



IDEA AND PERSPECTIVE

A mechanistic theory of personality-dependent movement behaviour based on dynamic energy budgets

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Abstract

Consistent between-individual differences in movement are widely recognised across taxa. In addition, foraging plasticity at the within-individual level suggests a behavioural dependency on the internal energy demand. Because behaviour co-varies with *fast-slow* life history (LH) strategies in an adaptive context, as theoretically predicted by the pace-of-life syndrome hypothesis, mass/energy fluxes should link behaviour and its plasticity with physiology at both between- and within-individual levels. However, a mechanistic framework driving these links in a fluctuating ecological context is lacking. Focusing on home range behaviour, we propose a novel behavioural-bioenergetics theoretical model to address such complexities at the individual level based on energy balance. We propose explicit mechanistic links between behaviour, physiology/metabolism and LH by merging two well-founded theories, the movement ecology paradigm and the dynamic energetic budget theory. Overall, our behavioural-bioenergetics model integrates the mechanisms explaining how (1) behavioural between- and within-individual variabilities connect with internal state variable dynamics, (2) physiology and behaviour are explicitly interconnected by mass/energy fluxes, and (3) different LHs may arise from both behavioural and physiological variabilities in a given ecological context. Our novel theoretical model reveals encouraging opportunities for empiricists and theoreticians to delve into the eco-evolutionary processes that favour or hinder the development of between-individual differences in behaviour and the evolution of personality-dependent movement syndromes.

Keywords

bioenergetics, dynamic energy budget (DEB) model, exploration rate, foraging behaviour, growth rate, home range, life history traits, metabolism, movement, personality.

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INTRODUCTION

The pace-of-life syndrome (POLS) hypothesis provides a theoretical framework explaining the co-variation between life history (LH) traits with diverse physiological and behavioural traits within an eco-evolutionary context (Réale *et al.* 2010), where ecological processes are the main drivers shaping these relationships and their co-evolution (Ricklefs & Wikelski 2002; Montiglio *et al.* 2018). However, the ways in which consistent within- and between-individual differences in behaviour (i.e. animal personality or behavioural types, BTs, Dall *et al.* 2004; Réale *et al.* 2007; Sih *et al.* 2004) are connected to the wide range of observed LH remains a fundamental yet unresolved question (Mathot & Frankenhuis 2018). BTs are often associated with consistent between-individual differences in metabolism (hereafter physiological types, PTs) (Biro & Stamps 2010; Metcalfe *et al.* 2016), which are certainly widespread (Nespolo & Franco 2007; Killen *et al.* 2016). Moreover, PTs correlate with variation in internal state dynamics and LH traits along the *fast-slow continuum* (Stearns 1992; Careau *et al.* 2008; Careau & Garland 2012; Holtmann *et al.* 2017a). Consequently, BTs have been associated with differences in growth rates, time to sexual maturation, lifetime, expected reproduction output (Stamps 2007; Biro & Stamps

2008) and, eventually, individual fitness (Mathot & Dingemanse 2015; Sih *et al.* 2015). However, phenotypic plasticity in both behaviour and physiology and the potentially confounding effects of environment may blur these co-variation patterns (Niemelä *et al.* 2013), which may be one of the causes of the scarce supporting empirical evidence of POLS (Niemelä & Dingemanse 2018).

Before considering behaviour as a putative candidate for driving LH at the evolutionary scale, two prerequisites must be met. First, behaviour cannot be only a plastic response to environmentally driven individual-level characteristics (Dingemanse *et al.* 2010) nor a random or stochastic component of the individual, but some consistency should exist (Réale *et al.* 2007; Doctermann *et al.* 2014). However, different processes may underlie behavioural consistency and the establishment of behavioural individuality, such as behavioural state dependency along with stable differences in states (Dall *et al.* 2004; Wolf & Weissing 2010; Sih *et al.* 2015; Holtmann *et al.* 2017a), genetic and/or environmental correlations (Niemelä *et al.* 2013; Doctermann *et al.* 2014; Santostefano *et al.* 2017), the integration of developmental (i.e. irreversible) plasticity (Dammhahn *et al.* 2018) and differences in stress physiology (i.e. coping styles Koolhaas *et al.* 1999; Di Rienzo *et al.* 2012). Moreover, other unidentified factors may exist

(Bierbach *et al.* 2017). Second, whenever related to fitness, individual behavioural differences should require an adaptive explanation (Wolf *et al.* 2007; Wolf & Weissing 2010; Vindenes & Langanen 2015), which is not expected to be simple but arises from intricate and complex interwoven connections (Fig. 1). Therefore, because the mechanisms underlying these associations are unclear, more explicit hypotheses on the within-individual internal state variable dynamics explaining behaviour from an adaptive perspective are still required (Mathot & Frankenhuys 2018; Montiglio *et al.* 2018).

