims to limit the incentive to rely on ad hoc estimates of energy use when constructing movement models. Advances in field technology used for collecting movement data are improving how we interpret energy use in movement ecology. These technologies include biologging, accelerometers, and GPS tags that allow us to gather enormous amounts of useful data. The challenge now is to interpret these data with useable concepts. For example, the concept of the energy landscape (Wilson et al. 2012; Shepard et al. 2013; Scharf et al. 2016) is a promising approach that has taken practical knowledge from the field summarised with an understanding of explicit space use by the animal. Exploring how this concept can be supplemented with a theory-based understanding of animal movement will present new avenues of research.

In Chapter 3, I integrated the i_{DEB} primer into a complete energy and mass budget-driven individual-based movement model (Individual Dynamic Energy Budget Movement model; IDEBM) of an ectothermic animal explicit in space and time. I tested data on the movement of the case study species, the sleepy lizard *Tiliqua rugosa*, together with data on the habitat and climate of the study site in southern Australia. I summarised the energetic and thermal costs of movement by exploring how environmental temperatures affect the thermal state of the animal. The IDEBM model integrates three coupled sub-models: a metabolic model of an animal's energy and mass balance, including direct movement costs, based on DEB theory; a transient heat budget model for calculating changes in the individual thermal state in response to varying habitat microclimates; and a decision-making model driving movement in space and time. From this, I generated movement and home range patterns under contrasting movement strategies (optimising and satisficing) and resources densities (dense and sparse) in a simulated model landscape. The model generates the activity budget of searching, feeding, and resting behaviours, T_b profiles, home range areas in space, and metabolic properties and costs. The IDEBM model successfully captured home range use by the wild sleepy lizard population at the study site and highlighted how movement behaviour of sleepy lizards is consistent with feeding requirements and thermal constraints on the individual. Movement strategy also influenced the metabolic consequences of space use, where a more active strategy (optimising) yielded no additional benefit in metabolic fitness outputs than a minimising strategy (satisficing).

The home range results from Chapter 3 identify some caveats when interpreting space use and home range patterns by animals. From the IDEBM model, I found home range size of adults was similar between sparse and dense resource patterns. However, the T_b profiles show animals with an active searching strategy (optimising) in a sparse resource landscape spent less time transitioning between shade and sun patches. The heat budget model captures T_b change at a finer scale than home range patterns emerging at the end of the breeding season. Therefore, rates of T_b change under low resources appear much lower and produces a smoother T_b curve compared to more erratic ones from animals in a dense resource landscape. Smoother T_b profiles when resources are low may lead us to

incorrectly assume lower rates of T_b change and thus low thermal stress to the animal (acute thermal stress; McKechnie & Wolf 2010); this could influence how we interpret the sensitivity of animals to thermal stress over long time periods. Therefore, we need to take caution when interpreting forecasts from this and similar models at fine space and time scales. A potential explanation for an erratic T_b profile under dense resources is animals more frequently encounter and pass over shade patches instead of sojourning, thus rapidly raising and dropping T_b. A possible solution here is to modify the correlated random walk (CRW) behaviour of the individual to avoid shade patches when moving within its activity range (T_{lower} and T_{upper}). However, this seems like an unnecessary assumption to implement given it detracts from expected behaviour in the wild.

In Chapter 4, I extended the IDEBM model to test how metabolic and thermal constraints on body size influence habitat requirements and space use across the individual life cycle. I used DEB theory estimates of body size together with the physical constraints on the heat balance of the animal for the juvenile and adult life stages. Body size is closely tied to metabolic rates that depend on environmental temperature, which restricts space use by the animal. The metabolic and thermal costs to the individual meant smaller-bodied juveniles were more vulnerable to environmental extremes, thus reducing home range size and available activity time. A landscape of low resources presented riskier and more immediate costs to juveniles than adults, such as more extreme rates of T_b change. By using two extremes in structural body size and associated maturation levels, I show that incorporating body size in a process-based model allows us to translate the habitat requirements of different life stages into physiological mechanisms.

Environmental temperatures limits the distance individuals can displace from refuges (Christian et al. 1983; Lyons et al. 2013; Merkle et al. 2016). However, as we have seen in Chapter 3 and 4, the relationship among space use, the individual, and movement costs can be subtle. For example, low resource density creates large distances between potential refuge sites, but also allows animals to displace further and thus widen their home range. To further tease apart this relationship, future work aims to highlight the fitness consequences of straying from refuges in environments that incur high costs to individual physiology. One approach is to simulate above average environmental temperatures and compare movement costs against those in the hottest days of the year when resources are sparse. The aim here is to highlight how distance from refuge sites influences costs to fitness and increased space use under environmental extremes, a common hazard to habitat use by animals (Villén-Pérez et al. 2013; Padie et al. 2015; Spiegel et al. 2015).

Further work aims to explore whether energy investment into movement versus metabolism, such as reproductive mass, is gender specific. For example, females invest substantial energy reserves into sexual maturation and offspring development (Wade 1979; Duncan et al. 1984; Gittleman & Thompson 1988; Castellano et al. 2004). In DEB theory, this energy is mobilised down the $1 - \kappa$ path for maturity and reproductive potential; comparatively, the fate of surplus energy costs of movement in males that females normally invest into reproduction may translate to considerable differences in movement costs and thus home range patterns. Metabolic costs of movement are more discernable over larger time scales; here, physical change in the individual and

environmental change, such as seasonal food cycles, can be more easily observed (Pérez-Barbería et al. 1998). Therefore, exploring how metabolic investment of movement varies with gender should be at appropriate and detectable scales. Gender-specific movement is closely linked to sociality (Komers & Brotherton 1997; Murray & Bull 2004; Godfrey et al. 2012; Spiegel et al. 2017). This suggests there are tractable ways to estimate differences in home range emergence from social behaviour, such as movement strategy.

This thesis explores the habitat constraints on individual movement of one type of ectotherm species at a given semi-arid site in southern Australia. There is much scope to extend this work to simulate other habitats and conditions, such as hotter or cooler mean daily temperatures. For example, the physical constraints on body size and the sociality of gender-specific movement are future steps in building the complete picture of habitat use at different stages of the life cycle. The bottom-up approach of the IDEBM model allows us to address common ecological challenges tied to model development, such as scaling from individuals to population (Ellis et al. 2012; Jeltsch et al. 2013; Martin et al. 2013; Bauer & Hoye 2014; Ayllón et al. 2016) and ecosystem levels (Jeltsch et al. 2013; Purves et al. 2013; Bauer & Hoye 2014). The IDEBM framework also shows potential to interpret how movement trade-offs translate from the individual to group (Huse & Giske 1998; Huse et al. 2004; Pettifor et al. 2000; Kramer-Schadt et al. 2005; Duriez et al. 2009; Bocedi et al. 2014; Aben et al. 2014; Hayes & Thompson 2013; Henry et al. 2014; Merkle et al. 2015). Movement outcomes at higher levels of biological complexity is primarily linked to the individual (Börger et al. 2008; Holyoak et al. 2008; Nathan et al. 2008; Duriez et al. 2009; Giuggioli & Bartumeus 2010; Sibly et al. 2013; Bauer & Klaassen 2013; Benhamou 2014). This type of modelling is becoming increasingly popular in its scope as computer power improves and data become more accessible and collaborative (Morales et al. 2004; Bauer et al. 2009; Nams 2014; Bird et al. 2014; Wilson et al. 2015; Scharf et al. 2016).

Future avenues for the IDEBM model will be to explore whether the framework can usefully capture movement and dispersal trade-offs at the many time and space scales of migration. Freely available movement data at the migration scale from online repositories, e.g. Movebank (https://www.movebank.org/), provide a sandbox to test the model capabilities. Further, these databases are supported by global environmental datasets, such as climate data and satellite imagery, from peer-supported sources, such as the Environmental Data Automated Track Annotation System (Env-DATA, https://www.movebank.org/node/6607). These combined data and toolboxes present an opportunity to apply the IDEBM framework to readily available systems. Using this approach, we can explore how interacting individuals influence the stability and performance of group migration from the perspective of individual limits. By combining migration data with climate and resource data, the IDEBM model can allow us to test 1) how animals use energy as a mechanism to define their activity budget and thus inform and adapt migration decisions from the patch to landscape scale and 2) whether these internal cues can accurately forecast individual and group migration when confronted with the uncertainty of resource, habitat, and climate availability across the patch and landscape scales of migration. Questions to ask include whether migrating animals aim to maximise return on their movement decisions or minimise risk under future uncertainty. With the individual as a scalable unit at the core, we can explore whether key constraints,

such as food or climate, are limiting to migration strategies and how migrants trade-off their energy and time costs to negotiate these in space and time.

The final potential scope for the IDEBM model is testing its capabilities to predict species ranges and dispersal at larger spatial scales. I have emphasised throughout this thesis that the individual level is scalable when we know something about the behaviour of a species and when we have data on habitat requirements. Collaborative efforts on major ecological problems, such as predicting the spread of invasive species, bridge diverse disciplines and merge extensive data on species occurrence, animal GPS and tracking, habitat and environment conditions, and location-specific climates. Testing the IDEBM model in this context with these available data is an ideal starting point that offers new modelling solutions to applied problems. Finally, the bottom-up approach of the IDEBM model allows us to add or subtract data layers of the model to match the ecology of the system. Explicitly focussing on different layers of the model not only informs us which elements of the problem are the most important to consider, but also how to populate the model with the type of data available. Here, individual properties of the animal may be more limiting to dispersal potential than others, such as body size related to age demographics within a population. Using appropriate properties of the individual to fit the resolution of available data allows us to make more accurate forecasts of movement and dispersal potential in habitats expected under future environmental change.

A

Appendix A

Matthew Malishev[1,2*], C. Michael Bull[3], & Michael R. Kearney[2]

[1] *Centre of Excellence for Biosecurity Risk Analysis,* [2] *School of BioSciences, University of Melbourne, Parkville, Melbourne, 3010, Australia*

[3] *School of Biological Sciences, Flinders University, Adelaide, 5001, Australia*

This Appendix is found at https://doi.org/10.5281/zenodo.998145 or on Github at https://github.com/darwinanddavis/Thesis/tree/master/AppendixA.

[*]Corresponding author: matthew.malishev@gmail.com

Table of Contents

Data collection 128
NicheMapR microclimate model overview 129
onelump_varenv.R. 130
DEB.R. 136
Appendix A1 145
space and time scales 145
interface 145
globals 145
turtles-own 146
patches-own 147
breeds 147
setup 147
go 149
update T_b 150
make-decision 150
search 154
bounce 155
handle food 155
shade search 155
rest 155
socialise 156
update food levels 156
report patch color 156
report patch type 157
report results 157
to save world 158
spatial plot 158
get home range 158
draw home range 158
Appendix A2 160

Initial setup.....160
Read in microclimate data 161
Read in DEB parameters.....162
Initialise decision-making and DEB models.....163
Run simulation 165
Example of data output files from simulation.....171
Figures.....172
References.....174

Data collection

All data were collected at the sleepy lizard habitat study site (139°21'E, 33°55'S) at the Bundey Bore field station in the mid-north of South Australia during the breeding season (September to December, 2009). Animal data are for the adult sleepy lizard (n = 60). Individual animals were tagged with GPS units, step counters ('waddleometers'), and skin surface temperature probes at the beginning of the breeding season and tracked throughout the season using radio telemetry. Animals were captured and GPS data downloaded every two weeks throughout the breeding season for each individual, with batteries for the units replaced when needed. GPS units reported locations every 10 minutes, waddleometers recorded step counts every 2 minutes, and temperature probes recorded skin surface temperature every 2 minutes.

The simulation model uses a 2-minute time step to correspond to the frequency of observed data.

A

NicheMapR microclimate model overview

The NicheMapR microclimate model calculates hourly estimates of solar and infrared radiation, air temperature at 1 m and 1 cm above ground level, wind velocity, relative humidity, and soil temperature at different intervals, e.g. 0 cm, 10 cm, 20 cm, 50 cm, 100 cm, and 200 cm. The model uses minimum and maximum daily air temperature, wind speed, relative humidity, soil properties (conductivity, specific heat, density, solar reflectivity, emissivity), as well as the roughness height, slope, and aspect. Climatic data are gathered from a global data set of monthly mean daily minimum and maximum air temperatures and monthly mean daily humidity and wind speeds. Soil surface temperatures are computed using heat balance equations, accounting for heat exchange via radiation, convection, conduction, and evaporation.

For simulation time steps, the microclimate model verifies the microclimate conditions for the current simulation hour of the day, e.g. noon or 18:00, and location in space, i.e. the study site for the observed animal data, and updates patches in the simulation landscape (either sun or shade) with these microenvironment conditions. As the simulated animal moves in or ut of these patches at each time step, the animal updates its current T_b, including rates of change in T_b per 2-minute ime step.

The *onelump_varenv.R* and *DEB.R* functions update the individual internal thermal and metabolic states, respectively. See below for both model functions.

A

onelump_varenv.R.

onelump_varenv.R available on **Github**.

```
onelump_varenv<-function (t = seq(1, 3600, 60), time = 0, Tc_init = 5, thresh = 29,
   AMASS = 500, lometry = 2, Tairf = Tairfun, Tradf = Tradfun,
   velf = velfun, Qsolf = Qsolfun, Zenf = Zenfun, Flshcond = 0.5,
   q = 0, Spheat = 3073, EMISAN = 0.95, rho = 932, ABS = 0.85,
   colchange = 0, lastt = 0, ABSMAX = 0.9, ABSMIN = 0.6, customallom = c(10.4713,
      0.688, 0.425, 0.85, 3.798, 0.683, 0.694, 0.743), shape_a = 1,
   shape_b = 0.5, shape_c = 0.5, posture = "n", FATOSK = 0.4,
   FATOSB = 0.4, sub_reflect = 0.2, PCTDIF = 0.1, press = 101325)
{
   sigma <- 5.67e-08
   Tair <- Tairf(time + t)
   vel <- velf(time + t)
   Qsol <- Qsolf(time + t)
   Trad <- Tradf(time + t)
   Zen <- Zenf(time + t)
   Zenith <- Zen * pi/180
   Tc <- Tc_init
   Tskin <- Tc + 0.1
   RHskin <- 100
   vel[vel < 0.01] <- 0.01
   abs2 <- ABS
   if (colchange >= 0) {
      abs2 <- min(ABS + colchange * (t - lastt), ABSMAX)
   }
   else {
      abs2 <- max(ABS + colchange * (t - lastt), ABSMIN)
   }
   S2 <- 1e-04
   DENSTY <- 101325/(287.04 * (Tair + 273))
   THCOND <- 0.02425 + (7.038 * 10^-5 * Tair)
   VISDYN <- (1.8325 * 10^-5 * ((296.16 + 120)/((Tair + 273) +
      120))) * (((Tair + 273)/296.16)^1.5)
   m <- AMASS/1000
   C <- m * Spheat
   V <- m/rho
   Qgen <- q * V
   L <- V^(1/3)
   Flshcond <- 0.5
   if (lometry == 0) {
      ALENTH <- (V/shape_b * shape_c)^(1/3)
      AWIDTH <- ALENTH * shape_b
      AHEIT <- ALENTH * shape_c
```

A

```
    ATOT <- ALENTH * AWIDTH * 2 + ALENTH * AHEIT * 2 + AWIDTH *
      AHEIT * 2
    ASILN <- ALENTH * AWIDTH
    ASILP <- AWIDTH * AHEIT
    L <- AHEIT
    if (AWIDTH <= ALENTH) {
      L <- AWIDTH
    }
    else {
      L <- ALENTH
    }
    R <- ALENTH/2
  }
  if (lometry == 1) {
    R1 <- (V/(pi * shape_b * 2))^(1/3)
    ALENTH <- 2 * R1 * shape_b
    ATOT <- 2 * pi * R1^2 + 2 * pi * R1 * ALENTH
    AWIDTH <- 2 * R1
    ASILN <- AWIDTH * ALENTH
    ASILP <- pi * R1^2
    L <- ALENTH
    R2 <- L/2
    if (R1 > R2) {
      R <- R2
    }
    else {
      R <- R1
    }
  }
  if (lometry == 2) {
    A1 <- ((3/4) * V/(pi * shape_b * shape_c))^0.333
    B1 <- A1 * shape_b
    C1 <- A1 * shape_c
    P1 <- 1.6075
    ATOT <- (4 * pi * (((A1^P1 * B1^P1 + A1^P1 * C1^P1 +
      B1^P1 * C1^P1))/3)^(1/P1))
    ASILN <- max(pi * A1 * C1, pi * B1 * C1)
    ASILP <- min(pi * A1 * C1, pi * B1 * C1)
    S2 <- (A1^2 * B1^2 * C1^2)/(A1^2 * B1^2 + A1^2 * C1^2 +
      B1^2 * C1^2)
    Flshcond <- 0.5 + 6.14 * B1 + 0.439
  }
  if (lometry == 3) {
    ATOT <- (10.4713 * AMASS^0.688)/10000
    AV <- (0.425 * AMASS^0.85)/10000
    ASILN <- (3.798 * AMASS^0.683)/10000
```

A

```
    ASILP <- (0.694 * AMASS^0.743)/10000
    R <- L
}
if (lometry == 4) {
    ATOT = (12.79 * AMASS^0.606)/10000
    AV = (0.425 * AMASS^0.85)/10000
    ZEN <- 0
    PCTN <- 1.38171e-06 * ZEN^4 - 0.000193335 * ZEN^3 + 0.00475761 *
        ZEN^2 - 0.167912 * ZEN + 45.8228
    ASILN <- PCTN * ATOT/100
    ZEN <- 90
    PCTP <- 1.38171e-06 * ZEN^4 - 0.000193335 * ZEN^3 + 0.00475761 *
        ZEN^2 - 0.167912 * ZEN + 45.8228
    ASILP <- PCTP * ATOT/100
    R <- L
}
if (lometry == 5) {
    ATOT = (customallom[1] * AMASS^customallom[2])/10000
    AV = (customallom[3] * AMASS^customallom[4])/10000
    ASILN = (customallom[5] * AMASS^customallom[6])/10000
    ASILP = (customallom[7] * AMASS^customallom[8])/10000
    R <- L
}
if (max(Zen) >= 90) {
    Qnorm <- 0
}
else {
    Qnorm <- (Qsol/cos(Zenith))
}
if (Qnorm > 1367) {
    Qnorm <- 1367
}
if (posture == "p") {
    Qabs <- (Qnorm * (1 - PCTDIF) * ASILP + Qsol * PCTDIF *
        FATOSK * ATOT + Qsol * sub_reflect * FATOSB * ATOT) *
        abs2
}
if (posture == "n") {
    Qabs <- (Qnorm * (1 - PCTDIF) * ASILN + Qsol * PCTDIF *
        FATOSK * ATOT + Qsol * sub_reflect * FATOSB * ATOT) *
        abs2
}
if (posture == "b") {
    Qabs <- (Qnorm * (1 - PCTDIF) * (ASILN + ASILP)/2 + Qsol *
        PCTDIF * FATOSK * ATOT + Qsol * sub_reflect * FATOSB *
        ATOT) * abs2
```