Animal movement and space-use [including home range (HR) behaviour] are a specific dimension of behaviour that has been recently integrated within the conceptual framework of POLS to better understand the adaptive value of movement-BTs (e.g. Kobler *et al.* 2009; Biro & Stamps 2010; Nakayama *et al.* 2017). HR behaviour typically refers to the animal movement that leads to the establishment of a bounded area that fulfils vital activities (Burt 1943; Börger *et al.* 2008); it has been widely reported in nature, and it may trigger many fundamental eco-evolutionary processes (McCauley *et al.* 2015). Consistent intraspecific variation in HR behaviour has been widely recognised across taxa (Olsen *et al.* 2012; Harrison *et al.* 2015; Villegas-Ríos *et al.* 2017)

facilitated by the fast development and miniaturisation of biotelemetry devices in the last two decades (Hays *et al.* 2016). Such consistent intraspecific variation allows the recognition of different movement-BTs ranging from *mobile* to *resident* (Harrison *et al.* 2015), where a *mobile*-type (vs. *resident*-type) is characterised by a large HR, high movement rates and little site fidelity at within species level.

Understanding the interactions, causes and outcomes between movement-BTs and their links with PTs, LH, internal state dynamics and environmental factors, is a fundamental question to address the adaptive value of movement behaviour within the POLS framework (Mathot & Frankenhuys 2018). Aiming to disentangle the possible mechanisms behind these associations, we frame our work around two well-established movement-related frameworks. First, the *movement ecology paradigm* proposes that the interplay among the internal state, motion and navigation capacities of the individual with external environmental factors is the main mechanism behind spatiotemporal patterns of animal movement (Nathan *et al.* 2008). Second, the *personality-dependent spatial ecology* framework extends the *movement ecology paradigm* by proposing that individual variability in movement may arise from both consistent between-individual differences in behavioural

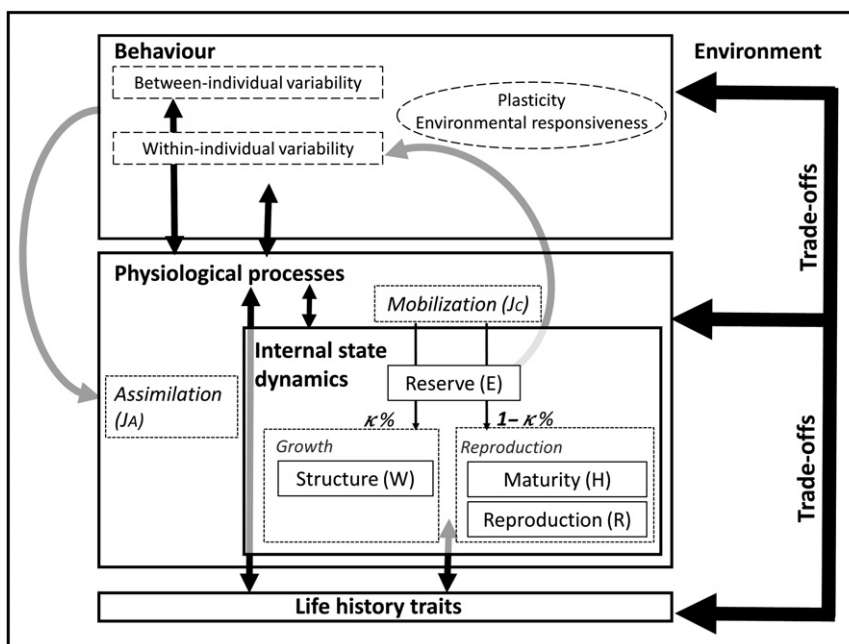


Figure 1 Individual behavioural-bioenergetics theory explaining life history (LH) variability from mechanistic links connecting interindividual differences in behaviour, physiology and internal state dynamics. Different mechanistic connections can explain the correlation between behaviour, physiology and LH in different ecological environments. Behaviour is a complex state of the organism that is connected with the dynamics of the internal states, physiological processes and environmental factors through an interweaving of interactions mediated by energy and mass flows (thin black arrows). Consistent interindividual differences in behaviour, along with its within-individual variability and plasticity, can affect the individual realised LHs through its direct connection with feeding behaviour and, consequently, the assimilation flux. Additionally, a feedback between behaviour, physiological processes and internal states may also induce consistency between correlated traits and mediate its responsiveness to environmental conditions. For instance, when connecting movement with feeding behaviour, the space-use dynamics should accommodate environmental conditions to achieve at least the necessary energy for internal requirements through feedback from the dynamics of the reserve energy (grey arrows). Black arrows show interactions (and direction) between the four main connected blocks: behaviour, physiology, internal states and environment (squares with thick continuous line). Within behaviour, squares with a dashed line outline different components of behavioural variability. Reserve, maturity and reproduction (boxes) dynamics are described by dynamic energy budget theory (dotted boxes). Grey arrows show interactions (and direction) between behaviour and the internal reserve dynamics, through the fluxes of assimilation and mobilisation (dotted boxes). A κ fraction of the mobilised energy is allocated for growth and structural maintenance, while the rest is invested for maturity and reproduction.

traits (e.g. exploration, activity) and proximate mechanisms (e.g. endocrinology, genetic variation) linking behaviour and movement and resulting in behavioural syndromes, along with behavioural responsiveness to environmental variation (Spiegel *et al.* 2017). However, explicit mechanisms that shape space-use dynamics and their connection with LH have not yet been proposed (Nathan *et al.* 2008; Spiegel *et al.* 2015), which limits their applicability when addressing the adaptive value of movement-BTs within POLS.

A prevalent role of foraging for HR behaviour has been suggested by, among other reasons, the existence of between-species scaling relationships between body size and optimal HR size (Minns 1995; Buchmann *et al.* 2011; McCauley *et al.* 2015; Nash *et al.* 2015). Therefore, this relationship may be shaped, at least in part, by energy availability. Thus, larger energy needs, which also scale with body size (Harestad & Bunnell 1979; Brown *et al.* 1993; Andersen *et al.* 2015), would be fulfilled by exploiting larger HR areas (McNab 1963; Jetz *et al.* 2004; Tamburello *et al.* 2015). This connection may provide a suitable mechanism linking HR behaviour and LH at the individual level. Accordingly, at least some of the variability in HR and space-use dynamics observed at the individual level may be mediated by internal energy-related states (Mueller & Fagan 2008; Higginson *et al.* 2018), underpinned by bioenergetics (Teal *et al.* 2012; Sih *et al.* 2015) and dependent on seasonal and spatial foraging opportunities (Shepard *et al.* 2013; Tao *et al.* 2016; Gallagher *et al.* 2017) and habitat quality (Börger *et al.* 2006). From an adaptive perspective, the optimal HR size and how animals move within it (i.e. optimal movement strategy) are expected to be those that maximise the cumulated energy profit (Yodzis & Innes 1992; Nathan *et al.* 2008) and minimise the mortality risk during an individual's lifespan (Graham 1984; Jørgensen *et al.* 2016) to enhance reproduction and maximise fitness. Therefore, when individual differences in space-use co-vary with fitness, some nexus should connect HR behaviour with LH itself. Overall, such an optimal context-dependent movement strategy (i.e. the rule specifying the dependence of behaviour on the internal state, organism's environment and time) would emerge from the interactions between PTs and other BT dimensions, where foraging-related behaviour is assumed as a key driver connecting space-use and environment with internal states and, eventually, LH.

To rigorously address these complexities, we propose a fully mechanistic (process-based) model that describes the functional connections between behavioural and physiological traits supporting growth, energetic maintenance costs and reproduction (Fig. 1). Mechanistically linking HR behaviour with the rules for the organisation of individual metabolism based on mass/energy fluxes (i.e. fluxes that determine the balance between all mass and energy that enter and exit an individual) would provide insight into the energetic dimension of behaviour and the processes that lead to between-individual differences in HR and LHs. In particular, our approach attempts to establish explicit links between movement-BTs and physiological/metabolic traits by enlarging a widely recognised bioenergetics model [dynamic energy budget (DEB); Kooijman 2010] to cope with the mechanisms that together would determine a suite of LH traits for an animal living in a

given environment. Accordingly, our proposed behavioural-bioenergetics theoretical model aims to shed light on how LH properties emerge from explicit mechanistic dependencies between behaviour and physiology.