A

```
}
Rrad <- ((Tskin + 273) - (Trad + 273))/(EMISAN * sigma *
   (FATOSK + FATOSB) * ATOT * ((Tskin + 273)^4 - (Trad +
   273)^4))
Rrad <- 1/(EMISAN * sigma * (FATOSK + FATOSB) * ATOT * ((Tc +
   273)^2 + (Trad + 273)^2) * ((Tc + 273) + (Trad + 273)))
Re <- DENSTY * vel * L/VISDYN
PR <- 1005.7 * VISDYN/THCOND
if (lometry == 0) {
   NUfor <- 0.102 * Re^0.675 * PR^(1/3)
}
if (lometry == 3 | lometry == 5) {
   NUfor <- 0.35 * Re^0.6
}
if (lometry == 1) {
   if (Re < 4) {
      NUfor = 0.891 * Re^0.33
   }
   else {
      if (Re < 40) {
         NUfor = 0.821 * Re^0.385
      }
      else {
         if (Re < 4000) {
           NUfor = 0.615 * Re^0.466
         }
         else {
           if (Re < 40000) {
             NUfor = 0.174 * Re^0.618
           }
           else {
             if (Re < 4e+05) {
               NUfor = 0.0239 * Re^0.805
             }
             else {
               NUfor = 0.0239 * Re^0.805
             }
           }
         }
      }
   }
}
if (lometry == 2 | lometry == 4) {
   NUfor <- 0.35 * Re^(0.6)
}
hc_forced <- NUfor * THCOND/L
```

A

```
GR <- abs(DENSTY^2 * (1/(Tair + 273.15)) * 9.80665 * L^3 *
   (Tskin - Tair)/VISDYN^2)
Raylei <- GR * PR
if (lometry == 0) {
   NUfre = 0.55 * Raylei^0.25
}
if (lometry == 1 | lometry == 3 | lometry == 5) {
   if (Raylei < 1e-05) {
      NUfre = 0.4
   }
   else {
      if (Raylei < 0.1) {
         NUfre = 0.976 * Raylei^0.0784
      }
      else {
         if (Raylei < 100) {
           NUfre = 1.1173 * Raylei^0.1344
         }
         else {
           if (Raylei < 10000) {
             NUfre = 0.7455 * Raylei^0.2167
           }
           else {
             if (Raylei < 1e+09) {
               NUfre = 0.5168 * Raylei^0.2501
             }
             else {
               if (Raylei < 1e+12) {
                 NUfre = 0.5168 * Raylei^0.2501
               }
               else {
                 NUfre = 0.5168 * Raylei^0.2501
               }
             }
           }
         }
      }
   }
}
if (lometry == 2 | lometry == 4) {
   Raylei = (GR^0.25) * (PR^0.333)
   NUfre = 2 + 0.6 * Raylei
}
hc_free <- NUfre * THCOND/L
hc_comb <- hc_free + hc_forced
Rconv <- 1/(hc_comb * ATOT)
```

A

```
  Nu <- hc_comb * L/THCOND
  hr <- 4 * EMISAN * sigma * ((Tc + Trad)/2 + 273)^3
  hc <- hc_comb
  if (lometry == 2) {
    j <- (Qabs + Qgen + hc * ATOT * ((q * S2)/(2 * Flshcond) +
      Tair) + hr * ATOT * ((q * S2)/(2 * Flshcond) + Trad))/C
  }
  else {
    j <- (Qabs + Qgen + hc * ATOT * ((q * R^2)/(4 * Flshcond) +
      Tair) + hr * ATOT * ((q * S2)/(2 * Flshcond) + Trad))/C
  }
  kTc <- ATOT * (Tc * hc + Tc * hr)/C
  k <- ATOT * (hc + hr)/C
  Tcf <- j/k
  Tci <- Tc
  Tc <- (Tci - Tcf) * exp(-1 * k * t) + Tcf
  timethresh <- log((thresh - Tcf)/(Tci - Tcf))/(-1 * k)
  tau <- (rho * V * Spheat)/(ATOT * (hc + hr))
  dTc <- j - kTc
  list(Tc = Tc, Tcf = Tcf, tau = tau, dTc = dTc, abs2 = abs2)
}
```

A

DEB.R.

DEB.R function available on **Github**.

```
DEB<-function (step = 1/24, z = 7.997, del_M = 0.242, F_m = 13290 *
   step, kap_X = 0.85, v = 0.065 * step, kap = 0.886, p_M = 32 *
   step, E_G = 7767, kap_R = 0.95, k_J = 0.002 * step, E_Hb = 73590,
   E_Hj = E_Hb, E_Hp = 186500, h_a = 2.16e-11/(step^2), s_G = 0.01,
   T_REF = 20, TA = 8085, TAL = 18721, TAH = 9E+4, TL = 288,
   TH = 315, E_0 = 1040000, f = 1, E_sm = 1116, K = 1, andens_deb = 1,
   d_V = 0.3, d_E = 0.3, d_Egg = 0.3, mu_X = 525000, mu_E = 585000,
   mu_V = 5e+05, mu_P = 480000, kap_X_P = 0.1, n_X = c(1, 1.8,
      0.5, 0.15), n_E = c(1, 1.8, 0.5, 0.15), n_V = c(1, 1.8,
      0.5, 0.15), n_P = c(1, 1.8, 0.5, 0.15), n_M_nitro = c(1,
      4/5, 3/5, 4/5), clutchsize = 2, clutch_ab = c(0.085,
      0.7), viviparous = 0, minclutch = 0, batch = 1, lambda = 1/2,
   VTMIN = 26, VTMAX = 39, ma = 1e-04, mi = 0, mh = 0.5, arrhenius = matrix(data =
 matrix(data = c(rep(TA,
      8), rep(TAL, 8), rep(TAH, 8), rep(TL, 8), rep(TH, 8)),
      nrow = 8, ncol = 5), nrow = 8, ncol = 5), acthr = 1,
   X = 10, E_pres = 6011.93, V_pres = 3.9752^3, E_H_pres = 73592,
   q_pres = 0, hs_pres = 0, surviv_pres = 1, Es_pres = 0, cumrepro = 0,
   cumbatch = 0, p_B_past = 0, stage = 1, breeding = 0, pregnant = 0,
   Tb = 33)
{
   q_init <- q_pres
   E_H_init <- E_H_pres
   hs_init <- hs_pres
   fecundity <- 0
   clutches <- 0
   clutchenergy = E_0 * clutchsize
   n_O <- cbind(n_X, n_V, n_E, n_P)
   CHON <- c(12, 1, 16, 14)
   wO <- CHON %*% n_O
   w_V = wO[3]
   M_V <- d_V/w_V
   y_EX<-kap_X*mu_X/mu_E # yield of reserve on food
   y_XE<-1/y_EX # yield of food on reserve
   y_VE<-mu_E*M_V/E_G  # yield of structure on reserve
   y_PX<-kap_X_P*mu_X/mu_P # yield of faeces on food
   y_PE<-y_PX/y_EX # yield of faeces on reserve  0.143382353
   nM <- matrix(c(1, 0, 2, 0, 0, 2, 1, 0, 0, 0, 2, 0, n_M_nitro),
      nrow = 4)
   n_M_nitro_inv <- c(-1 * n_M_nitro[1]/n_M_nitro[4], (-1 *
      n_M_nitro[2])/(2 * n_M_nitro[4]), (4 * n_M_nitro[1] +
      n_M_nitro[2] - 2 * n_M_nitro[3])/(4 * n_M_nitro[4]),
```

A

```
    1/n_M_nitro[4])
n_M_inv <- matrix(c(1, 0, -1, 0, 0, 1/2, -1/4, 0, 0, 0, 1/2,
    0, n_M_nitro_inv), nrow = 4)
JM_JO <- -1 * n_M_inv %*% n_O
etaO <- matrix(c(y_XE/mu_E * -1, 0, 1/mu_E, y_PE/mu_E, 0,
    0, -1/mu_E, 0, 0, y_VE/mu_E, -1/mu_E, 0), nrow = 4)
w_N <- CHON %*% n_M_nitro
Tcorr = exp(TA * (1/(273 + T_REF) - 1/(273 + Tb)))/(1 + exp(TAL *
    (1/(273 + Tb) - 1/TL)) + exp(TAH * (1/TH - 1/(273 + Tb))))
M_V = d_V/w_V
p_MT = p_M * Tcorr
k_Mdot = p_MT/E_G
k_JT = k_J * Tcorr
p_AmT = p_MT * z/kap
vT = v * Tcorr
E_m = p_AmT/vT
F_mT = F_m * Tcorr
g = E_G/(kap * E_m)
E_scaled = E_pres/E_m
V_max = (kap * p_AmT/p_MT)^(3)
h_aT = h_a * Tcorr
L_T = 0
L_pres = V_pres^(1/3)
L_max = V_max^(1/3)
scaled_l = L_pres/L_max
kappa_G = (d_V * mu_V)/(w_V * E_G)
yEX = kap_X * mu_X/mu_E
yXE = 1/yEX
yPX = kap_X_P * mu_X/mu_P
mu_AX = mu_E/yXE
eta_PA = yPX/mu_AX
w_X = wO[1]
w_E = wO[3]
w_V = wO[2]
w_P = wO[4]
if (E_H_pres <= E_Hb) {
    dLdt = (vT * E_scaled - k_Mdot * g * V_pres^(1/3))/(3 *
        (E_scaled + g))
    V_temp = (V_pres^(1/3) + dLdt)^3
    dVdt = V_temp - V_pres
    rdot = vT * (E_scaled/L_pres - (1 + L_T/L_pres)/L_max)/(E_scaled +
        g)
}
else {
    rdot = vT * (E_scaled/L_pres - (1 + L_T/L_pres)/L_max)/(E_scaled +
        g)
```

A

```
    dVdt = V_pres * rdot
    if (dVdt < 0) {
        dVdt = 0
    }
}
V = V_pres + dVdt
if (V < 0) {
    V = 0
}
svl = V^(0.3333333333333)/del_M * 10
if (E_H_pres <= E_Hb) {
    Sc = L_pres^2 * (g * E_scaled)/(g + E_scaled) * (1 +
        ((k_Mdot * L_pres)/vT))
    dUEdt = -1 * Sc
    E_temp = ((E_pres * V_pres/p_AmT) + dUEdt) * p_AmT/(V_pres +
        dVdt)
    dEdt = E_temp - E_pres
}
else {
    if (Es_pres > 1e-07 * E_sm * V_pres) {
        dEdt = (p_AmT * f - E_pres * vT)/L_pres
    }
    else {
        dEdt = (p_AmT * 0 - E_pres * vT)/L_pres
    }
}
E = E_pres + dEdt
if (E < 0) {
    E = 0
}
p_M = p_MT * V_pres
p_J = k_JT * E_H_pres
if (Es_pres > 1e-07 * E_sm * V_pres) {
    p_A = V_pres^(2/3) * p_AmT * f
}
else {
    p_A = 0
}
p_X = p_A/kap_X
p_C = (E_m * (vT/L_pres + k_Mdot * (1 + L_T/L_pres)) * (E_scaled *
    g)/(E_scaled + g)) * V_pres
p_R = (1 - kap) * p_C - p_J
if (E_H_pres < E_Hp) {
    if (E_H_pres <= E_Hb) {
        U_H_pres = E_H_pres/p_AmT
        dUHdt = (1 - kap) * Sc - k_JT * U_H_pres
```

A

```
        dE_Hdt = dUHdt * p_AmT
    }
    else {
        dE_Hdt = (1 - kap) * p_C - p_J
    }
}
else {
    dE_Hdt = 0
}
E_H = E_H_init + dE_Hdt
if (E_H_pres >= E_Hp) {
    p_D = p_M + p_J + (1 - kap_R) * p_R
}
else {
    p_D = p_M + p_J + p_R
}
p_G = p_C - p_M - p_J - p_R
if ((E_H_pres <= E_Hp) | (pregnant == 1)) {
    p_B = 0
}
else {
    if (batch == 1) {
        batchprep = (kap  R/lambda) * ((1 - kap) * (E  m *
            (vT * V_pres^(2/3) + k_Mdot * V_pres)/(1 + (1/g))) -
            p_J)
        if (breeding == 0) {
            p_B = 0
        }
        else {
            if (cumrepro < batchprep) {
              p_B = p_R
            }
            else {
              p_B = batchprep
            }
        }
    }
    else {
        p_B = p_R
    }
}
if (E_H_pres > E_Hp) {
    if (cumrepro < 0) {
        cumrepro = 0
    }
    else {
```

```
        cumrepro = cumrepro + p_R * kap_R - p_B_past
    }
}
cumbatch = cumbatch + p_B
if (stage == 2) {
    if (cumbatch < 0.1 * clutchenergy) {
        stage = 3
    }
}
if (E_H <= E_Hb) {
    stage = 0
}
else {
    if (E_H < E_Hj) {
        stage = 1
    }
    else {
        if (E_H < E_Hp) {
            stage = 2
        }
        else {
            stage = 3
        }
    }
}
if (cumbatch > 0) {
    if (E_H > E_Hp) {
        stage = 4
    }
    else {
        stage = stage
    }
}
if ((cumbatch > clutchenergy) | (pregnant == 1)) {
    if (viviparous == 1) {
        if ((pregnant == 0) & (breeding == 1)) {
            v_baby = v_init_baby
            e_baby = e_init_baby
            EH_baby = 0
            pregnant = 1
            testclutch = floor(cumbatch/E_0)
            if (testclutch > clutchsize) {
              clutchsize = testclutch
              clutchenergy = E_0 * clutchsize
            }
            if (cumbatch < clutchenergy) {
```

A

```
            cumrepro_temp = cumrepro
            cumrepro = cumrepro + cumbatch - clutchenergy
            cumbatch = cumbatch + cumrepro_temp - cumrepro
          }
        }
        if (hour == 1) {
          v_baby = v_baby_init
          e_baby = e_baby_init
          EH_baby = EH_baby_init
        }
        if (EH_baby > E_Hb) {
          if ((Tb < VTMIN) | (Tb > VTMAX)) {
          }
          cumbatch(hour) = cumbatch(hour) - clutchenergy
          repro(hour) = 1
          pregnant = 0
          v_baby = v_init_baby
          e_baby = e_init_baby
          EH  baby = 0
          newclutch = clutchsize
          fecundity = clutchsize
          clutches = 1
          pregnant = 0
        }
      }
      else {
        if ((Tb < VTMIN) | (Tb > VTMAX)) {
        }
        if ((Tb < VTMIN) | (Tb > VTMAX)) {
        }
        testclutch = floor(cumbatch/E_0)
        if (testclutch > clutchsize) {
          clutchsize = testclutch
        }
        cumbatch = cumbatch - clutchenergy
        repro = 1
        fecundity = clutchsize
        clutches = 1
      }
    }
    if (E_H_pres > E_Hb) {
      if (acthr > 0) {
        dEsdt = F_mT * (X/(K + X)) * V_pres^(2/3) * f - 1 *
          (p_AmT/kap_X) * V_pres^(2/3)
      }
      else {
```

```
        dEsdt = -1 * (p_AmT/kap_X) * V_pres^(2/3)
    }
}
else {
    dEsdt = -1 * (p_AmT/kap_X) * V_pres^(2/3)
}
if (V_pres == 0) {
    dEsdt = 0
}
Es = Es_pres + dEsdt
if (Es < 0) {
    Es = 0
}
if (Es > E_sm * V_pres) {
    Es = E_sm * V_pres
}
gutfull = Es/(E_sm * V_pres)
if (gutfull > 1) {
    gutfull = 1
}
JOJx = p_A * etaO[1, 1] + p_D * etaO[1, 2] + p_G * etaO[1,
    3]
JOJv = p_A * etaO[2, 1] + p_D * etaO[2, 2] + p_G * etaO[2,
    3]
JOJe = p_A * etaO[3, 1] + p_D * etaO[3, 2] + p_G * etaO[3,
    3]
JOJp = p_A * etaO[4, 1] + p_D * etaO[4, 2] + p_G * etaO[4,
    3]
JOJx_GM = p_D * etaO[1, 2] + p_G * etaO[1, 3]
JOJv_GM = p_D * etaO[2, 2] + p_G * etaO[2, 3]
JOJe_GM = p_D * etaO[3, 2] + p_G * etaO[3, 3]
JOJp_GM = p_D * etaO[4, 2] + p_G * etaO[4, 3]
JMCO2 = JOJx * JM_JO[1, 1] + JOJv * JM_JO[1, 2] + JOJe *
    JM_JO[1, 3] + JOJp * JM_JO[1, 4]
JMH2O = JOJx * JM_JO[2, 1] + JOJv * JM_JO[2, 2] + JOJe *
    JM_JO[2, 3] + JOJp * JM_JO[2, 4]
JMO2 = JOJx * JM_JO[3, 1] + JOJv * JM_JO[3, 2] + JOJe * JM_JO[3,
    3] + JOJp * JM_JO[3, 4]
JMNWASTE = JOJx * JM_JO[4, 1] + JOJv * JM_JO[4, 2] + JOJe *
    JM_JO[4, 3] + JOJp * JM_JO[4, 4]
JMCO2_GM = JOJx_GM * JM_JO[1, 1] + JOJv_GM * JM_JO[1, 2] +
    JOJe_GM * JM_JO[1, 3] + JOJp_GM * JM_JO[1, 4]
JMH2O_GM = JOJx_GM * JM_JO[2, 1] + JOJv_GM * JM_JO[2, 2] +
    JOJe_GM * JM_JO[2, 3] + JOJp_GM * JM_JO[2, 4]
JMO2_GM = JOJx_GM * JM_JO[3, 1] + JOJv_GM * JM_JO[3, 2] +
    JOJe_GM * JM_JO[3, 3] + JOJp_GM * JM_JO[3, 4]
```