A NOVEL INDIVIDUAL BEHAVIOURAL-BIOENERGETICS THEORY

Two theoretically and empirically well-founded bodies of theories are merged here into a unique theory (hereafter the behavioural-bioenergetics model) to bridge the gap between movement-BTs and LH dynamics (Fig. 1). These theories are the *movement ecology paradigm* (Nathan *et al.* 2008) and its recent link to the *personality-dependent spatial ecology* framework (Spiegel *et al.* 2017), which we extend to LH theory (Stearns 1992) through explicit links with the DEB theory (Kooijman 2010), which explains mechanistically the individual metabolic organisation. The emerging patterns from the proposed behavioural-bioenergetics model (Box 1) are then explored to mechanistically understand the relationships between contrasting behavioural (*mobile* and *resident*) and physiological/metabolic (*fast* and *slow*) types in different environments, and whether these interactions may lead to the emergence of *fast-slow* POLS.

Describing HR movement

Several mechanistic processes leading to the establishment of a HR have been proposed (see Moorcroft *et al.* 2006 and Börger *et al.* 2008 for a review). One of the simplest approaches assumes that HR results from animal movements within an isotropic environment following random stimuli such as food items, but with an additional tendency (drift) to remain around a specific point (e.g. the refuge), designed as the HR centre (Palmer *et al.* 2011). The resulting path is a *biased random walk* (BRW) described by a Langevin process (Gardiner 1990):

$$\frac{d\vec{r}}{dt} = -\gamma(\vec{r}(t) - \vec{r}_o) + \sqrt{\epsilon}\vec{\xi}(t), \quad (1)$$

where $\vec{r}(t)$ denotes the time-dependent animal displacement with respect to the location \vec{r}_o (HR centre) and γ defines the strength of the tendency to remain around \vec{r}_o (in mathematical terms, this tendency is described in eqn 1 by the dynamics of a particle subjected to the influence of an harmonic force of constant γ). The stochastic term $\sqrt{\epsilon}\vec{\xi}(t)$ is considered to have a Gaussian distribution (white noise), with a zero mean, uncorrelated between the two spatial coordinates with the same variance (ϵ) on each spatial dimension. The stationary spatial pattern (after a period of time large enough to reach an asymptote in the cumulative space explored) is a circular HR with radius HR_r (the radius of the area within which an animal has a 95% probability of being found), as described by Palmer *et al.* (2011):

$$HR_r \propto \sqrt{\frac{\epsilon}{\gamma}}. \quad (2)$$

The parameters of the HR-type movement described in eqns 1 and 2 can be ecologically interpreted in terms of the *searching*

rate (ε , visited area by unit of time, with dimensions L^2T^{-1}) and *drift force (or damping) coefficient* γ (strength of the tendency to keep near to the HR centre, with dimensions T^{-1}). The *searching rate* ε can be interpreted as a proxy of *activity level*, and among others, it may depend on energy requirements (see below). The *drift force* coefficient γ , which determines the readiness of the individual to move away from the home location \bar{r}_o and how the individual moves within the HR, can be interpreted as a proxy of the *exploration rate* (i.e. the ratio between exploring new areas vs. exploiting familiar resources, Réale et al. 2007). The *drift force* coefficient may depend on extrinsic factors, such as environmental fluctuations, landscape heterogeneity, intraspecific avoidance, attraction, competition or other social interactions, predation risk or intrinsic factors such as other BTs (e.g. shier behavioural types are expected to be closer to their refuge). Both together, the ratio ε/γ determines the characteristic size of the circular HR and essentially measures the tendency to be *mobile* vs. *sedentary*.