A

```
JMNWASTE_GM = JOJx_GM * JM_JO[4, 1] + JOJv_GM * JM_JO[4,
    2] + JOJe_GM * JM_JO[4, 3] + JOJp_GM * JM_JO[4, 4]
O2FLUX = -1 * JMO2/(T_REF/Tb/24.4) * 1000
CO2FLUX = JMCO2/(T_REF/Tb/24.4) * 1000
MLO2 = (-1 * JMO2 * (0.082058 * (Tb + 273.15))/(0.082058 *
    293.15)) * 24.06 * 1000
GH2OMET = JMH2O * 18.01528
#metabolic heat production (Watts) = growth overhead plus dissipation power (mainte
nance, maturity maintenance,
#maturation/repro overheads) plus assimilation overheads. correct to 20 degrees so it c
an be temperature corrected
#in MET.f for the new guessed Tb
DEBQMET = ((1 - kappa_G) * p_G + p_D + (p_X - p_A - p_A *
    mu_P * eta_PA))/3600/Tcorr
DRYFOOD = -1 * JOJx * w_X
FAECES = JOJp * w_P
NWASTE = JMNWASTE * w_N
if (pregnant == 1) {
    wetgonad = ((cumrepro/mu_E) * w_E)/d_Egg + ((((v_baby *
        e_baby)/mu_E) * w_E)/d_V + v_baby) * clutchsize
}
else {
    wetgonad = ((cumrepro/mu_E) * w_E)/d_Egg + ((cumbatch/mu_E) *
        w_E)/d_Egg
}
wetstorage = ((V * E/mu_E) * w_E)/d_V
wetfood = Es/21525.37/(1 - 0.18)
wetmass = V * andens_deb + wetgonad + wetstorage + wetfood
gutfreemass = V * andens_deb + wetgonad + wetstorage
potfreemass = V * andens_deb + (((V * E_m)/mu_E) * w_E)/d_V
dqdt = (q_pres * (V_pres/V_max) * s_G + h_aT) * (E_pres/E_m) *
    ((vT/L_pres) - rdot) - rdot * q_pres
if (E_H_pres > E_Hb) {
    q = q_init + dqdt
}
else {
    q = 0
}
dhsds = q_pres - rdot * hs_pres
if (E_H_pres > E_Hb) {
    hs = hs_init + dhsds
}
else {
    hs = 0
}
h_w = ((h_aT * (E_pres/E_m) * vT)/(6 * V_pres^(1/3)))^(1/3)
```

A

```
  dsurvdt = -1 * surviv_pres * hs
  surviv = surviv_pres + dsurvdt
  p_B_past = p_B
  E_pres = E
  V  pres = V
  E_H_pres = E_H
  q_pres = q
  hs_pres = hs
  suriv  pres = surviv_pres
  Es_pres = Es
  deb.names <- c("E_pres", "V_pres", "E_H_pres", "q_pres",
     "hs_pres", "surviv_pres", "Es_pres", "cumrepro", "cumbatch",
     "p_B_past", "O2FLUX", "CO2FLUX", "MLO2", "GH2OMET", "DEBQMET",
     "DRYFOOD", "FAECES", "NWASTE", "wetgonad", "wetstorage",
     "wetfood", "wetmass", "gutfreemass", "gutfull", "fecundity",
     "clutches")
  results_deb <- c(E_pres, V_pres, E_H_pres, q_pres, hs_pres,
     surviv_pres, Es_pres, cumrepro, cumbatch, p_B_past, O2FLUX,
     CO2FLUX, MLO2, GH2OMET, DEBQMET, DRYFOOD, FAECES, NWASTE,
     wetgonad, wetstorage, wetfood, wetmass, gutfreemass,
     gutfull, fecundity, clutches)
  names(results_deb) <- deb.names
  return(results_deb)
}
```

A

Appendix A1

Netlogo IBM decision making model (.nlogo). Available on **Github**.

space and time scales

```
; Spatial scale: 1500 * 1500 m
; 1 patch = 2 m
; 1 tick = 2 min
; 1 day = 720 ticks
; 1 tick = 2 bites possible for small food; 4 bites possible for large food
```

interface

```
; Energy cost of individual
; ========================
; Movement-cost:    Cost (J) of moving one patch (2 m). Calculated from DEB model.
; Maintenance-cost: Cost (J) of paying maintenance. Calculated from DEB model.

; Energy gain of individual
; =================
; Low-food gain:  Energy gain (J) from small food items (Brown 1991).
; kap_X:          Conversion efficiency of assimilated energy from food (J) (Kooijman 201
0).

; Food patch growth
; =================
; Large-food-initial: Initial energy level (J) of large food items at setup. Parameterised fro
m literature.
; Small-food-initial: Initial energy level (J) of small food items at setup. Parameterised fro
m literature.

; Individual attributes
; ===================
; Maximum-reserve: Maximum reserve level (J). Appears in 'to setup' and 'to make decisi
on'.
; Minimum-reserve: Define the critical starvation period. Individuals can survive without
food for two hours in this state (reasonable estimate).
```

globals

```
globals
[
  in-shade?          ; Reports TRUE if turtle is in shade
  in-food?           ; Reports TRUE if turtle is in a food patch
```

```
  min-energy        ; Minimum food unit level for individual to lose interest and move awa
y from patch. This eliminates the incentive for individuals to return immediately to the pr
eviously visited food patch after vacating it.
  reserve-level     ; Reserve level of individual.
  min-vision        ; Minimum (normal) vision range of individuals (Auburn et al. 2009).
  max-vision        ; Maximum vision range of individuals activated by starvation mode. S
ee 'to starving' procedure (Auburn et al. 2009)
  ctmincount        ; Counter for time spent under min_T_b_
  feedcount         ; Counter for time spent in feeding state.
  restcount         ; Counter for the time spent resting in shade
  searchcount       ; Counter for time spent searching for food.
  starvecount       ; Counter for time spent in starvation state.
  shadecount        ; Counter for time spent searching for shade following a feeding bout.
  transcount        ; Counter for frequency of transitions between any of the three activity s
tates--searching, feeding, resting.
  zenith            ; Zenith angle of sun (update-sun procedure).
  tempXY            ; XY coords for drawing homerange
  gutfull           ; Reports gut level of DEB model
  movelist          ; List of cumulative movement costs
  fh_               ; String for working dir to export results
  ]
```

turtles-own

```
turtles-own
[
  activity-state    ; Individual is either under a Searching, Feeding, or Resting state for eac
h tick. The transition between the various activity states defines the global behavioural re
pertoire.
  energy-gain       ; Converted energy gained from food
  T_b_              ; Body temperature (T_b) of individual (Celsius)
  T_b_basking_      ; Basking body temperature of individual (Celsius)
  T_opt_range       ; Foraging body temperature range of individual (Celsius)
  T_opt             ; Median foraging body temperature of individual (Celsius)
  T_opt_lower_      ; Lower foraging body temperature of individual (Celsius)
  T_opt_upper_      ; Upper foraging body temperature of individual (Celsius)
  min-T_b_          ; Lower critical body temperature (min-T_b) of individual (Celsius)
  max-T_b_          ; Upper critical body temperature (max-T_b) of individual (Celsius)
  vision-range      ; Vision (no. of patches) range of individual.
  has-been-starving? ; Results reporter only variable for reporting stavation time only if in
dividual has starved
  has-been-feeding?  ; Results reporter only variable for reporting feeding time only if ind
ividual has been feeding
  X                 ; List of x coords for homerange
  Y                 ; List of y coords for homerange
  gutthresh_        ; Threshold for gutlevel to motivate turtle to move
  V_pres_           ; DEB structural volume
```

A

```
  wetgonad_          ; DEB wet mass reproductive organ volume
  wetstorage_        ; DEB wet mass storage
  wetfood_           ; DEB converted food mass
  ]
```

patches-own

```
patches-own
[
  patch-type    ; Defines type of patches in environment as either Food or Shade.
  food-level    ; *> Interface <* Defines the initial and updated level of energy (J) in food
patches. Food level increases (plant growth; see 'Food patch growth' in Interface) and dec
reases (feeding by individual) with each tick.
  shade-level   ; *> Interface <* Defines the initial and updated level of shade in shade pat
ches. Shade levels remain constant throughout simulation.
  ]
```

breeds

```
breed
[homeranges homerange]
```

setup

```
to setup
  ca
  if Food-patches + Shade-patches > count patches
  [ user-message (word "Lower the sum of shade and food patches to < " count patches "."
)
    stop ]
  random-seed 1                        ; Outcomment to generate seed for spatial configuration
of all patches in the landscape (food and shade). For reproducibility. NB: turtle movemen
t is still stochastic. See below random-seed primitive for complete function.
  set min-energy Small-food-initial
  set min-vision 5                     ; 10m (Auburn et al. 2009)

  ask patches
  [set patch-type "Sun"
    set pcolor (random 1 + blue)]

  let NumFoodPatches Food-patches / 10
  ask n-of NumFoodPatches patches [
    ask n-of 10 patches in-radius 4 [ ; Sets 10 random food patches within a 5-patch radius
of Food-patches
    let food-amount random 100
    ifelse food-amount < 50
    [set food-level (Small-food-initial) + random-float 1 * 10 ^ -5] ; Makes only one food
```

```
patch attractive to turtle because turtles love good chow
    [set food-level (Large-food-initial) + random-float 1 * 10 ^ -5]
      set pcolor PatchColor
      set patch-type "Food"
      ]
  ]

ifelse Shade-density = "Random"[ ; chooser for setting Random or Clumped shade patche
s (similar to food patch arrangement)
  let NumShadePatches Shade-patches
  ask n-of NumShadePatches patches [
    let shade-amount random 100
    ifelse shade-amount < 50
    [set shade-level (Low-shade + random-float 1 * 10 ^ -5) ; Makes only one shade patch
attractive to turtle
      set pcolor black + 2]
    [set shade-level (High-shade + random-float 1 * 10 ^ -5)
      set pcolor black]
      set patch-type "Shade"
      ]
]
[
    let NumShadePatches Shade-patches / 10
    ask n-of NumShadePatches patches [
    ask n-of 10 patches in-radius 4 [ ; Sets 10 random food patches within a 5-patch radius
of Food-patches
    let shade-amount random 100
    ifelse shade-amount < 50
    [set shade-level (Low-shade + random-float 1 * 10 ^ -5) ; Makes only one shade patch
attractive to turtle
      set pcolor black + 2]
    [set shade-level (High-shade + random-float 1 * 10 ^ -5)
      set pcolor black]
      set patch-type "Shade"
      ]
]
]; close else shade loop

ask patch 0 0 [set patch-type "Shade"
  set pcolor black]

set movelist (list 0)
;  ask one-of patches with [patch-type = "Shade"]
;  [sprout 1]
crt 1
```

A

```
 random-seed new-seed ; Outcomment to generate seed for spatial configuration of all pat
ches in the landscape (food and shade).

  ask turtle 0
  [
    setxy 0 0 ;random-xcor random-ycor
    set reserve-level Maximum-reserve
    set T_b_basking_ 14
    set T_opt_range (list 26 27 28 29 30 31 32 33 34 35 )        ; From Pamula thesis
    set T_opt_upper last T_opt_range
    set T_opt_lower first T_opt_range
    set T_opt median T_opt_range
    set min-T_b_ min-T_b
    set max-T_b_ max-T_b
    set V_pres_ V_pres
    set wetgonad_ wetgonad
    set wetstorage_ wetstorage
    set wetfood_ wetfood
    set activity-state "S"
    set vision-range min-vision
    if [patch-type] of patch-here = "Shade"
    [set in-shade? TRUE]
     if [patch-type] of patch-here = "Food"
    [set in-food? TRUE]
    set shape "lizard"
    set size 2
    set color red
    pen-down
    set X (list xcor)
    set Y (list ycor)
    ]
setup-spatial-plot
set fh_ fh
reset-ticks
end

go

to go
  tick
  if not any? turtles
  [
    get-homerange
    print "All turtles dead. Check output of model results."
    repeat 3 [beep wait 0.2]
    stop
    save-world
```

A

```
  ]
 if (ticks * 2 / 60 / 24) = No.-of-days
 [
   ask turtle 0
   [report-results]
   stop
   save-world
   ]
 ifelse show-plots?
 []
 [clear-all-plots]
 ask turtle 0
 [
   report-patch-type
   ask turtles with [reserve-level > Minimum-reserve]
   [set vision-range min-vision]
   update-T_b
   make-decision
   set X lput xcor X ; populate X list with turtle X coords to generate home range
   set Y lput ycor Y ; populate Y list with turtle Y coords to generate home range
 ]
 if any? turtles with [reserve-level <= 0]
 [ask turtle 0 [report-results]
   stop
   ]
 ask patches with [patch-type = "Food"]
   [update-food-levels]
end
```

update T_b

```
to update-T_b
 ask turtles with [T_b >= max-T_b]
   [stop]
 if T_b <= min-T_b
   [set ctmincount ctmincount + 1]
   if (ctmincount * 2 / 60) = ctminthresh
   [stop]
end
```

make-decision

```
to make-decision

;-----------------------------------------------------------------------------------
;-------------------------------------Optimising-------------------------------------
;-----------------------------------------------------------------------------------
```

```
 ifelse (strategy = "Optimising")
 [; start optimising loop
   ifelse (T_b > T_opt_upper) or (T_b < T_opt_lower)
 [
   ask turtle 0
   [;set label "Resting"
     set activity-state "R"
       if [patch-type] of patch-here != "Shade"
     [shade-search]
     if ([patch-type] of patch-here = "Shade") and (T_b < T_b_basking_)
     [set in-shade? TRUE]
     ]
   if (activity-state = "R") and (T_b >= T_b_basking_) and (T_b < T_opt_upper) ; Baskin
g behaviour
   [set in-shade? FALSE
 ;      set transcount transcount + 1 ; Outcomment to include basking behaviour as activity
state
 ;      plotxy xcor ycor
   ]
 set restcount restcount + 1
   ]
    [; else optimising loop
       if (activity-state = "R")
   [
       set restcount restcount + 1
      ; set label "Resting"
     if ((T_b <= T_opt_upper) and (T_b >= T_opt_lower)); and reserve-level < search-ene
rgy
     [set transcount transcount + 1
       plotxy xcor ycor
       set activity-state "S"]
    ; [set activity-state "R"]
   ]


   if (activity-state = "F");
   [
     ifelse (gutfull < gutthresh) ;and ([patch-type] of patch-here = "Food") ; if gut is not fu
ll, keep feeding
     [
     ask turtle 0
     [handle-food
       ;set label "Feeding"
       set has-been-feeding? TRUE]
     if [patch-type] of patch-here != "Food" ; if patch isn not food, search for food
     [set activity-state "S"
```

```
      set transcount transcount + 1
      plotxy xcor ycor
      set energy-gain 0]
    if reserve-level >= Maximum-reserve ;
    [set transcount transcount + 1
      plotxy xcor ycor
;       ifelse (strategy = "Optimising")
;       [set activity-state "S"]
      set activity-state "R"
      stop]
    ]
    [;set label "Gut is full" ; otherwise, turtle moves during active hours of the day
      socialise
      set searchcount searchcount + 1
      plotxy xcor ycor
      ]
  ]

  if (activity-state = "S")
  [
    ask turtle 0
    [search
     ; set label "Searching for food"
     ]
    set searchcount searchcount + 1
    if ([patch-type] of patch-here = "Food") and (gutfull < gutthresh)
    [set transcount transcount + 1
      plotxy xcor ycor
      set activity-state "F"]
    ]
 ]
 ]; end optimising loop


;-----------------------------------------------------------------------------------
;-------------------------------------Satisficing-------------------------------------
;-----------------------------------------------------------------------------------

 [; else satisfice, i.e. move only when gutfull is below the gut threshold
 ifelse (T_b > T_opt_upper) or (T_b < T_opt_lower) or (gutfull >= gutthresh); 'gutfull' is
DEB.R input
 [
  ask turtle 0
  [;set label "Resting"
    set activity-state "R"
    ifelse gutfull >= gutthresh and T_b < T_opt_upper and T_b > T_opt_lower
```

A

```
    [;set label "Full gut"
      stop ]
    [if [patch-type] of patch-here != "Shade"
    [shade-search]]
    if ([patch-type] of patch-here = "Shade") and (T_b < T_b_basking_)
    [set in-shade? TRUE]
    ]
   if (activity-state = "R") and (T_b >= T_b_basking_) and (T_b < T_opt_upper) ; Baskin
g behaviour
   [set in-shade? FALSE
 ;     set transcount transcount + 1 ; Outcomment to include basking behaviour as activity
state
 ;     plotxy xcor ycor
   ]
 set restcount restcount + 1
   ]

  [
      if (activity-state = "R")
   [
      set restcount restcount + 1
     ; set label "Resting"
    if ((T_b <= T_opt_upper) and (T_b >= T_opt_lower)); and reserve-level < search-ene
rgy
    [set transcount transcount + 1
      plotxy xcor ycor
      set activity-state "S"]
   ; [set activity-state "R"]
   ]


   if (activity-state = "F")
   [
    ifelse (gutfull < gutthresh) ;and ([patch-type] of patch-here = "Food") ; if gut is not fu
ll, keep feeding, else stop.
    [
    ask turtle 0
    [handle-food
      ;set label "Feeding"
      set has-been-feeding? TRUE]
    if [patch-type] of patch-here != "Food"
    [set activity-state "S"
      set transcount transcount + 1
      plotxy xcor ycor
      set energy-gain 0]
    if reserve-level >= Maximum-reserve ; Turtle will fight between feeding and resting i
```

```
f DEB model not activated i.e. reserve incurs no cost.
      [set transcount transcount + 1
        plotxy xcor ycor
        set activity-state "R"
        stop]
      ]
      [;set label "Gut is full"
        stop]
    ]

    if (activity-state = "S")
    [
      ask turtle 0
      [search
       ; set label "Searching for food"
       ]
      set searchcount searchcount + 1
      if ([patch-type] of patch-here = "Food")  ;and ([food-level] of patch-here > min-energ
y)
      [set transcount transcount + 1
        plotxy xcor ycor
        set activity-state "F"]
      ]
    ]
  ]; end satisficing loop
end
```

search

```
to search
  set reserve-level reserve-level - Movement-cost
  set movelist lput Movement-cost movelist
  bounce
  let local-food-patches patches with [(distance myself < [vision-range] of turtle 0) and (p
atch-type = "Food")]
  ifelse any? local-food-patches
  [let my-food-patch local-food-patches with-min [distance myself] ;with-max [food-level
]
  face one-of my-food-patch]
  [lt random 180 - 90 ]
  fd 1
  if [patch-type] of patch-here = "Food"
  [set activity-state "F"]
end
```

A

bounce

```
to bounce
; Turtles turn a random angle ~180 when encountering a wall
  ask turtle 0
 [ if abs pxcor = abs max-pxcor or
      abs pycor = abs max-pycor
    [lt random-float 180 ]
 ]
end
```

handle food

```
to handle-food
  set energy-gain Low-food-gain
  ;set in-food? TRUE
  set feedcount feedcount + 1
  set-current-plot "Spatial coordinates of transition between activity states"
  set-current-plot-pen "Feeding"
  ifelse [pcolor] of patch-here = 45
  [set-plot-pen-color 45]
  [set-plot-pen-color 55]
  plotxy xcor ycor
end
```

A

shade search

```
to shade-search
  set reserve-level reserve-level - Movement-cost ; add miniscule movement cost to avoid
turtle exiting green food patches for one time step when feeding
  set movelist lput Movement-cost movelist
  let local-shade-patches patches with [(distance myself < [vision-range] of turtle 0) and (
patch-type = "Shade")]
  ifelse any? local-shade-patches
  [let my-shade-patch local-shade-patches with-min [distance myself] with-max [shade-le
vel]
    face one-of my-shade-patch
    set shadecount shadecount + 1]
  [lt random 180 - 90]
  fd 1
end
```

rest

```
to rest
  ifelse strategy = "Optimising"
  [set activity-state "S"]
```

```
  [set activity-state "R"]
end
```

socialise

```
to socialise
  set reserve-level reserve-level - Movement-cost ; add miniscule movement cost to avoid
turtle exiting green food patches for one time step when feeding
  set movelist lput Movement-cost movelist
  bounce
  lt random 180 - 90
  fd 1
  if gutfull < gutthresh
  [set activity-state "S"]
end
```

update food levels

```
to update-food-levels
  let food-deplete food-level - Low-food-gain
  if (count turtles-here with [activity-state = "F"] > 0) and (gutfull < gutthresh)
; [ifelse food-level < Large-food-initial
  [set food-level food-deplete ; yellow food
    set in-food? TRUE
    print "In food"]
;  [set food-level food-level - (Low-food-gain * 2)] ; green food
;  ]
  if food-level < Small-food-initial
    [set patch-type "Sun"]
set pcolor PatchColor
end
```

report patch color

```
to-report PatchColor
  let PatColor 0
  ifelse food-level >= Large-food-initial
  [set PatColor green]
  [ifelse food-level >= Small-food-initial
    [set PatColor yellow]
    [set PatColor brown]
  ]
  report PatColor
end
```

A

report patch type

```
to report-patch-type
ifelse [patch-type] of patch-here = "Food"
   [set in-food? TRUE]
   [
     ifelse [patch-type] of patch-here = "Shade"
     [set in-shade? TRUE]
     [set in-shade? FALSE
       set in-food? FALSE]
   ]
end
```

report results

```
to report-results
   output-print (word "Number of real days:,, " precision (ticks * 2 / 60 / 24) 5)
   output-print ""
   output-print (word "Time spent searching for food (mins/days):, " (searchcount * 2) " ,
" precision (searchcount * 2 / 60 / 24) 3 "")
   output-print ""
   output-print (word "Time spent feeding (mins/days):, " (feedcount * 2) " , " precision (f
eedcount * 2 / 60 / 24) 3 "")
   output-print ""
   output-print (word "Time spent searching for shade  (mins/days):, " (shadecount * 2) "
, " precision (shadecount * 2 / 60 / 24) 3 "")
   output-print ""
   output-print (word "Time spent resting in shade (mins/days):, " (restcount * 2) " , " pre
cision (restcount * 2 / 60 / 24) 3 "")
   output-print ""
   output-print (word "Time spent in critical starvation (mins/days):, " (starvecount * 2) "
, " precision (starvecount * 2 / 60 / 24) 3 "")
   output-print ""
   output-print (word "Number of transitions between activity states:, " transcount)
   output-print ""
   ifelse has-been-feeding? = TRUE
   [output-print (word "Proportion of feeding to searching:, " precision (feedcount / searc
hcount) 3)]
   [output-print (word "Proportion of feeding to searching:, " 0)]
   output-print ""
   ifelse has-been-starving? = TRUE
   [output-print (word "Proportion of feeding to starving:, " precision (feedcount / starvec
ount) 3)]
   [output-print (word "Proportion of feeding to starving:, " 0)]
   output-print ""
   output-print (word "Patches with pcolor = brown (eaten): " patches with [pcolor = 35])
```

A

```
    stop;die
end
```

to save world

```
to save-world ; This procedure saves the model world. The file output procedure then out
puts the saved model world as a .txt file to the local dir.
  let world user-new-file
  if ( world != false )
  [
    file-write world
    ask patches
    [
      file-write pxcor
      file-write pycor
       if patch-type = "Food"
       [file-write pxcor and pycor and (patch-type = "Food") and food-level]
       if patch-type = "Shade"
       [file-write pxcor and pycor and (patch-type = "Shade") and shade-level]
    ]
    file-close
  ]
end
```

spatial plot

```
to setup-spatial-plot
  set-current-plot "Spatial coordinates of transition between activity states"
  set-plot-x-range min-pxcor max-pxcor
  set-plot-y-range min-pycor max-pycor
  clear-plot
end
```

get home range

```
to get-homerange
draw-homerange
end
```

draw home range

```
to draw-homerange
  clear-drawing
  if any? turtles [
    ask turtle 0
  [pu
   hatch-homeranges 1
```

A

```
  [hide-turtle
 ;  set ID [ID] of myself
    set color red
    ]
  ; draw the homerange
  foreach tempXY
  [ask homeranges
    [move-to patch (item 0 ?) (item 1 ?)
      pd
      ]
    ]
  ; close the homerange polygon
  ask homeranges
  [let lastpoint first tempXY
    move-to patch (item 0 lastpoint) (item 1 lastpoint)
    ]
  ]
 ]
end
```

A

Appendix A2

Energy and heat budget models, including microclimate model (.R). Available on **Github**.

Initial setup

```
# RNL_new trans model_with DEB_1.6.2

# ----------------------------------------------------------------
# ------------------- initial Mac OS and R config ----------------
# ----------------------------------------------------------------

#if using Mac OSX Mountain Lion + and not already in JQR, download and open JGR
# after downloading, load JGR
install.packages("JGR")
Sys.setenv(NOAWT=1)
library(JGR)
Sys.unsetenv("NOAWT")
JGR()

# in JGR onwards
# if already loaded, uninstall RNetlogo and rJava
p<-c("rJava", "RNetLogo")
remove.packages(p)

# install Netlogo and rJava from source if haven't already
dir<- "<your working directory>"
install.packages(paste0(dir,"/RNetLogo_1.0-2.tar.gz", repos = NULL, type="source"))
install.packages(paste0(dir,"/rJava_0.9-8.tar.gz", repos = NULL, type="source"))
library(RNetlogo); library(rJava)
```

For PC and working Mac OSX

Source DEB.R and onelump_varenv.R from **Github**

```
# ------------------- for PC and working Mac OSX -----------------
# ------------------- model setup --------------------------
# get packages
install.packages(c("NicheMapR","adehabitatHR","rgeos","sp", "maptools", "raster","rw
orldmap","rgdal","dplyr"))
library(NicheMapR); library(adehabitatHR); library(rgeos); library(sp); library(mapt
ools); library(raster); library(rworldmap); library(rgdal); library(dplyr)

#source DEB and heat budget models from https://github.com/darwinanddavis/Thesis/tre
```

```
e/master/AppendixA
source('DEB.R')
source('onelump_varenv.R')

# set dirs
setwd("<your working dir>") # set wd
results.path<- "<dir path to store result outputs>" # set results path
```

Read in microclimate data

Source metout, soil, shadmet, and shadsoil from **Github**

```
# read in microclimate data (metout, soil, shadmet, and shadsoil)
tzone<-paste("Etc/GMT-",10,sep="")
metout<-read.csv('metout.csv')
soil<-read.csv('soil.csv')
shadmet<-read.csv('shadmet.csv')
shadsoil<-read.csv('shadsoil.csv')
micro_sun_all<-cbind(metout[,2:5],metout[,9],soil[,6],metout[,14:16])
colnames(micro_sun_all)<-c('dates','JULDAY','TIME','TALOC','VLOC','TS','ZEN','SOL
R','TSKYC')
micro_shd_all<-cbind(shadmet[,2:5],shadmet[,9],shadsoil[,6],shadmet[,14:16])
colnames(micro_shd_all)<-c('dates','JULDAY','TIME','TALOC','VLOC','TS','ZEN','SOL
R','TSKYC')

# choose a day(s) to simulate
daystart<-paste('09/09/05',sep="") # yy/mm/dd
dayfin<-paste('10/12/31',sep="") # yy/mm/dd
micro_sun<-subset(micro_sun_all, format(as.POSIXlt(micro_sun_all$dates), "%y/%m/
%d")>=daystart & format(as.POSIXlt(micro_sun_all$dates), "%y/%m/%d")<=dayfin)
micro_shd<-subset(micro_shd_all, format(as.POSIXlt(micro_shd_all$dates), "%y/%m/
%d")>=daystart & format(as.POSIXlt(micro_shd_all$dates), "%y/%m/%d")<=dayfin)
days<-as.numeric(as.POSIXlt(dayfin)-as.POSIXlt(daystart))

# create time vectors
time<-seq(0,(days+1)*60*24,60) #60 minute intervals from microclimate output
time<-time[-1]
times2<-seq(0,(days+1)*60*24,2) #two minute intervals for prediction
time<-time*60 # minutes to seconds
times2<-times2*60 # minutes to seconds

# apply interpolation functions
velfun<- approxfun(time, micro_sun[,5], rule = 2)
Zenfun<- approxfun(time, micro_sun[,7], rule = 2)
Qsolfun_sun<- approxfun(time, micro_sun[,8], rule = 2)
Tradfun_sun<- approxfun(time, rowMeans(cbind(micro_sun[,6],micro_sun[,9])), rule =
 2)
```

A

```
Tairfun_sun<- approxfun(time, micro_sun[,4], rule = 2)
Qsolfun_shd<- approxfun(time, micro_shd[,8]*.1, rule = 2)
Tradfun_shd<- approxfun(time, rowMeans(cbind(micro_shd[,6],micro_shd[,9])), rule =
 2)
Tairfun_shd<- approxfun(time, micro_shd[,4], rule = 2)

# upper and lower activity thermal limits
VTMIN<- 26
VTMAX<- 35
```

Read in DEB parameters

Source DEB_pars_Tiliqua_rugosa.csv from **Github**

```
# ************************** read in DEB parameters *********************
*****

debpars=as.data.frame(read.csv('DEB_pars_Tiliqua_rugosa.csv',header=FALSE))$V1
# read in DEB pars

# set core parameters
z=debpars[8] # zoom factor (cm)
F_m = 13290 # max spec searching rate (l/h.cm^2)
kap  X=debpars[11] # digestion efficiency of food to reserve (-)
v=debpars[13] # energy conductance (cm/h)
kap=debpars[14] # kappa, fraction of mobilised reserve to growth/maintenance (-)
kap_R=debpars[15] # reproduction efficiency (-)
p  M=debpars[16] # specific somatic maintenance (J/cm3)
k_J=debpars[18] # maturity maint rate coefficient (1/h)
E_G=debpars[19] # specific cost for growth (J/cm3)
E_Hb=debpars[20] # maturity at birth (J)
E_Hp=debpars[21] # maturity at puberty (J)
h_a=debpars[22]*10^-1 # Weibull aging acceleration (1/h^2)
s_G=debpars[23] # Gompertz stress coefficient (-)

# set thermal respose curve paramters
T_REF = debpars[1]-273
TA = debpars[2] # Arrhenius temperature (K)
TAL = debpars[5] # low Arrhenius temperature (K)
TAH = debpars[6] # high Arrhenius temperature (K)
TL = debpars[3] # low temp boundary (K)
TH = debpars[4] # hight temp boundary (K)

# set auxiliary parameters
del_M=debpars[9] # shape coefficient (-)
E_0=debpars[24] # energy of an egg (J)
mh = 1 # survivorship of hatchling in first year
```

A

```
mu_E = 585000 # molar Gibbs energy (chemical potential) of reserve (J/mol)
E_sm=186.03*6
gutfull <- 1
# set initial state
E_pres_init = (debpars[16]*debpars[8]/debpars[14])/(debpars[13]) # initial reserve
E_m <- E_pres_init
E_H_init = debpars[21] + 5

#### change inital size here by multiplying by < 0.85 ####
V_pres_init = (debpars[26] ^ 3) * 0.85
d_V<-0.3
mass <- V_pres_init + V_pres_init*E_pres_init/mu_E/d_V*23.9

# ***************** end TRANSIENT MODEL SETUP ***************
# ************************************************************
```

Initialise decision-making and DEB models

Source Netlogo model from **Github**

```
# ********************* start NETLOGO SIMULATION  ********************
**

nl.path<- "<dir path to Netlogo program>"
NLStart(nl.path)
model.path<- "<dir path to Netlogo model>"
NLLoadModel(model.path)

# ************************ setup NETLOGO MODEL ************************
*

# 1. update animal and env traits
month<-"sep"
NL_days<-117      # No. of days simulated
NL_gutthresh<-0.75
gutfull<-0.8

# set resource density
if(density=="high"){
   NL_shade<-100000L      # Shade patches
   NL_food<-100000L       # Food patches
   }else{
   NL_shade<-1000L     # Shade patches
   NL_food<-1000L  # Food patches
}

# 2. update initial conditions for DEB model
```

A

```
Es_pres_init<-(E_sm*gutfull)*V_pres_init
acthr<-1
Tb_init<-20
step = 1/24
debout<-DEB(step = step, z = z, del_M = del_M, F_m = F_m *
   step, kap_X = kap_X, v = v * step, kap = kap, p_M = p_M *
   step, E_G = E_G, kap_R = kap_R, k_J = k_J * step, E_Hb = E_Hb,
   E_Hj = E_Hb, E_Hp = E_Hp, h_a = h_a/(step^2), s_G = s_G,
   T_REF = T_REF, TA = TA, TAL = TAL, TAH = TAH, TL = TL,
   TH = TH, E_0 = E_0, E_pres=E_pres_init, V_pres=V_pres_init, E_H_pres=E_H_init,
acthr = acthr, breeding = 1, Es_pres = Es_pres_init, E_sm = E_sm)

# 3. calc direct movement cost
V_pres<-debout[2]
step<-1/24 #hourly

p_M2<-p_M*step #J/h
p_M2<-p_M2*V_pres # loco cost * structure
names(p_M2)<-NULL # remove V_pres name attribute from p_M

# movement cost for time period
VO2<-0.45 # O2/g/h JohnAdler etal 1986

# multiple p_M by structure = movement cost (diff between p_M with loco cost and struct
ure for movement period)
# p_M with loco cost
loco<-VO2*mass*20.1 # convert ml O2 to J = J/h
loco<-loco+p_M2 # add to p_M = J/h
loco<-loco/30/V_pres ; loco #J/cm3/2min

Es_pres_init<-(E_sm*gutfull)*V_pres_init
X_food<-3000
V_pres<-debout[2]
wetgonad<-debout[19]
wetstorage<-debout[20]
wetfood<-debout[21]
ctminthresh<-120000
Tairfun<-Tairfun_shd
Tc_init<-Tairfun(1)+0.1 # Initial core temperature

NL_T_b<-Tc_init      # Initial T_b
NL_T_b_min<-VTMIN        # Min foraging T_b
NL_T_b_max<-VTMAX        # Max foraging T_b
NL_ctminthresh<-ctminthresh # No. of consecutive hours below CTmin that leads to deat
h
NL_reserve<-E_m       # Initial reserve density
```

A

```
NL_max_reserve<-E_m    # Maximum reserve level
NL_maint<-round(p_M, 3)              # Maintenance cost
NL_move<-round(loco, 3)              # Movement cost
NL_zen<-Zenfun(1*60*60)     # Zenith angle

strategy<-function(strategy){ # set movement strategy
  if (strategy == "O"){
    NLCommand("set strategy \"Optimising\" ")
    }else{
    NLCommand("set strategy \"Satisficing\" ")
    }
  }
strategy("O") # "S"

shadedens<-function(shadedens){ # set movement strategy
  if (shadedens == "Random"){
    NLCommand("set Shade-density \"Random\" ")
    }else{
    NLCommand("set Shade-density \"Clumped\" ")
    }
  }
shadedens("Clumped") # set clumped resources
```

A

Run simulation

```
sc<-1 # set no. of desired simualations---for automating writing of each sim results to file
. N = N runs
for (i in 1:sc){ # start sc sim loop

NLCommand("set Shade-patches",NL_shade,"set Food-patches",NL_food,"set No.-of-d
ays",NL  days,"set T  b precision",
NL_T_b, "2","set T_opt_lower precision", NL_T_b_min, "2","set T_opt_upper precision
", NL_T_b_max, "2",
"set reserve-level", NL_reserve, "set Maximum-reserve", NL_max_reserve, "set Mainten
ance-cost", NL_maint,
"set Movement-cost precision", NL_move, "3", "set zenith", NL_zen, "set ctminthresh",
NL_ctminthresh,
"set gutthresh", NL_gutthresh, 'set gutfull', gutfull, 'set V_pres precision', V_pres, "5", 'se
t wetstorage precision', wetstorage, "5",
'set wetfood precision', wetfood, "5", 'set wetgonad precision', wetgonad, "5","setup")

#NLCommand("inspect turtle 0")

NL_ticks<-NL_days / (2 / 60 / 24) # No. of NL ticks (measurement of days)
NL_T_opt_l<-NLReport("[T_opt_lower] of turtle 0")
NL_T_opt_u<-NLReport("[T_opt_upper] of turtle 0")
```

```
# data frame setup for homerange polygon
turtles<-data.frame() # make an empty data frame
NLReport("[X] of turtle 0"); NLReport("[Y] of turtle 0")
who<-NLReport("[who] of turtle 0")

# ********************************************************************
**
# ******************* start NETLOGO SIMULATION  **********************
**

debcall<-0 # check for first call to DEB
stepcount<-0 # DEB model step count

for (i in 1:NL_ticks){
stepcount<-stepcount+1
NLDoCommand(1, "go")

######### Reporting presence of shade
shade<-NLGetAgentSet("in-shade?","turtles", as.data.frame=T); shade<-as.numeric(sha
de) # returns an agentset of whether turtle is currently on shade patch

# choose sun or shade
tick<-i
times3<-c(times2[tick],times2[tick+1])

if(shade==0){
  Qsolfun<-Qsolfun_sun
  Tradfun<-Tradfun_sun
  Tairfun<-Tairfun_sun
}else{
  Qsolfun<-Qsolfun_shd
  Tradfun<-Tradfun_shd
  Tairfun<-Tairfun_shd
}
if(i==1){
Tc_init<-Tairfun(1)+0.1 #initial core temperature
}

# one_lump_trans params
Qsol<-Qsolfun(mean(times3)); Qsol
vel<-velfun(mean(times3)) ;vel
Tair<-Tairfun(mean(times3));Tair
Trad<-Tradfun(mean(times3)); Trad
Zen<-Zenfun(mean(times3)); Zen

# calc Tb params at 2 mins interval
```