The dynamic bioenergetics model

Bioenergetics models mechanistically predict the ontogenetic trajectory of internal state variables and LH traits in different environmental contexts (Persson et al. 1998; Nisbet et al. 2012; Jusup et al. 2017). Bioenergetics models are being gradually extended beyond conventional bioenergetics to include behaviour and performance (Jørgensen et al. 2016). In such a behaviour-related paradigm, DEB theory (Kooijman 2010) offers a well-supported bioenergetics framework over which the way in which different BTs and/or PTs may connect with the emergent LHs can be explored. In essence, DEB theory addresses the major mass/energy fluxes of living organisms and predicts the changes in a set of internal state variables that includes structure (W), reserve (E), maturity (H) and reproduction (R) at the individual level (van der Meer 2006; Ledder 2014). In brief, energy for life is assimilated from food, stored as reserve and then mobilised to fuel all internal processes related to growth and reproduction. The rate of change of E (dE/dt , Table 1) depends on the energy inflow (i.e. the assimilation rate, J_A , Table 1), and the rate of stored energy outflow to fuel any physiological process (i.e. the mobilisation rate, J_C , Table 1). How fast E is mobilised depends on a parameter called the *energy conductance* v (Ledder 2014). Moreover, the proportion of the reserve allocated to different processes is described by the κ -rule, which is a particularity of DEB theory. κ represents a fixed and constant fraction of the mobilised energy that is allocated for growth and structural maintenance, while the rest, a $1 - \kappa$ proportion of the mobilised energy, is invested for maturity and reproduction. Thus, growth and development are parallel processes (Kooijman 2010). The growth rate (dW/dt , Table 1) depends on the κ fraction of the energy mobilised for growth (κJ_C) after first covering the maintenance costs of W , J_S (Table 1). Movement costs, whenever proportional to the structural volume, are considered as a fixed part of maintenance costs (Kooijman 2010; Jusup et al. 2011; Nisbet et al. 2012). In contrast, the fraction $1 - \kappa$ of the mobilisation flux ($(1 - \kappa) J_C$) goes towards H , which includes reorganisation processes, the development of reproductive organs and regulatory

systems. The maturity level at birth is zero, and it increases (dH/dt , Table 1) after paying for maturity maintenance costs (J_H , Table 1). Juveniles become adults when arriving at a threshold maturity level H_p . Then, after puberty, maturation stops, and this fraction of mobilised energy is redirected to reproduction (dR/dt , Table 1). More details can be found elsewhere (van der Meer 2006; Kooijman 2010; Ledder 2014).

With the purpose of avoiding dependence on the choice of currency, either energy or mass (i.e. moles of carbon atoms), Ledder (2014) replaced the original variables E and W with the reserve density (U) and structural length (L). In such a way, $W = \Gamma L^3$ and $E = U \Gamma L^3$, where Γ represents the density of energy (or moles of carbon atoms) contained in a unit volume of structure. Therefore, U becomes a dimensionless internal state variable describing the amount of reserve in terms of its equivalent contained in a unit volume of structure (i.e. $U = E/\Gamma L^3$). Aiming to explore the general performance of the model, we propose a scaled version to work with dimensionless internal state variables (see Appendix S1 in Supporting Information).

Incorporating between- and within-individual differences in HR behaviour into a bioenergetics model

To provide insights into the interconnection between movement-BTs and mass/energy fluxes, we enlarged a standard-DEB model by including two relationships with HR behaviour (Fig. 1). In particular, we propose one direct connection through the assimilation flux to match foraging behaviour (Lika & Papandroulakis 2005; Watkins 2012; van Gils et al. 2015), and an indirect connection through the dynamics of the reserve density U .

According to DEB theory (Kooijman 2010), J_A is proportional to the animal surface area, and following Ledder's notation (2014), it can be described as:

$$\frac{J_A}{\Gamma L^2} = Q, \quad (3)$$

where Q refers to the *assimilation conductance* (dimensions LT^{-1}). Importantly, Q describes how fast energy is assimilated from the environment, and it does not depend on any internal state but on food availability. This dependence occurs through a functional response, with a physiological maximum bound because an animal cannot assimilate an unlimited amount of food even if available. Hence, Q is given by:

$$Q = Q_m f, \quad (4)$$

where f is a functional response that is dependent on the resource density representing a non-dimensional fraction, bounded between 0 and 1, of the maximum metabolic limit Q_m for Q .