A

```
Tbs<-onelump_varenv(t=120,time=times3[2],Tc_init=Tc_init,thresh = 30, AMASS = m
ass, lometry = 3, Tairf=Tairfun,Tradf=Tradfun,velf=velfun,Qsolf=Qsolfun,Zenf=Zenfun)
Tb<-Tbs$Tc
rate<-Tbs$dTc
Tc_init<-Tb

NLCommand("set T_b precision", Tb, "2") # Updating Tb
NLCommand("set zenith", Zenfun(times3[2])) # Updating zenith

# time spent below VTMIN
ctminhours<-NLReport("[ctmincount] of turtle 0") * 2/60 # ticks to hours
if (ctminhours == NL_ctminthresh) {NLCommand("ask turtle 0 [stop]")}

# ******************** start DEB SIMULATION  ****************************

if(stepcount==1) { # run DEB loop every time step (2 mins)
stepcount<-0

# report activity state
actstate<-NLReport("[activity-state] of turtle 0")
 # Reports true if turtle is in food
actfeed<-NLGetAgentSet("in-food?","turtles", as.data.frame=T); actfeed<-as.numeric(a
ctfeed)

n<-1 # time steps
step<-2/1440 # step size (2 mins). For hourly: 1/24
# update direct movement cost
if(actstate == "S"){
   NLCommand("set Movement-cost", NL_move)
   }else{
      NLCommand("set Movement-cost", 1e-09)
      }
# if within activity range, it's daytime, and gut below threshold
if(Tbs$Tc>=VTMIN & Tbs$Tc<=VTMAX & Zen!=90 & gutfull<=NL_gutthresh){
  acthr=1 # activity state = 1
if(actfeed==1){ # if in food patch
   X_food<-NLReport("[energy-gain] of turtle 0") # report joules intake
   }
   }else{
      X_food = 0
      acthr=0
      }

# calculate DEB output
if(debcall==0){
   # initialise DEB
```

A

```
   debout<-matrix(data = 0, nrow = n, ncol = 26)
   deb.names<-c("E_pres","V_pres","E_H_pres","q_pres","hs_pres","surviv_pres","Es_p
res","cumrepro","cumbatch","p_B_past","O2FLUX","CO2FLUX","MLO2","GH2OMET
","DEBQMET","DRYFOOD","FAECES","NWASTE","wetgonad","wetstorage","wetfo
od","wetmass","gutfreemass","gutfull","fecundity","clutches")
   colnames(debout)<-deb.names
   # initial conditions
   debout<-DEB(E_pres=E_pres_init, V_pres=V_pres_init, E_H_pres=E_H_init, acthr =
acthr, Tb = Tb  init, breeding = 1, Es_pres = Es_pres_init, E_sm = E_sm, step = step, z, d
el_M = del_M, F_m = F_m *
   step, kap_X = kap_X, v = v * step, kap = kap, p_M = p_M *
   step, E_G = E_G, kap_R = kap_R, k_J = k_J * step, E_Hb = E_Hb,
   E_Hj = E_Hb, E_Hp = E_Hp, h_a = h_a/(step^2), s_G = s_G,
   T_REF = T_REF, TA = TA, TAL = TAL, TAH = TAH, TL = TL,
   TH = TH, E_0 = E_0)
   debcall<-1
   }else{
      debout<-DEB(step = step, z = z, del_M = del_M, F_m = F_m *
   step, kap  X = kap  X, v = v * step, kap = kap, p  M = p  M *
   step, E_G = E_G, kap_R = kap_R, k_J = k_J * step, E_Hb = E_Hb,
   E_Hj = E_Hb, E_Hp = E_Hp, h_a = h_a/(step^2), s_G = s_G,
   T_REF = T_REF, TA = TA, TAL = TAL, TAH = TAH, TL = TL,
   TH = TH, E  0 = E  0,
        X=X_food,acthr = acthr, Tb = Tbs$Tc, breeding = 1, E_sm = E_sm, E_pres=debou
t[1],V_pres=debout[2],E_H_pres=debout[3],q_pres=debout[4],hs_pres=debout[5],surviv
_pres=debout[6],Es_pres=debout[7],cumrepro=debout[8],cumbatch=debout[9],p_B_past
=debout[10])
      }
mass<-debout[22]
gutfull<-debout[24]
NL_reserve<-debout[1]
V_pres<-debout[2]
wetgonad<-debout[19]
wetstorage<-debout[20]
wetfood<-debout[21]

#update NL wetmass properties
NLCommand("set V_pres precision", V_pres, "5")
NLDoCommand("plot xcor ycor")
NLCommand("set wetgonad precision", wetgonad, "5")
NLDoCommand("plot xcor ycor")
NLCommand("set wetstorage precision", wetstorage, "5")
NLDoCommand("plot xcor ycor")
NLCommand("set wetfood precision", wetfood, "5")
NLDoCommand("plot xcor ycor")
```

A

```
} #-- end DEB loop

NLCommand("set reserve-level", NL_reserve) # update reserve
NLCommand("set gutfull", debout[24])# update gut level

# ******************* end DEB SIMULATION ************************

# generate results, with V_pres, wetgonad, wetstorage, and wetfood from debout
if(i==1){
   results<-cbind(tick,Tb,rate,shade,V_pres,wetgonad,wetstorage,wetfood,NL_reserve)
   }else{
      results<-rbind(results,c(tick,Tb,rate,shade,V_pres,wetgonad,wetstorage,wetfood,NL
_reserve))
      }
results<-as.data.frame(results)

# generate data frames for homerange polygon
if (tick == NL  ticks - 1){
   X<-NLReport("[X] of turtle 0"); head(X)
   Y<-NLReport("[Y] of turtle 0"); head(Y)
   turtles<-data.frame(X,Y)
   who1<-rep(who,NL  ticks); who # who1<-rep(who,NL  ticks - 1); who
   turtledays<-rep(1:NL_days,length.out=NL_ticks,each=720)
   turtle<-data.frame(ID = who1,days=turtledays)
   turtles<-cbind(turtles,turtle)
   }

} # ************************* end NL loop ******************************
*

# get hr data
spdf<-SpatialPointsDataFrame(turtles[1:2], turtles[3]) # creates a spatial points data fr
ame (adehabitatHR package)
homerange<-mcp(spdf,percent=95)

# writing new results
if (exists("results")){  #if results exist
   sc<-sc-1
   nam <- paste("results", sc, sep = "") # generate new name with added sc count
   rass<-assign(nam,results) #assign new name to results. call 'results1, results2 ... result
sN'
   namh <- paste("turtles", sc, sep = "")  #generate new name with added sc count
   rassh<-assign(namh,turtles) #assign new name to results. call 'results1, results2 ... resu
ltsN'
   nams <- paste("spdf", sc, sep = "")
```

```
  rasss<-assign(nams,spdf)
  namhr <- paste("homerange", sc, sep = "")
  rasshr<-assign(namhr,homerange)

  fh<-results.path; fh
  for (i in rass){
     # export all results
     write.table(results,file=paste(fh,nam,".R",sep=""))
     }
  for (i in rassh){
     # export turtle location data
     write.table(turtles,file=paste(fh,namh,".R",sep=""))
     }
     #export NL plots
     month<-"sep"
     #spatial plot
     sfh<-paste(month,NL_days,round(mass,0),NL_shade,as.integer(NL_food*10),"_",
sc,"_move","",sep="");sfh
     NLCommand(paste("export-plot \"Spatial coordinates of transition between activit
y states\" \"",results.path,sfh,".csv\"",sep=""))
     #temp plot
     tfh<-paste(month,NL_days,round(mass,0),NL_shade,as.integer(NL_food*10),"_",
sc,"  temp",sep="")
     NLCommand(paste("export-plot \"Body temperature (T_b)\" \"",results.path,tfh,".c
sv\"",sep=""))
     #activity budget
     afh<-paste(month,NL_days,round(mass,0),NL_shade,as.integer(NL_food*10),"_",
sc,"_act","",sep="");afh
     NLCommand(paste("export-plot \"Global time budget\" \"",results.path,afh,".csv\"
",sep=""))
     #text output
     xfh<-paste(month,NL_days,round(mass,0),NL_shade,as.integer(NL_food*10),"_",
sc,"  txt",sep="");xfh
     NLCommand(paste("export-output \"",results.path,xfh,".csv\"",sep=""))
     #gut level
     gfh<-paste(month,NL_days,round(mass,0),NL_shade,as.integer(NL_food*10),"_",
 sc,"_gut","",sep="");gfh
     NLCommand(paste("export-plot \"Gutfull\" \"",results.path,gfh,".csv\"",sep=""))
     #wet mass
     mfh<-paste(month,NL_days,round(mass,0),NL_shade,as.integer(NL_food*10),"_"
,sc,"_wetmass","",sep="");mfh
     NLCommand(paste("export-plot \"Total wetmass plot\" \"",results.path,mfh,".csv\"
",sep=""))
     #movement cost (loco)
     lfh<-paste(month,NL_days,round(mass,0),NL_shade,as.integer(NL_food*10),"_",
sc,"_loco","",sep="");lfh
```

A

```
      NLCommand(paste("export-plot \"Movement costs\" \"",results.path,lfh,".csv\"",se
p=""))
   }
} # ********************** end sc sim loop ****************************

#************************ end NETLOGO SIMULATION **********************
******
#*********************************************************************
****
```

Example of data output files from simulation

```
# example files of results output in results.path
list.files(results.path)
# [1] "results0.R"                "sep572310001000_0_act.csv"
# [3] "sep572310001000_0_gut.csv"    "sep572310001000_0_loco.csv"
# [5] "sep572310001000_0_move.csv"   "sep572310001000_0_temp.csv"
# [7] "sep572310001000_0_txt.csv"    "sep572310001000_0_wetmass.csv"
# [9] "turtles0.R"
```

A

Figures

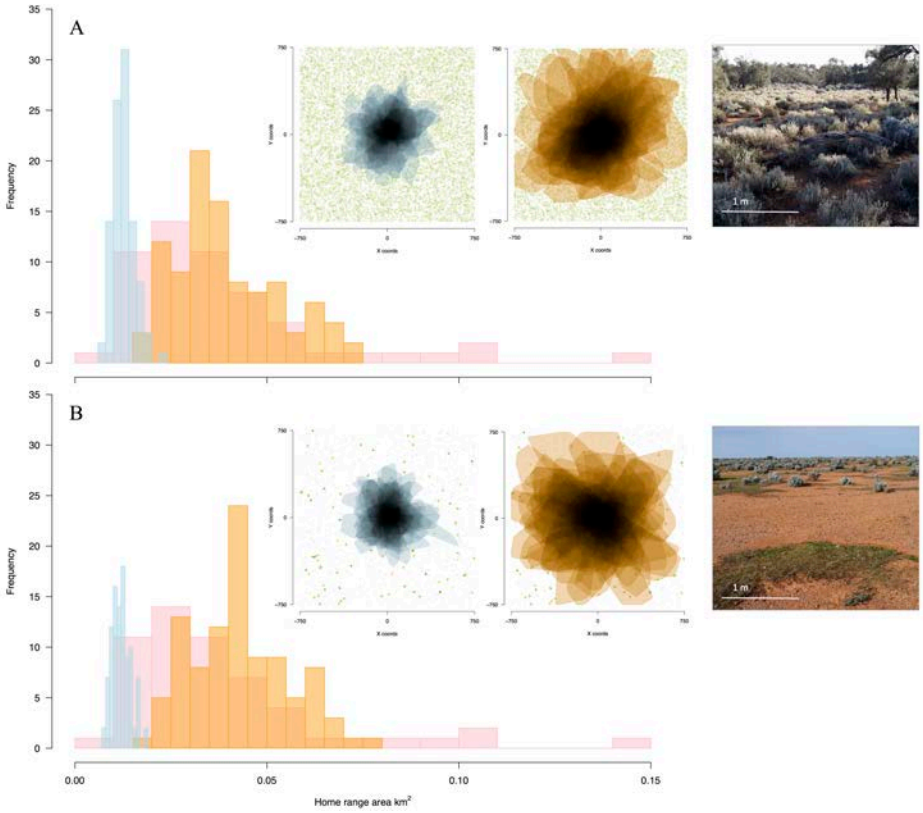

Figure A1. Distributions of home range area (km^2) of real animals (pink) and simulated optimising (orange) and satisficing (blue) movement strategies under (A) dense and (B) sparse resource distribution (food and shade). Insets (L–R): Home range polygons in space showing overlap of simulated satisficing (blue) and optimising (orange) movement strategies, and examples of (upper) dense and (lower) sparse resource distributions in the study site.

A

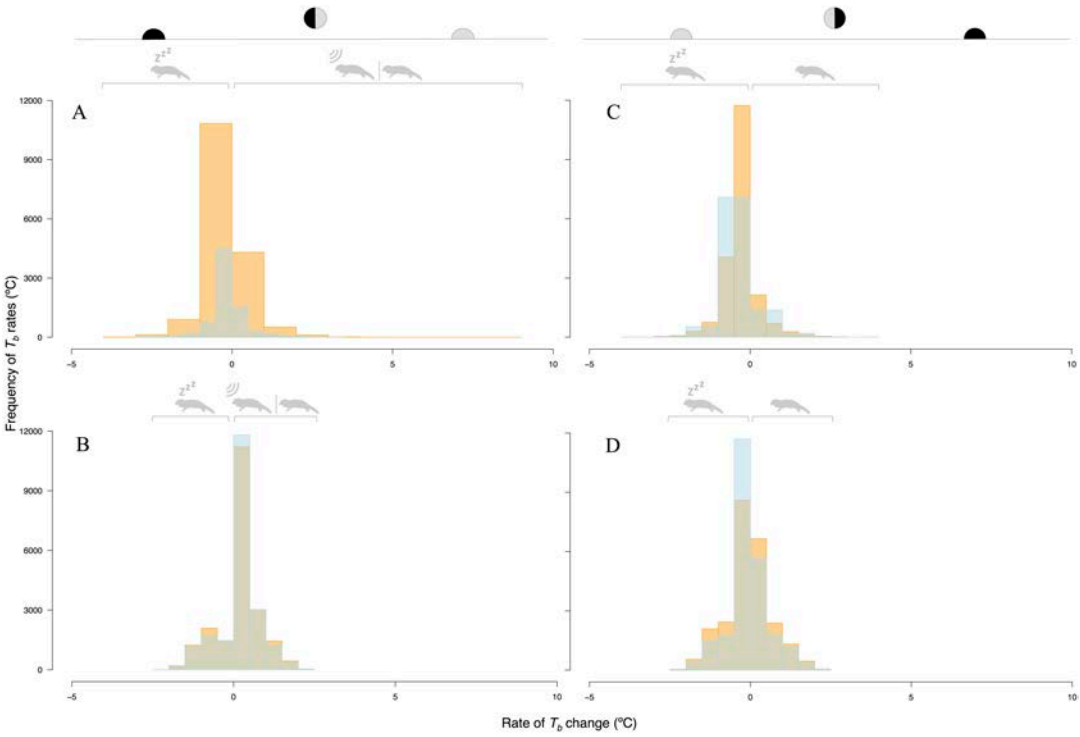

Figure A2. Rates of T_b change (ºC 2 min^{-1}) comparing (A) observed active (orange; #11885) and passive (blue; #11533) movement and (B) simulated optimising (orange) and satisficing (blue) movement for the morning hours (heating period; 06:00–12:00). (C) Observed active (orange) and passive (blue) movement and (D) simulated optimising (orange) and satisficing (blue) movement for the afternoon hours (cooling period; 12:00–18:00) throughout the breeding season. Animal graphics represent the most probable activity state of the animal (from Fig. 5).

References

Auburn, Z. M., Bull, C. M. and Kerr G. D. 2009. The visual perceptual range of a lizard, *Tiliqua rugosa*, *Journal of Ethology*, pp. 27:75-81.

Brown, G. W. 1991. Ecological feeding analysis of south-eastern Australian Scincids (Reptilia—Lacertilia), *Australian Journal of Zoology*, 39:9-29.

Kearney, M. R., Simpson, S. J., Raubenheimer, D. & Kooijman, S. A. L. M. 2012. Balancing heat, water and nutrients under environmental change: a thermodynamic niche framework. *Functional Ecology,* 27(4): 950–966.

Kooijman, S. A. L. M. 2010. Dynamic Energy Budget Theory, Cambridge, UK: Cambridge University Press.

Pamula, Y. 1997. Ecological and physiological aspects of reproduction in the viviparous skink *Tiliqua rugosa*, Ph.D. thesis, Flinders University, South Australia, Australia.

A

Bibliography

Aben, J., Strubbe, D., Adriaensen, F., Palmer, S. C. F., Travis, J. M. J., Lens, L., & Matthysen, E. 2014. Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. *Journal of Applied Ecology*, 51(3), pp.693–702.

Achenbach, G.G. & Snowdon, C.T., 2002. Costs of Caregiving: Weight Loss in Captive Adult Male Cotton-Top Tamarins (Saguinus oedipus) Following the Birth of Infants. *International Journal of Primatology*, 23(1), pp.179–189.

Adolph, S.C. & Porter, W.P., 1993. Temperature, activity and lizard life histories. *American Naturalist*, 142(2), pp.273–295.

Álvarez, D. & Nicieza, A.G., 2002. Effects of temperature and food quality on anuran larval growth and metamorphosis. *Functional Ecology*, 16(5), pp.640–648.

nderson, B. J., Akçakaya, H. R., Araújo, M. B., Fordham, D. A., Martinez-Meyer, E., Thuiller, W., & Brook, B. W. 2009. Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, 276, pp.1415–1420.

Angilletta, M.J., Steury, T.D. & Sears, M.W., 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, 44(6), pp.498–509.

Atkinson, D., 1994. Temperature and Organism Size—A Biological Law for Ectotherms? *Advances in Ecological Research*, 25, pp.1–58.

Auburn, Z.M., Bull, C.M. & Kerr, G.D., 2009. The visual perceptual range of a lizard, Tiliqua rugosa. *Journal of Ethology*, 27(1), pp.75–81.

Avgar, T., Deardon, R. & Fryxell, J.M., 2013. An empirically parameterized individual based model of animal movement, perception, and memory. *Ecological Modelling*, 251, pp.158–172.

Ayers, D.Y. & Shine, R., 1997. Thermal influences on foraging ability: body size, posture and cooling rate of an ambush predator, the python Morelia spilota. *Functional Ecology*, 11(3), pp.342–347.

Ayllón, D., Railsback, S. F., Vincenzi, S., Groeneveld, J., Almodóvar, A., & Grimm, V. 2016. InSTREAM-Gen: Modelling eco-evolutionary dynamics of trout populations under anthropogenic environmental change. *Ecological Modelling*, 326, pp.36–53.

Bacher, C. & Gangnery, A., 2006. Use of dynamic energy budget and individual based models to simulate the dynamics of cultivated oyster populations. *Journal of Sea Research*, 56(2), pp.140–155.

Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J. P., & Courtois, R. 2015. Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, 96(10), pp.2622–2631.

Bateman, A. W., Lewis, M. A., Gall, G., Manser, M. B., & Clutton-Brock, T. H. 2015. Territoriality and home-range dynamics in meerkats, Suricata suricatta: a mechanistic modelling approach. *The Journal of Animal Ecology*, 84(1), pp.260–271.

Bauer, S., Barta, Z., Ens, B. J., Hays, G. C., McNamara, J. M., & Klaassen, M. 2009.

Animal migration: linking models and data beyond taxonomic limits. *Biology letters*, 5(4), pp.433–435.
Bauer, S. & Hoye, B.J., 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science (New York, N.Y.)*, 344(6179), p.1242552.
Bauer, S. & Klaassen, M., 2013. Mechanistic models of animal migration behaviour - their diversity, structure and use. *Journal of Animal Ecology*, 82(3), pp.498–508.
Belliure, J., Carrascal, L.M. & Díaz, J.A., 1996. Covariation of thermal biology and foraging mode in two mediterranean lacertid lizards. *Ecology*, 77(4), pp.1163–1173.
Benhamou, S., 2014. Of scales and stationarity in animal movements. *Ecology Letters*, 17(3), pp.261–272.
Bergman, C.M., Fryxell, J.M., Gates, C.C. & Fortin, D. 2001. Ungulate foraging strategies : energy maximizing or time minimizing ? *Journal of Animal Ecology*, 70, pp.289–300.
Blouin-Demers, G. & Nadeau, P., 2005. The cost–benefit model of thermoregulation does not predict lizard thermoregulatory behavior. *Ecology*, 86(3), pp.560–566.
Bocedi, G., Zurell, D., et al., 2014. Mechanistic modelling of animal dispersal offers new insights into range expansion dynamics across fragmented landscapes. *Ecography*, 37(12), pp.1240–1253.
Bocedi, G., Zurell, D., Reineking, B., & Travis, J. M. J. 2014. RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Methods in Ecology and Evolution*, 5(4), pp.388–396.
Bode, N.W.F. & Delcourt, J., 2013. Individual-to-Resource Landscape Interaction Strength Can Explain Different Collective Feeding Behaviours. *PLoS ONE*, 8(10).
Bonnell, T. R., Campennì, M., Chapman, C. A., Gogarten, J. F., Reyna-Hurtado, R. A., Teichroeb, J. A., … Sengupta, R. 2013. Emergent Group Level Navigation: An Agent-Based Evaluation of Movement Patterns in a Folivorous Primate. *PLoS ONE*, 8(10), pp.1–12.
Bonte, D., van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., … Travis, J. M. J. 2012. Costs of dispersal. *Biological Reviews*, 87(2), pp.290–312.
Boone, R.B., Thirgood, S.J. & Hopcraft, J.G.C., 2006. Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. *Ecology*, 87(8), pp.1987–1994.
Börger, L., Matthiopoulos, J., Holdo, R. M., Morales, J. M., Couzin, I., & McCauley, E. 2011. Migration quantified: constructing models and linking them with data. In *Animal Migration*. Oxford: Oxford University Press.
Börger, L., Dalziel, B.D. & Fryxell, J.M., 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, 11(6), pp.637–650.
Bowler, D.E. & Benton, T.G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological reviews of the Cambridge Philosophical Society*, 80(2), pp.205–225.
Brown, C.R. & Brown, M.B., 2000. Weather-mediated natural selection on arrival time in cliff swallows (Petrochelidon pyrrhonota). *Behavioral Ecology and Sociobiology*, 47(5), pp.339–345.
Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. 2004. Toward a metabolic theory of ecology. *Ecology*, 85(7), pp.1771–1789.

Brown, J.H. & Nicoletto, P.F., 1991. Spatial scaling of species composition: body masses of North American land mammals. *The American Naturalist*, 138(6), pp.1478–1512.
Brown, J.S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral ecology and sociobiology*, 22(1), pp.37–47.
Buchmann, C. M., Schurr, F. M., Nathan, R., & Jeltsch, F. 2011. An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. *Oikos*, 120(1), pp.106–118.
Buchmann, C. M., Schurr, F. M., Nathan, R., & Jeltsch, F. 2013. Habitat loss and fragmentation affecting mammal and bird communities-The role of interspecific competition and individual space use. *Ecological Informatics*, 14, pp.90–98.
Buchmann, C. M., Schurr, F. M., Nathan, R., & Jeltsch, F. 2012. Movement upscaled - the importance of individual foraging movement for community response to habitat loss. *Ecography*, 35(5), pp.436–445.
Buckley, L.B., 2008. Linking Traits to Energetics and Population Dynamics to Predict Lizard Ranges in Changing Environments. *The American Naturalist*, 171(1), pp.1–19.
Buckley, L.B., 2010. The range implications of lizard traits in changing environments. *Global Ecology and Biogeography*, 19(4), pp.452–464.
Cagnacci, F., Focardi, S., Ghisla, A., van Moorter, B., Merrill, E. H., Gurarie, E., … Hebblewhite, M. 2015. How many routes lead to migration? Comparison of methods to assess and characterise migratory movements. *Journal of Animal Ecology*, *85*(1), 54–68.
Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., … Purvis, A. 2005. Multiple causes of high extinction risk in large mammal species. *Science*, 309(5738), pp.1239–1241.
Chambers, J.M., Becker, R.A. & Wilks, A.R., 1988. *The new S language : a programming environment for data analysis and graphics.*, Wadsworth and Brooks, CA, USA.
Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, 9(2), pp.129–136.
Christian, K.A. & Weavers, B.W., 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecological monographs*, 66(2), pp.139–157.
Christian, K., Tracey, C.R. & Porter, W.P., 1983. Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (Conolophus pallidus). *Ecology*, 64(3), pp.463–468.
Clissold, F.J., Coggan, N. & Simpson, S.J., 2013. Insect herbivores can choose microclimates to achieve nutritional homeostasis. *The Journal of Experimental Biology*, 216(Pt 11), pp.2089–96.
Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., & Massot, M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12(3), pp.197–209.
Cooper, W.E., 2000. Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard (Holbrookia propinqua). *Behaviour*, 137(10), pp.1299–1315.
Cote, J., Bocedi, G., Debeffe, L., Chudzińska, M. E., Weigang, H. C., Dytham, C., …

Hewison, A. J. M. 2016. Behavioural synchronization of large-scale animal movements - disperse alone, but migrate together? *Biological reviews of the Cambridge Philosophical Society*, 33.

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. 2005. Effective leadership and decision-making in animal groups on the move. *Nature*, 433(7025), pp.513–516.

Crawford, R. J. M., Barham, P. J., Underhill, L. G., Shannon, L. J., Coetzee, J. C., Dyer, B. M., ... Upfold, L. 2006. The influence of food availability on breeding success of African penguins Spheniscus demersus at Robben Island, South Africa. *Biological Conservation*, 132(1), pp.119–125.

Crespi, E.J. & Denver, R.J., 2005. Roles of stress hormones in food intake regulation in anuran amphibians throughout the life cycle. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 141(4), pp.381–390.

Crick, H.Q.P., 2004. The impact of climate change on birds. *Ibis*, 146(s1), pp.48–56.

Crouse, D.T., Crowder, L.B. & Caswell, H., 1987. A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology*, 68(5), pp.1412–1423.

Crozier, L. & Dwyer, G., 2006. Combining Population-Dynamic and Ecophysiological Models to Predict Climate-Induced Insect Range Shifts. *The American Naturalist*, 167(6), pp.853–866.

Damuth, J., 1981. Population density and body size in mammals. *Nature*, 290(5808), pp.699–700.

Davies, Z. G., Wilson, R. J., Coles, S., & Thomas, C. D. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology*, 75(1), pp.247–256.

DeAngelis, D.L. & Mooij, W.M., 2005. Individual-Based Modeling of Ecological and Evolutionary Processes. *Annual Review of Ecology, Evolution, and Systematics*, 36(1), pp.147–168.

Delgado, M. D. M., Penteriani, V., Morales, J. M., Gurarie, E., & Ovaskainen, O. 2014. A statistical framework for inferring the influence of conspecifics on movement behaviour. *Methods in Ecology and Evolution*, 5(2), pp.183–189.

Diaz, J.A., 1997. Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. *Functional Ecology*, 11(1), pp.79–89.

Dietz, J.M., Baker, A.J. & Miglioretti, D., 1994. Seasonal variation in reproduction, juvenile growth, and adult body mass in golden lion tamarins (Leontopithecus rosalia). *American Journal of Primatology*, 34(2), pp.115–132.

Van Dijk, P.L.M., Hardewig, I. & Hölker, F., 2005. Energy reserves during food deprivation and compensatory growth in juvenile roach: the importance of season and temperature. *Journal of Fish Biology*, 66(1), pp.167–181.

Duffy, K.J., 2011. Simulations to investigate animal movement effects on population dynamics. *Natural Resource Modeling*, 24(1), pp.48–60.

Dumont, B. & Hill, D.R.C., 2004. Spatially explicit models of group foraging by herbivores: what can Agent-Based Models offer? *Animal Research*, 53(5), pp.419–428.

Duriez, O., Bauer, S., Destin, A., Madsen, J., Nolet, B. A., Stillman, R. a., & Klaassen, M. 2009. What decision rules might pink-footed geese use to depart on migration?

An individual-based model. *Behavioral Ecology*, 20(3), pp.560–569.
van Dyck, H. & Baguette, M., 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology*, 6(6), pp.535–545.
Earl, J.E. & Zollner, P.A., 2014. Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecological Modelling*, 283, pp.45–52.
Eliassen, S., Jørgensen, C., Mangel, M., & Giske, J. 2007. Exploration or exploitation: Life expectancy changes the value of learning in foraging strategies. *Oikos*, 116(3), pp.513–523.
Eliassen, S., Jørgensen, C., Mangel, M., & Giske, J. 2009. Quantifying the adaptive value of learning in foraging behavior. *The American Naturalist*, 174(4), pp.478–489.
Ellis, R.D., McWhorter, T.J. & Maron, M., 2012. Integrating landscape ecology and conservation physiology. *Landscape Ecology*, 27(1), pp.1–12.
Fagan, W. F., Lewis, M. a., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., … Mueller, T. 2013. Spatial memory and animal movement. *Ecology Letters*, 16(10), pp.1316–1329.
Fahrig, L., 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), pp.487–515.
Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, 21(6), pp.1003–1015.
Fiksen, O. & Carlotti, F., 1998. A model of optimal life history and diel vertical migration in Calanus finmarchicus. *Sarsia*, 83, pp.129–147.
Floeter, J. & Temming, A., 2003. Explaining diet composition of North Sea cod (Gadus morhua): prey size preference vs. prey availability. *Canadian Journal of Fisheries and Aquatic Sciences*, 60(2), pp.140–150.
Fourcade, Y., Engler, J. O., Rodder, D., & Secondi, J. 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: A performance assessment of methods for correcting sampling bias. *PLoS ONE*, 9(5), pp.1–13.
Franklin, C.E., Davison, W. & Seebacher, F., 2007. Antarctic fish can compensate for rising temperatures: thermal acclimation of cardiac performance in Pagothenia borchgrevinki. *The Journal of Experimental Biology*, 210(Pt 17), pp.3068–74.
Fronhofer, E.A., Hovestadt, T. & Poethke, H.J., 2013. From random walks to informed movement. *Oikos*, 122(6), pp.857–866.
Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. 2011. Declining body size: a third universal response to warming? *Trends in Ecology & Evolution*, 26(6), pp.285–291.
Garland, T., 1983. Scaling the Ecological Cost of Transport to Body Mass in Terrestrial Mammals. *The American Naturalist*, 121(4), pp.571–587.
Gates, D.M., 1980. *Biophysical ecology*, New York: Springer Verlag.
Genner, M. J., Sims, D. W., Southward, A. J., Budd, G. C., Masterson, P., McHugh, M., … Hawkins, S. J. 2010. Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biology*, 16(2), pp.517–527.
Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. 2001. Effects of size and temperature on metabolic rate. *science*, 293(5538), pp.2248–2251.

Giske, J., Eliassen, S., Fiksen, Ø., Jakobsen, P. J., Aksnes, D. L., Jørgensen, C., & Mangel, M. 2013. Effects of the emotion system on adaptive behavior. *The American Naturalist*, 182(6), pp.689–703.

Giuggioli, L. & Bartumeus, F., 2010. Animal movement, search strategies and behavioural ecology: A cross-disciplinary way forward. *Journal of Animal Ecology*, 79(4), pp.906–909.

Gleiss, A.C., Wilson, R.P. & Shepard, E.L.C., 2011. Making overall dynamic body acceleration work: On the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution*, 2(1), pp.23–33.

Godfrey, S. S., Bradley, J. K., Sih, A., & Bull, C. M. 2012. Lovers and fighters in sleepy lizard land: where do aggressive males fit in a social network? *Animal Behaviour*, 83(1), pp.209–215.

Grant, B.W. & Dunham, A.E., 1990. Elevational covariation in environmental constraints and life histories of the desert lizard Sceloporus merriami. *Ecology*, 71(5), pp.1765–1776.

Grant, J.W.A., Chapman, C.A. & Richardson, K.S., 1992. Defended versus undefended home range size of carnivores, ungulates and primates. *Behavioral Ecology and Sociobiology*, 31(3), pp.149–161.

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. 2007. Bee foraging ranges and their relationship to body size. *Oecologia*, 153(3), pp.589–596.

Grieco, F., 2002. Time constraint on food choice in provisioning blue tits, Parus caeruleus: the relationship between feeding rate and prey size. *Animal Behaviour*, 64(4), pp.517–526.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., … DeAngelis, D. L. 2006. A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, 198(1–2), pp.115–126.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., … DeAngelis, D. L. 2005. Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. *Science*, 310(5750), pp.987–991.

Grimm, V. & Railsback, S.F., 2005. *Individual-based Modeling and Ecology:* STU-Stud., Princeton: Princeton University Press.

Grimm, V. & Railsback, S.F., 2011. Pattern-oriented modelling: a "multi-scope" for predictive systems ecology. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 367(1586), pp.298–310.

Grünbaum, D. & Veit, R.R., 2003. Black-browed albatrosses foranging on antarctic krill: Denesty-dependence trough local enhancement? *Ecology*, 84(12), pp.3265–3275.

Guensch, G.R., Hardy, T.B. & Addley, R.C., 2001. Examining feeding strategies and position choice of drift-feeding salmonids using an individual-based, mechanistic foraging model. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(3), pp.446–457.

Gustafson, E.J., 2013. When relationships estimated in the past cannot be used to predict the future: Using mechanistic models to predict landscape ecological dynamics in a changing world. *Landscape Ecology*, 28(8), pp.1429–1437.

Harley, C.D.G., 2011. Climate change, keystone predation, and biodiversity loss. *Science*, 334(6059), pp.1124–1127.

Haskell, J.P., Ritchie, M.E. & Olff, H., 2002. Fractal geometry predicts varying body size

scaling relationships for mammal and bird home ranges. *Nature*, 418(6897), p.527.
Hawkes, C., 2009. Linking movement behaviour, dispersal and population processes: Is individual variation a key? *Journal of Animal Ecology*, 78(5), pp.894–906.
Hawkes, L. A., Balachandran, S., Batbayar, N., Butler, P. J., Chua, B., Douglas, D. C., … Bishop, C. M. 2013. The paradox of extreme high-altitude migration in bar-headed geese Anser indicus. *Proceedings of the Royal Society B: Biological Sciences*, 280(1750), p.20122114.
Hayes, D.B. & Thompson, B.E., 2013. Movement rules for juvenile steelhead: Dynamic linking of movement behaviour to habitat and density. *Ecology of Freshwater Fish*, pp.1–13.
Hein, A.M., Hou, C. & Gillooly, J.F., 2012. Energetic and biomechanical constraints on animal migration distance. *Ecology Letters*, 15(2), pp.104–110.
Helmuth, B., Kingsolver, J.G. & Carrington, E., 2005. Biophysics, physiological ecology, and climate change: Does mechanism matter? *Annual Review of Physiology*, 67(1), pp.177–201.
Helmuth, B.S.T. & Hofmann, G.E., 2001. Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *Biological Bulletin*, 201(3), pp.374–384.
Henry, R. C., Bocedi, G., Dytham, C., & Travis, J. M. J. 2014. Inter-annual variability influences the eco-evolutionary dynamics of range-shifting. *PeerJ*, 2, pp.e228–e228.
Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91(7), pp.385–398.
Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., & Spiegel, O. 2008. Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences of the United States of America*, 105(49), pp.19060–19065.
Hosseini, P.R., 2006. Pattern formation and individual-based models: The importance of understanding individual-based movement. *Ecological Modelling*, 194(4), pp.357–371.
Hoyle, J.A. & Keast, A., 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (Micropterus salmoides). *Canadian Journal of Zoology*, 65(8), pp.1972–1977.
Huey, R.B., 1974. Behavioral thermoregulation in lizards: importance of associated costs. In American Association for the Advancement of Science.
Huey, R. B., Peterson, C. R., Arnold, S. J., & Porter, W. P. 1989. Hot Rocks and Not-So-Hot Rocks: Retreat-Site Selection by Garter Snakes and Its Thermal Consequences. *Ecology*, 70(4), pp.931–944.
Huey, R.B., 1991. Physiological Consequences of Habitat Selection. *The American Naturalist*, 137, pp.91–115.
Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M., & Williams, S. E. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1596), p.1665 LP-1679.
Huey, R. B., Deutsch, C. A., Tewksbury, J. J., Vitt, L. J., Hertz, P. E., Álvarez Pérez, H. J., & Garland, T. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B: Biological Sciences*, 276(1664), p.1939 LP-1948.

Huey, R.B. & Pianka, E.R., 1981. Ecological consequences of foraging mode. *Ecology*, 62(4), pp.991–999.

Hurlbert, A.H., 2004. Species–energy relationships and habitat complexity in bird communities. *Ecology Letters*, 7(8), pp.714–720.

Huse, G., Johansen, G. O., Bogstad, B., & Gjøsæter, H. 2004. Studying spatial and trophic interactions between capelin and cod using individual-based modelling. *ICES Journal of Marine Science*, 61(7), pp.1201–1213.

Huse, G. & Giske, J., 1998. Ecology in mare pentium: An individual-based spatio-temporal model for fish with adapted behaviour. *Fisheries Research*, 37(1–3), pp.163–178.

Huse, G., Railsback, S. & Fernö, A., 2002. Modelling changes in migration pattern of herring: collective behaviour and numerical domination. *Journal of Fish Biology*, 60(3), pp.571–582.

Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., … Bauer, S. 2013. Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology*, 1(1), p.6.

John-Alder, H.B., Garland, T. & Bennett, A.F., 1986. Locomotory capacities, oxygen consumption, and the cost of locomotion of the shingle-back lizard (Trachydosaurus rugosus). *Physiological Zoology*, 59(5), pp.523–531.

Jones, D.A., Wang, W. & Fawcett, R., 2009. High-quality spatial climate data-sets for Australia. *Australian Meteorological and Oceanographic Journal*, 58(4), pp.233–248.