We consider the classical consumer–resource concept of the functional response f between the consumption rate (i.e. amount of food eaten per unit time) and food density (Solomon 1949) to mechanistically link foraging and assimilation (Visser 2007; Pawar et al. 2012). For simplicity, we define this relationship as a scaled version of the Holling type II functional response (Holling 1959), which in its canonical form defines the intake rate (IR , with dimension n food items T^{-1}) as:

Table 1 State variables, parameters and dynamic equations of the behavioural-bioenergetics model. Standard-DEB formulae are from Ledder (2014). Specific formulae for the behavioural-bioenergetics model* and dimensionless version† have been developed in this work.

Symbol	Interpretation (description)	Dimension
State variables		
$W = \Gamma L^3$	Structure (corporeal material of the organism) <i>L structural length (L)</i>	ML^2T^{-2}
$E = U\Gamma L^3$	Reserve (stored energy for future allocation to other components or processes) <i>U reserve energy density (reserve energy per unit of energy in structure)</i>	ML^2T^{-2}
H	Maturity (energy required to prepare reproduction)	ML^2T^{-2}
R	Reproduction (energy used for reproduction)	ML^2T^{-2}
Dynamic equations†		
$\frac{dE}{dt} = J_A - J_C$	Reserve dynamics	ML^2T^{-3}
$\frac{dW}{dt} = y(\kappa J_C - J_S)$	Structure dynamics	ML^2T^{-3}
$\frac{dH}{dt} = (1 - \kappa)J_C - J_H(H < H_P)$	Maturity dynamics	ML^2T^{-3}
$\frac{dR}{dt} = (1 - \kappa)J_C - J_H(H \geq H_P)$	Reproduction dynamics	ML^2T^{-3}
Fluxes		
$J_A = \Gamma L^2 Q$	Assimilation rate (rate at which energy is assimilated from food)	ML^2T^{-3}
$Q = \tilde{Q}_m f_{(e,x)}$	<i>Q Assimilation conductance</i>	LT^{-1}
$J_C = \frac{yU\Gamma L^2 + yUJ_S}{1 + \kappa yU}$	Mobilisation rate (rate at which energy is mobilised from the reserve for internal processes)	ML^2T^{-3}
$J_S = k\Gamma L^3$	Structural maintenance rate (costs required for somatic maintenance)	ML^2T^{-3}
$J_H = K_H H$	Maturation maintenance rate (costs required for maturity maintenance)	ML^2T^{-3}
Parameters		
Γ	Energy (or moles of carbon atoms) per unit of structure (Γ is used to convert quantities measured in energy units into an equivalent of structural length (Ledder 2014))	$ML^{-1}T^{-2}$
κ	κ (fraction of the mobilised energy that is invested for growth and structural maintenance)	–
v	Energy conductance	LT^{-1}
Q_m	Maximum assimilation conductance	LT^{-1}
y	Yield in structure of the fraction of invested resources	–
k	Structural maintenance coefficient	T^{-1}
k_H	Maturity costs coefficient	T^{-1}
H_P	Threshold maturity level in the puberty time	ML^2T^{-2}
Link between HR and DEB*		
$f_{(e,x)} = \frac{\varepsilon x}{1 + \varepsilon x}$	Functional response ε HR-exploration rate x scaled resource levels	–
$\varepsilon = \frac{\varepsilon_m}{1 + \frac{U}{U_{th}}}$	Exploration rate ε_m maximum HR-exploration rate (behavioural trait) U_{th} threshold level of density of energy at which ε is half its maximum	L^2T^{-1} L^2T^{-1}
$HR_r \propto \sqrt{\frac{\varepsilon}{\gamma}}$	Radius of the circular HR area γ drift force (behavioural trait)	L T^{-1}
Dimensionless states‡		
$U = \frac{E}{\Gamma L^3}$	Reserve energy density (reserve energy per unit of energy in structure)	–
$l = \frac{k}{\kappa Q_m} \cdot L$	Scaled length by its maximum (values range from 0 to 1) $L_m = \frac{\kappa Q_m}{k}$	–
$h = \frac{k^3}{\Gamma \kappa^2 Q_m^3} \cdot H$	Scaled maturity	–
$r = \frac{k^3}{\Gamma \kappa^2 Q_m^3} \cdot R$	Scaled reproduction	–
$\tau = k \cdot t$	Scaled time	–
Dimensionless dynamic equations‡		
$\frac{dU}{d\tau} = \frac{1}{\kappa l} (f - \frac{v}{Q_m} U)$	Reserve energy density dynamics	–
$\frac{dl}{d\tau} = \frac{v}{3} \left(\frac{x}{Q_m} \right) \frac{U-l}{1+y\kappa U}$	Scaled length dynamics	–
$\frac{dh}{d\tau} = (1 - \kappa) U l^2 \left(\frac{x}{Q_m + y\kappa l} \right) - \sigma h (h < h_P)$	Scaled maturity dynamics $\sigma = \frac{k_H}{k}$ dimensionless parameter (maturity and structural maintenance coefficient ratio)	–
$\frac{dr}{d\tau} = (1 - \kappa) U l^2 \left(\frac{x}{Q_m + y\kappa l} \right) - \sigma h_P (h \geq h_P)$	Scaled reproduction dynamics	–
$U^{st} = \frac{Q_m f}{v}$	Steady dimensionless reserve energy density, U^{st} , and length, l^{st} , states when scaled dynamic equations equal 0‡	–
$l^{st} = \frac{v}{Q_m} U^{st} = f$		–