Kanagaraj, R., Wiegand, T., Kramer-Schadt, S., & Goyal, S. P. 2013. Using individual-based movement models to assess inter-patch connectivity for large carnivores in fragmented landscapes. *Biological Conservation*, 167, pp.298–309.

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. 2015. Terrestrial animal tracking as an eye on life and planet. *Science*, 348(6240), p.aaa2478-aaa2478.

Kearney, M.R., 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology Letters*, 16(12), pp.1470–1479.

Kearney, M. R., Simpson, S. J., Raubenheimer, D., & Kooijman, S. A. L. M. 2013. Balancing heat, water and nutrients under environmental change: A thermodynamic niche framework. *Functional Ecology*, 27(4), pp.950–966.

Kearney, M. R., Simpson, S. J., Raubenheimer, D., & Helmuth, B. 2010. Modelling the ecological niche from functional traits. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365(1557), pp.3469–3483.

Kearney, M.R. & Porter, W.P., 2004. Mapping the fundamental niche: Physiology, climate, and the distribution of a nocturnal lizard. *Ecology*, 85(11), pp.3119–3131.

Kearney, M.R. & Porter, W.P., 2009. Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, 12(4), pp.334–350.

Kearney, M.R., Shine, R. & Porter, W.P., 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 106(10), pp.3835–3840.

Kerr, G.D. & Bull, C.M., 2006. Movement patterns in the monogamous sleepy lizard

(Tiliqua rugosa): effects of gender, drought, time of year and time of day. *Journal of Zoology*, 269(2), pp.137–147.

Kerr, G.D., Bull, C.M. & Cottrell, G.R., 2004. Use of an "on board" datalogger to determine lizard activity patterns, body temperature and microhabitat use for extended periods in the field. *Wildlife Research*, 31(2), pp.171–176.

Kilner, R.M., 2001. A growth cost of begging in captive canary chicks. *Proceedings of the National Academy of Sciences* , 98(20), pp.11394–11398.

Kingsolver, J.G., Diamond, S.E. & Buckley, L.B., 2013. Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Functional Ecology*, 27(6), pp.1415–1423.

Kitaysky, A.S., Wingfield, J.C. & Piatt, J.F., 1999. Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Functional Ecology*, 13(5), pp.577–584.

Kokko, H. & López-Sepulcre, A., 2006. From individual dispersal to species ranges: perspectives for a changing world. *Science*, 313(5788), pp.789–791.

Kooijman, S.A.L.M., 2010. *Dynamic Energy Budget Theory*, Cambridge, UK: Cambridge University Press.

Kramer-Schadt, S., Revilla, E., & Wiegand, T. (2005). Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? *Biological Conservation*, *125*(2), 169–182. http://doi.org/http://dx.doi.org/10.1016/j.biocon.2005.02.015

Kramer-Schadt, S., Revilla, E., Wiegand, T., & Breitenmoser, U. R. S. (2004). Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology*, *41*(4), 711–723. http://doi.org/10.1111/j.0021-8901.2004.00933.x

Kramer-Schadt, S., S. Kaiser, T., Frank, K., & Wiegand, T. (2011). Analyzing the effect of stepping stones on target patch colonisation in structured landscapes for Eurasian lynx. *Landscape Ecology*, *26*(4), 501–513. http://doi.org/10.1007/s10980-011-9576-4

Kranstauber, B., Kays, R., Lapoint, S. D., Wikelski, M., & Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology*, *81*(4), 738–746. http://doi.org/10.1111/j.1365-2656.2012.01955.x

Kubisch, A., Holt, R. D., Poethke, H. J., & Fronhofer, E. a. (2014). Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal. *Oikos*, *123*(1), 5–22. http://doi.org/10.1111/j.1600-0706.2013.00706.x

Kułakowska, K., Kułakowski, T. M., Inglis, I. R., Smith, G. C., Haynes, P. J., Prosser, P., … Sibly, R. M. (2014). Using an individual-based model to select among alternative foraging strategies of woodpigeons: Data support a memory-based model with a flocking mechanism. *Ecological Modelling*, *280*, 89–101. http://doi.org/10.1016/j.ecolmodel.2013.09.019

Langrock, R., Hopcraft, J. G. C., Blackwell, P. G., Goodall, V., King, R., Niu, M., … Schick, R. S. (2014). Modelling group dynamic animal movement. *Methods in Ecology and Evolution*, *5*(2), 190–199. http://doi.org/10.1111/2041-210X.12155

Latombe, G., Parrott, L., Basille, M., & Fortin, D. (2014). Uniting Statistical and Individual-Based Approaches for Animal Movement Modelling. *PLoS ONE*, *9*(6),

e99938. http://doi.org/10.1371/journal.pone.0099938
Laundré, J. W., Hernández, L., Medina, P. L., Campanella, A., López-Portillo, J., González-Romero, A., … Browning, D. M. (2014). The landscape of fear: The missing link to understand top-down and bottom-up controls of prey abundance? *Ecology*, *95*(5), 1141–1152. http://doi.org/10.1890/13-1083.1
Leising, A. W. (2001). Copepod foraging in patchy habitats and thin layers using a 2-d individual-based model. *Marine Ecology Progress Series*, *216*, 167–179. http://doi.org/10.3354/meps216167
Leu, S. T., Bashford, J., Kappeler, P. M., & Bull, C. M. (2010). Association networks reveal social organization in the sleepy lizard. *Animal Behaviour*, *79*(1), 217–225. http://doi.org/http://dx.doi.org/10.1016/j.anbehav.2009.11.002
Leu, S. T., Farine, D. R., Wey, T. W., Sih, A., & Bull, C. M. (2016). Environment modulates population social structure: experimental evidence from replicated social networks of wild lizards. *Animal Behaviour*, *111*, 23–31. http://doi.org/http://dx.doi.org/10.1016/j.anbehav.2015.10.001
Lika, K., Kearney, M. R., Freitas, V., van der Veer, H. W., van der Meer, J., Wijsman, J. W. M., … Kooijman, S. A. L. M. (2011). The "covariation method" for estimating the parameters of the standard Dynamic Energy Budget model I: Philosophy and approach. *Journal of Sea Research*, *66*(4), 270–277. http://doi.org/http://dx.doi.org/10.1016/j.seares.2011.07.010
Lima, S. L., Bednekoff, P. A., & Sih, A. E. A. (1999). Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. *The American Naturalist*, *153*(6), 649–659. http://doi.org/10.1086/303202
Louzao, M., Wiegand, T., Bartumeus, F., & Weimerskirch, H. (2014). Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. *Movement Ecology*, *2*(1), 8. http://doi.org/10.1186/2051-3933-2-8
Lyons, A., Turner, W., & Getz, W. (2013). Home range plus: a space-time characterization of movement over real landscapes. *Movement Ecology*, *1*(1), 2. http://doi.org/10.1186/2051-3933-1-2
Malishev, M., Bull, C. M., & Kearney, M. R. (n.d.). An individual-based model of ectotherm movement integrating metabolic and microclimatic constraints. *Methods in Ecology and Evolution*, *In press.*
Martin, B. T., Jager, T., Nisbet, R. M., Preuss, T. G., Grimm, V., Rohani, A. E. P., & Day, E. T. (2013). Predicting Population Dynamics from the Properties of Individuals: A Cross-Level Test of Dynamic Energy Budget Theory. *The American Naturalist*, *181*(4), 506–519. http://doi.org/10.1086/669904
Martin, B., Zimmer, E., Grimm, V., & Jager, T. (2012). Dynamic Energy Budget theory meets individual-based modelling: a generic and accessible implementation. *Methods in Ecology and Evolution*, *3*(2), 445–449. http://doi.org/10.1111/j.2041-210X.2011.00168.x
Martin, J., Calenge, C., Quenette, P. Y., & Allainé, D. (2008). Importance of movement constraints in habitat selection studies. *Ecological Modelling*, *213*(2), 257–262. http://doi.org/10.1016/j.ecolmodel.2007.12.002
Martín, J., & López, P. (2003). Ontogenetic variation in antipredator behavior of Iberian rock lizards (Lacerta monticola): effects of body-size-dependent thermal-exchange

rates and costs of refuge use. *Canadian Journal of Zoology*, *81*(7), 1131–1137. http://doi.org/10.1139/z03-094

McClure, M., Cannell, E., & Despland, E. (2011). Thermal ecology and behaviour of the nomadic social forager Malacosoma disstria. *Physiological Entomology*, *36*(2), 120–127. http://doi.org/10.1111/j.1365-3032.2010.00770.x

McKechnie, A. E., & Wolf, B. O. (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, *6*(2), 253–256.

McNamara, J. M., Barta, Z., Klaassen, M., & Bauer, S. (2011). Cues and the optimal timing of activities under environmental changes. *Ecology Letters*, *14*(12), 1183–1190. http://doi.org/10.1111/j.1461-0248.2011.01686.x

McNamara, J. M., & Houston, A. I. (1990). The value of fat reserves and the tradeoff between starvation and predation. *Acta Biotheoretica*, *38*(1), 37–61. http://doi.org/10.1007/BF00047272

McVicar, T. R., Van Niel, T. G., Li, L. T., Roderick, M. L., Rayner, D. P., Ricciardulli, L., & Donohue, R. J. (2008). Wind speed climatology and trends for Australia, 1975-2006: Capturing the stilling phenomenon and comparison with near-surface reanalysis output. *Geophysical Research Letters*, *35*(20), L20403. http://doi.org/10.1029/2008GL035627

Merkle, J. A., Fortin, D., & Morales, J. M. (2014). A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecology Letters*, *17*(8), 924–931. http://doi.org/10.1111/ele.12294

Merkle, J. A., Sigaud, M., & Fortin, D. (2015). To follow or not? How animals in fusion-fission societies handle conflicting information during group decision-making. *Ecology Letters*, *18*(8), 799–806. http://doi.org/10.1111/ele.12457

Metcalfe, N. B., Fraser, N. H. C., & Burns, M. D. (1999). Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology*, *68*(2), 371–381.

Millar, J. S., & Hickling, G. J. (1990). Fasting endurance and the evolution of mammalian body size. *Functional Ecology*, *4*(1), 5–12.

Mitchell, M. S., & Powell, R. A. (2004). A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling*, *177*(1–2), 209–232. http://doi.org/http://dx.doi.org/10.1016/j.ecolmodel.2004.01.015

Mitchell, M. S., & Powell, R. A. (2007). Optimal use of resources structures home ranges and spatial distribution of black bears. *Animal Behaviour*, *74*(2), 219–230. http://doi.org/10.1016/j.anbehav.2006.11.017

Mitchell, M. S., & Powell, R. A. (2012). Foraging optimally for home ranges. *Journal of Mammalogy*, *93*(4), 917–928. http://doi.org/10.1644/11-MAMM-S-157.1

Mittelbach, G. G. (1981). Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology*, *62*(5), 1370–1386.

Miwa, M., Oishi, K., Nakagawa, Y., Maeno, H., Anzai, H., Kumagai, H., … Hirooka, H. (2015). Application of overall dynamic body acceleration as a proxy for estimating the energy expenditure of grazing farm animals: Relationship with heart rate. *PLoS ONE*, *10*(6), 1–20. http://doi.org/10.1371/journal.pone.0128042

Monaghan, P., Walton, P., Wanless, S., Uttley, J. D., & Bljrns, M. D. (1994). Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of

breeding Guillemots Uria aalge. *Ibis*, *136*(2), 214–222. http://doi.org/10.1111/j.1474-919X.1994.tb01087.x

Mooij, W. M., & DeAngelis, D. L. (2003). Uncertainty in spatially-explicit animal dispersal models. *Ecological Applications*, *13*(3), 794–805.

Moorcroft, P. R., Lewis, M. A., & Crabtree, R. L. (2006). Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*(1594), 1651–1659.

Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E., & Fryxell, J. M. (2004). Extracting more out of relocation data: Building movement models as mixtures of random walks. *Ecology*, *85*(9), 2436–2445.

Mueller, T., & Fagan, W. F. (2008). Search and navgation in dynamic environments - from individual behaviours to population distributions. *Oikos*, *117*(December 2007), 654–664. http://doi.org/10.1111/j.2008.0030-1299.16291.x

Mueller, T., Fagan, W. F., & Grimm, V. (2011). Integrating individual search and navigation behaviors in mechanistic movement models. *Theoretical Ecology*, *4*(3), 341–355. http://doi.org/10.1007/s12080-010-0081-1

Müller, T., Fagan, W. F., & Grimm, V. (2011). Integrating individual search and navigation behaviors in mechanistic movement models. *Theoretical Ecology*, *4*(3), 341–355. http://doi.org/10.1007/s12080-010-0081-1

Mysterud, A., Pérez-Barbería, F. J., & Gordon, I. J. (2001). The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oecologia*, *127*(1), 30–39.

Nabe-Nielsen, J., Tougaard, J., Teilmann, J., Lucke, K., & Forchhammer, M. C. (2013). How a simple adaptive foraging strategy can lead to emergent home ranges and increased food intake. *Oikos*, *122*(9), 1307–1316. http://doi.org/10.1111/j.1600-0706.2013.00069.x

Naef-Daenzer, L., Naef-Daenzer, B., & Nager, R. G. (2000). Prey selection and foraging performance of breeding Great Tits Parus major in relation to food availability. *Journal of Avian Biology*, *31*(2), 206–214.

Nagy, K. A. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs*, *57*(2), 111–128.

Nagy, K. A. (1994). Seasonal Water, Energy and Food Use by Free-Living, Arid-Habitat Mammals. *Australian Journal of Zoology*, *42*(1), 55–63.

Nams, V. O. (2014). Combining animal movements and behavioural data to detect behavioural states. *Ecology Letters*. http://doi.org/10.1111/ele.12328

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19052–19059. http://doi.org/10.1073/pnas.0800375105

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M., & Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *The Journal of Experimental Biology*, *215*(Pt 6), 986–96. http://doi.org/10.1242/jeb.058602

Newton, I. (2007). Weather-related mass-mortality events in migrants. *Ibis*, *149*(3), 453–467. http://doi.org/10.1111/j.1474-919X.2007.00704.x

Nisbet, R. M., Jusup, M., Klanjscek, T., & Pecquerie, L. (2012). Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models. *Journal of Experimental Biology*, *215*(7), 1246. http://doi.org/10.1242/jeb.071845

Nisbet, R. M., Muller, E. B., Lika, K., & Kooijman, S. A. L. M. (2000). From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology*, *69*(6), 913–926. http://doi.org/10.1111/j.1365-2656.2000.00448.x

Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., … Coulson, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, *466*(7305), 482.

Pamula, Y. (1997). *Ecological and physiological aspects of reproduction in the viviparous skink Tiliqua rugosa*. Flinders University, South Australia, Australia.

Patterson, T. a., Thomas, L., Wilcox, C., Ovaskainen, O., & Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends in Ecology and Evolution*, *23*(2), 87–94. http://doi.org/10.1016/j.tree.2007.10.009

Pauli, B. P., McCann, N. P., Zollner, P. A., Cummings, R., Gilbert, J. H., & Gustafson, E. J. (2013). SEARCH: Spatially Explicit Animal Response to Composition of Habitat. *PLoS ONE*, *8*(5). http://doi.org/10.1371/journal.pone.0064656

Pe'er, G., & Kramer-Schadt, S. (2008). Incorporating the perceptual range of animals into connectivity models. *Ecological Modelling*, *213*(1), 73–85. http://doi.org/10.1016/j.ecolmodel.2007.11.020

Pearson, R. G., Thuiller, W., Araújo, M. B., Martinez-Meyer, E., Brotons, L., McClean, C., … Lees, D. C. (2006). Model-based uncertainty in species range prediction. *Journal of Biogeography*, *33*(10), 1704–1711. http://doi.org/10.1111/j.1365-2699.2006.01460.x

Peck, M. a., & Daewel, U. (2007). Physiologically based limits to food consumption, and individual-based modeling of foraging and growth of larval fishes. *Marine Ecology Progress Series*, *347*, 171–183. http://doi.org/10.3354/meps06976

Pélabon, C. (1997). Is weight at birth a good predictor of weight in winter for fallow deer? *Journal of Mammalogy*, *78*(1), 48–54.

Pettifor, R. A., Caldow, R. W. G., Rowcliffe, J. M., Goss-Custard, J. D., Black, J. M., Hodder, K. H., … Webb, J. (2000). Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. *Journal of Applied Ecology*, *37*, 103–135. http://doi.org/10.1046/j.1365-2664.2000.00536.x

Phillips, B. L., Brown, G. P., Greenlees, M., Webb, J. K., & Shine, R. (2007). Rapid expansion of the cane toad (Bufo marinus) invasion front in tropical Australia. *Austral Ecology*, *32*(2), 169–176. http://doi.org/10.1111/j.1442-9993.2007.01664.x

Porter, W. P., & Kearney, M. (2009). Size, shape, and the thermal niche of endotherms. *Proceedings of the National Academy of Sciences* , *106*(Supplement 2), 19666–19672. http://doi.org/10.1073/pnas.0907321106

Porter, W. P., Mitchell, J. W., Beckman, W. A., & DeWitt, C. B. (1973). Behavioral implications of mechanistic ecology. *Oecologia*, *13*(1), 1–54. http://doi.org/10.1007/BF00379617

Porter, W. P., Munger, J. C., Stewart, W. E., Budaraju, S., & Jaeger, J. (1994). Endotherm Energetics - From a Scalable Individual-Based Model to Ecological Applications. *Australian Journal of Zoology*, *42*(1), 125–162.

Porter, W. P., Vakharia, N., Klousie, W. D., & Duffy, D. (2006). Po'ouli landscape

bioinformatics models predict energetics, behavior, diets, and distribution on Maui. In *Integrative and Comparative Biology* (Vol. 46, pp. 1143–1158). http://doi.org/10.1093/icb/icl051

Purves, D., Scharlemann, J., Harfoot, M., Newbold, T., Tittensor, D. P., Hutton, J., & Emmott, S. (2013). Time to model all life on Earth. *Nature*, *493*(7432), 295–297. http://doi.org/10.1038/493295a

Pyke, G. H. (2015). Understanding movements of organisms: it's time to abandon the Levy foraging hypothesis. *Methods in Ecology and Evolution*, *6*(1), 1–16. http://doi.org/10.1111/2041-210X.12298

Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal Foraging: A Selective Review of Theory and Tests. *The Quarterly Review of Biology*, *52*(2), 137–154.

Radchuk, V., Turlure, C., & Schtickzelle, N. (2013). Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, *82*(1), 275–285. http://doi.org/10.1111/j.1365-2656.2012.02029.x

R Development Core Team. (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/. *R Foundation for Statistical Computing, Vienna, Austria.*, 2015. http://doi.org/10.1007/978-3-540-74686-7

Railsback, S. F. (2001). Concepts from complex adaptive systems as a framework for individual-based modelling. *Ecological Modelling*, *139*(1), 47–62. http://doi.org/http://dx.doi.org/10.1016/S0304-3800(01)00228-9

Railsback, S. F., & Harvey, B. C. (2002). Analysis of Habitat-Selection Rules Using an Individual-Based Model. *Ecology*, *83*(7), 1817–1830. http://doi.org/10.1890/0012-9658(2002)083[1817:AOHSRU]2.0.CO;2

Railsback, S. F., Lamberson, R. H., Harvey, B. C., & Duffy, W. E. (1999). Movement rules for individual-based models of stream fish. *Ecological Modelling*, *123*(2–3), 73–89. http://doi.org/10.1016/S0304-3800(99)00124-6

Randin, C. F., Dirnböck, T., Dullinger, S., Zimmermann, N. E., Zappa, M., & Guisan, A. (2006). Are niche-based species distribution models transferable in space? *Journal of Biogeography*, *33*(10), 1689–1703. http://doi.org/10.1111/j.1365-2699.2006.01466.x

Ricklefs, R. E., & Hainsworth, F. R. (1968). Temperature dependent behavior of the cactus wren. *Ecology*, *49*(2), 227–233.

Ringelman, K. M. (2014). Predator foraging behavior and patterns of avian nest success: What can we learn from an agent-based model? *Ecological Modelling*, *272*, 141–149. http://doi.org/http://dx.doi.org/10.1016/j.ecolmodel.2013.09.028

Rittenhouse, T. A. G., & Semlitsch, R. D. (2006). Grasslands as movement barriers for a forest-associated salamander: Migration behavior of adult and juvenile salamanders at a distinct habitat edge. *Biological Conservation*, *131*(1), 14–22. http://doi.org/10.1016/j.biocon.2006.01.024

Roese, J. H., Risenhoover, K. L., & Folse, L. J. (1991). Habitat heterogeneity and foraging efficiency: an individual-based model. *Ecological Modelling*, *57*(1–2), 133–143. http://doi.org/10.1016/0304-3800(91)90058-9

Sachs, G., Traugott, J., Nesterova, A. P., & Bonadonna, F. (2013). Experimental verification of dynamic soaring in albatrosses. *The Journal of Experimental Biology*,

216(4), 4222–32. http://doi.org/10.1242/jeb.085209
Safi, K., Kranstauber, B., Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., … Bohrer, G. (2013). Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight. *Movement Ecology*, *1*(1), 4. http://doi.org/10.1186/2051-3933-1-4
Saunders, G., & McLeod, S. (1999). Predicting home range size from the body mass or population densities of feral pigs, Sus scrofa (Artiodactyla: Suidae). *Australian Journal of Ecology*, *24*(5), 538–543. http://doi.org/10.1046/j.1442-9993.1999.01001.x
Scharf, A. K., LaPoint, S., Wikelski, M., & Safi, K. (2016). Acceleration data reveal highly individually structured energetic landscapes in free-ranging fishers (Pekania pennanti). *PLoS ONE*, *11*(2), e0145732. http://doi.org/10.1371/journal.pone.0145732
Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., … Clark, J. S. (2008). Understanding movement data and movement processes: Current and emerging directions. *Ecology Letters*, *11*(12), 1338–1350. http://doi.org/10.1111/j.1461-0248.2008.01249.x
Schoener, T. W. (1968). Sizes of feeding territories among birds. *Ecology*, *49*(1), 123–141. http://doi.org/10.2307/1933567
Schurr, F. M., Pagel, J., Cabral, J. S., Groeneveld, J., Bykova, O., O'Hara, R. B., … Zimmermann, N. E. (2012). How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, *39*(12), 2146–2162. http://doi.org/10.1111/j.1365-2699.2012.02737.x
Sears, M. W., & Angilletta, M. J. (2015). Costs and benefits of thermoregulation revisited: both the heterogeneity and spatial structure of temperature drive energetic costs. *American Naturalist*, *185*(4), E94–E102. http://doi.org/10.1086/680008
Sears, M. W., Angilletta Jr., M. J., Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., … Mitchell, W. A. (2016). Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proc Natl Acad Sci U S A*, *113*(38), 10595–10600. http://doi.org/10.1073/pnas.1604824113
Sears, M. W., Raskin, E., & Angilletta, M. J. (2011). The world is not flat: Defining relevant thermal landscapes in the context of climate change. *Integrative and Comparative Biology*, *51*(5), 666–675. http://doi.org/10.1093/icb/icr111
Shaw, A. K., & Couzin, I. D. (2013). Migration or residency? The evolution of movement behavior and information usage in seasonal environments. *The American Naturalist*, *181*(1), 114–124. http://doi.org/10.1086/668600
Shelly, T. E. (1982). Comparative foraging behavior of light- versus shade-seeking adult damselflies in a lowland Neotropical forest (Odonata: Zygoptera). *Physiological Zoology*, *55*(4), 335–343. http://doi.org/10.1086/physzool.55.4.30155861
Shepard, E. L. C., & Lambertucci, S. A. (2013). From daily movements to population distributions: weather affects competitive ability in a guild of soaring birds. *Journal of The Royal Society Interface*, *10*(88), 20130612. http://doi.org/10.1098/rsif.2013.0612
Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A., & Vosper, S. B. (2013). Energy landscapes shape animal movement ecology. *The American Naturalist*, *182*(3), 298–312. http://doi.org/10.1086/671257

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, *1*(8), 401.

Sibly, R. M., Grimm, V., Martin, B. T., Johnston, A. S. a, Kułakowska, K., Topping, C. J., … Deangelis, D. L. (2013). Representing the acquisition and use of energy by individuals in agent-based models of animal populations. *Methods in Ecology and Evolution*, *4*(2), 151–161. http://doi.org/10.1111/2041-210x.12002

Sinervo, B., Mendez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagran-Santa Cruz, M., … Sites, J. W. (2010). Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches. *Science*, *328*(5980), 894–899. http://doi.org/10.1126/science.1184695

Singer, A., Johst, K., Banitz, T., Fowler, M. S., Groeneveld, J., Guti??rrez, A. G., … Travis, J. M. J. (2016). Community dynamics under environmental change: How can next generation mechanistic models improve projections of species distributions? *Ecological Modelling*, *326*, 63–74. http://doi.org/10.1016/j.ecolmodel.2015.11.007

Sousa, T., Domingos, T., & Kooijman, S. A. L. M. (2008). From empirical patterns to theory: a formal metabolic theory of life. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *363*(1502), 2453–2464.

Sousa, T., Domingos, T., Poggiale, J.-C., & Kooijman, S. A. L. M. (2010). Dynamic energy budget theory restores coherence in biology. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1557), 3413–3428.

Spiegel, O., Leu, S. T., Bull, C. M., & Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters*, *20*(1), 3–18. http://doi.org/10.1111/ele.12708

Spiegel, O., Leu, S. T., Sih, A., & Bull, C. M. (2016). Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. *Methods in Ecology and Evolution*, *7*(8), 971–979. http://doi.org/10.1111/2041-210X.12553

Stamps, J. A. (2007). Growth-mortality tradeoffs and "personality traits" in animals. *Ecology Letters*, *10*(5), 355–363. http://doi.org/10.1111/j.1461-0248.2007.01034.x

Stevenson, R. D. (1985a). Body Size and Limits to the Daily Range of Body Temperature in Terrestrial Ectotherms. *The American Naturalist*, *125*(1), 102–117. http://doi.org/10.1086/284330

Stevenson, R. D. (1985b). The Relative Importance of Behavioral and Physiological Adjustments Controlling Body Temperature in Terrestrial Ectotherms. *American Naturalist*, *126*(3), 362–386. http://doi.org/10.1086/284423

Stillman, R. A., Railsback, S. F., Giske, J., Berger, U., & Grimm, V. (2015). Making predictions in a changing world: The benefits of individual-based ecology. *BioScience*, *65*(2), 140–150. http://doi.org/10.1093/biosci/biu192

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., … Aureli, F. (2011). Collective decision-making and fission-fusion dynamics: A conceptual framework. *Oikos*, *120*(11), 1608–1617. http://doi.org/10.1111/j.1600-0706.2011.19685.x

Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences* , *111*(15), 5610–5615.

http://doi.org/10.1073/pnas.1316145111
Tang, W., & Bennett, D. (2010). Agent based Modeling of Animal Movement: A Review. *Geography Compass*, *7*, 1–30.
Teplitsky, C., Mills, J. A., Alho, J. S., Yarrall, J. W., & Merilä, J. (2008). Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population. *Proceedings of the National Academy of Sciences*, *105*(36), 13492–13496.
Thaler, J. S., McArt, S. H., & Kaplan, I. (2012). Compensatory mechanisms for ameliorating the fundamental trade-off between predator avoidance and foraging. *Proceedings of the National Academy of Sciences* , *109*(30), 12075–12080. http://doi.org/10.1073/pnas.1208070109
Thiele, J. C., Kurth, W., & Grimm, V. (2012). RNetLogo: An R package for running and exploring individual-based models implemented in NetLogo. *Methods in Ecology and Evolution*, *3*(3), 480–483. http://doi.org/10.1111/j.2041-210X.2011.00180.x
Toïgo, C., Gaillard, J., Van Laere, G., Hewison, M., & Morellet, N. (2006). How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography*, *29*(3), 301–308.
Torres-Contreras, H., & Bozinovic, F. (1997). Food selection in an herbivorous rodent: balancing nutrition with thermoregulation. *Ecology*, *78*(7), 2230–2237.
Tracy, C. R., & Christian, K. A. (1986). Ecological relations among space, time and thermal niche axes. *Ecology*. http://doi.org/10.2307/1937684
Travis, J. M. J., Brooker, R. W., & Dytham, C. (2005). The interplay of positive and negative species interactions across an environmental gradient: insights from an individual-based simulation model. *Biology Letters*, *1*(1), 5–8. http://doi.org/10.1098/rsbl.2004.0236
Travis, J. M. J., & Dytham, C. (1998). The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1390), 17–23. http://doi.org/10.1098/rspb.1998.0258
Turchin, P. (1998). *Quantitative analysis of movement : measuring and modeling population redistribution in animals and plants*. Sunderland: Sinauer.
van der Meer, J. (2006). An introduction to Dynamic Energy Budget (DEB) models with special emphasis on parameter estimation. *Journal of Sea Research*, *56*(2), 85–102. http://doi.org/http://dx.doi.org/10.1016/j.seares.2006.03.001
Van Dijk, P. L. M., Hardewig, I., & HÖlker, F. (2005). Energy reserves during food deprivation and compensatory growth in juvenile roach: the importance of season and temperature. *Journal of Fish Biology*, *66*(1), 167–181. http://doi.org/10.1111/j.0022-1112.2005.00590.x
van Dyck, H., & Baguette, M. (2005). Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology*, *6*(6), 535–545. http://doi.org/10.1016/j.baae.2005.03.005
Van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C. M., Solberg, E. J., & Sæther, B. E. (2013). Understanding scales of movement: Animals ride waves and ripples of environmental change. *Journal of Animal Ecology*, *82*(4), 770–780. http://doi.org/10.1111/1365-2656.12045
Van Moorter, B., Rolandsen, C. M., Basille, M., & Gaillard, J.-M. (2015). Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology*,

85(1), 21–31. http://doi.org/10.1111/1365-2656.12394
Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M. S., & Gaillard, J. M. (2009). Memory keeps you at home: A mechanistic model for home range emergence. *Oikos*, *118*(5), 641–652. http://doi.org/10.1111/j.1600-0706.2008.17003.x
Vickers, M., Manicom, C., & Schwarzkopf, L. (2011). Extending the cost-benefit model of thermoregulation: high-temperature environments. *American Naturalist*, *177*(4), 452–461. http://doi.org/10.1086/658150
Vickers, M., & Schwarzkopf, L. (2016). A random walk in the park: an individual-based null model for behavioral thermoregulation. *The American Naturalist*, *187*(4), 481–490.
Villén-Pérez, S., Carrascal, L. M., & Seoane, J. (2013). Foraging Patch Selection in Winter: A Balance between Predation Risk and Thermoregulation Benefit. *PLoS ONE*, *8*(7). http://doi.org/10.1371/journal.pone.0068448
Wajnberg, E., Hoffmeister, T. S., & Coquillard, P. (2013). Optimal within-patch movement strategies for optimising patch residence time: An agent-based modelling approach. *Behavioral Ecology and Sociobiology*, *67*(12), 2053–2063. http://doi.org/10.1007/s00265-013-1615-5
Walker, L. E., Walker, J. E., Palca, Joseph, W., & Berger, R. J. (1983). A Continuum of Sleep and Shallow Torpor in Fasting Doves. *Science*, *221*(4606), 194–195.
Walther, B., & Gosler, A. (2001). The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (Aves: Parus). *Oecologia*, *129*(2), 312–320.
Wang, M., & Grimm, V. (2007). Home range dynamics and population regulation: An individual-based model of the common shrew Sorex araneus. *Ecological Modelling*, *205*(3–4), 397–409. http://doi.org/10.1016/j.ecolmodel.2007.03.003
Webb, J. K., Brook, B. W., & Shine, R. (2003). Does foraging mode influence life history traits? A comparative study of growth, maturation and survival of two species of sympatric snakes from south-eastern Australia. *Austral Ecology*, *28*(6), 601–610.
Wehner, R., Marsh, A. C., & Wehner, S. (1992). Desert ants on a thermal tightrope. *Nature*, *357*(6379), 586–587.
Weimerskirch, H., Doncaster, C. P., & Cuenot-Chaillet, F. (1994). Pelagic Seabirds and the Marine Environment: Foraging Patterns of Wandering Albatrosses in Relation to Prey Availability and Distribution. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *255*(1343), 91–97.
Weimerskirch, H., Pinaud, D., Pawlowski, F., & Bost, C.-A. (2007). Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *The American Naturalist*, *170*(5), 734–743. http://doi.org/10.1086/522059
Weiss, S. B., Murphy, D. D., & White, R. R. (1988). Sun, slope, and butterflies: topographic determinants of habitat quality for Euphydryas editha. *Ecology*, *69*(5), 1486–1496.
Werner, E. E. (1986). Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *The American Naturalist*, *128*(3), 319–341.
Werner, E. E., & Anholt, B. R. (1993). Ecological Consequences of the Trade-Off between Growth and Mortality Rates Mediated by Foraging Activity. *The American*

Naturalist, *142*(2), 242–272.
Wilensky, U. (1999). NetLogo. *Http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and ComputerBased Modeling Northwestern University Evanston IL*.
Wilson, K. J., & Lee, A. K. (1974). Energy expenditure of Large Herbivorous Lizard. *Copeia*, *2*(2), 338–348.
Wilson, R. P., Griffiths, I. W., Legg, P. A., Friswell, M. I., Bidder, O. R., Halsey, L. G., … Shepard, E. L. C. (2013). Turn costs change the value of animal search paths. *Ecology Letters*, *16*(9), 1145–1150. http://doi.org/10.1111/ele.12149
Wilson, R. P., Grundy, E., Massy, R., Soltis, J., Tysse, B., Holton, M., … Butt, T. (2014). Wild state secrets: ultra-sensitive measurement of micro-movement can reveal internal processes in animals. *Frontiers in Ecology and the Environment*, *12*(10), 582–587. http://doi.org/10.1890/140068
Wilson, R. P., Quintana, F., & Hobson, V. J. (2012). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1730), 975–980. http://doi.org/10.1098/rspb.2011.1544
Wilson, R. S., Husak, J. F., Halsey, L. G., & Clemente, C. J. (2015). Predicting the Movement Speeds of Animals in Natural Environments. *Integrative and Comparative Biology*, *55*(6), 1125–1141. http://doi.org/10.1093/icb/icv106
Wilson, W. G. (1998). Resolving discrepancies between deterministic population models and individual-based simulations. *The American Naturalist*, *151*(2), 116–134. http://doi.org/10.1086/286106
Wood, K. A., Stillman, R. A., Wheeler, D., Groves, S., Hambly, C., Speakman, J. R., … O'Hare, M. T. (2013). Go with the flow: Water velocity regulates herbivore foraging decisions in river catchments. *Oikos*, *122*(12), 1720–1729. http://doi.org/10.1111/j.1600-0706.2013.00592.x
Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology & Evolution*, *20*(7), 402–409.
Woodward, G., & Hildrew, A. G. (2002). Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology*, *71*(6), 1063–1074. http://doi.org/10.1046/j.1365-2656.2002.00669.x
Wright, J. T., Williams, S. L., & Dethier, M. N. (2004). No zone is always greener: variation in the performance of Fucus gardneri embryos, juveniles and adults across tidal zone and season. *Marine Biology*, *145*(6), 1061–1073. http://doi.org/10.1007/s00227-004-1399-2
Yen, J. D. L., Thomson, J. R., Keith, J. M., Paganin, D. M., Fleishman, E., Dobkin, D. S., … Mac Nally, R. (2017). Balancing generality and specificity in ecological gradient analysis with species abundance distributions and individual size distributions. *Global Ecology and Biogeography*, *26*(3), 318–332. http://doi.org/10.1111/geb.12537
Zollner, P. A., & Lima, S. L. (2005). Behavioral tradeoffs when dispersing across a patchy landscape. *Oikos*, *108*(2), 219–230.

List of publications

Malishev M, Bull CM & Kearney MR An individual-based model of ectotherm movement integrating metabolic and microclimatic constraints. *Methods in Ecology and Evolution*. In press.

Fraser H, Soanes K, Jones C, Jones S & **Malishev M** 2017. The value of virtual conferencing for ecology and conservation. *Conservation Biology*, 31(3), pp.540–546.

Sperfeld E, Wagner ND[#], Halvorson HM[#], **Malishev M**[#] & Raubenheimer D 2017. Bridging Ecological Stoichiometry and Nutritional Geometry with homeostasis concepts and integrative models of organism nutrition. *Functional Ecology*, 31(2), pp.286–296.

Sperfeld E[#], Halvorson HM[#], **Malishev M**, Clissold F & Wagner ND 2016. Woodstoich III: Integrating tools of nutritional geometry and ecological stoichiometry to advance nutrient budgeting and the prediction of consumer-driven nutrient recycling. *Oikos*, 125, pp.1539–1553.

Malishev M & Sanson GD 2015. Leaf mechanics and herbivory defence: How tough tissue along the leaf body deters growing insect herbivores. *Austral Ecology*, 40(3), pp.300–308.

Malishev M & Kramer-Schadt S Individual-based energy budgets as next-generation extensions for modelling animal movement across scales. In revision.

Kearney MR, Munns SL, Moore D, **Malishev M** & Bull CM How well do mechanistic niche models work? A detailed test reveals how water can be more limiting than temperature for lizards under climate change. In review.

[#] Equal contribution