Notes *A non-monotonic relationship between HR and DEB is explored in Appendix S1 in Supporting Information.

†For the details of standard-DEB dynamic equations and ‡ the derivation of the scaled version in this work see Appendix S1.

$$IR = \frac{ap}{1 + ah\rho}, \quad (5)$$

where ρ is the resource density (dimensions n food items L^{-2} when considering 2D), h is the handling time (time needed for processing a single food item, with dimensions T), and a is usually referred as the *attack rate* (dimensions L^2T^{-1}) (Schröder *et al.* 2016). The maximum intake rate (IR_{max}) is attained at $1/h$, and thus, a convenient scaled definition of f may be obtained as:

$$f = IR/IR_{max} = \frac{ah\rho}{1 + ah\rho}. \quad (6)$$

The *attack rate* a depends on successful completion of the sequential processes of the encounter rate, probability of a successful pursuit-attack and probability of eating given the consumer has captured the prey (Lika & Papandroulakis 2005; van der Meer & Smallegange 2009). In the context of an animal with HR behaviour, the encounter rate (i.e. the amount of actually accessible resources) must be correlated with both ρ and the *searching rate* or *activity level* (Bartumeus *et al.* 2002; Lika & Papandroulakis 2005; Viswanathan *et al.* 2008; van Gils *et al.* 2015), defined as ε in the HR-movement model (eqns 1 and 2). By assuming h as a constant at the between- and within-individual level, we propose to simplify $f(a, \rho)$ into $f(\varepsilon, x)$:

$$f = \frac{\varepsilon x}{1 + \varepsilon x}, \quad (7)$$

where x is the *scaled resource density* equalling h times ρ (i.e. $x = h\rho$), which can be interpreted as the time needed to assimilate the resource items available per unit area (dimensions TL^{-2}).

In addition, we propose the existence of a state dependency of ε on the *reserve energy density* U . Conceptually, when the energy demand of an individual is low because the internal U is enough to cover any physiological process, the animal can reduce its activity and thus any ecological movement-related cost (Higginson *et al.* 2018). Conversely, when the energy balance is close to zero, the animal must explore larger areas and increase its activity close to a maximum limited only by biological (and/or ecological) constraints to acquire enough energy to cover the energy costs for structural maintenance. A simple functional link between the pattern of space-use and U can be given by:

$$\varepsilon = \frac{\varepsilon_m}{1 + \frac{U}{U_{th}}}, \quad (8)$$

where ε_m defines the *maximum searching rate* for the individual that leads to its maximum HR size (eqn 2) for a given value of γ . According to eqns 7 and 8, the attained ε will be close to ε_m only when U is close to zero. Then, ε will increase to allow greater food intake, which in turn will cause Q to approach Q_m . However, after increasing U because of the latter food intake increase, ε will drop again. Thus, at least in part, reserve levels may play a certain 'memory' role acting as a source of information of recent environmental conditions (Higginson *et al.* 2018). Note that U_{th} is a constant defining the threshold of U at which ε reaches half its maximum ε_m . This simple approximation is defined beforehand to evaluate the responsiveness of ε with

respect U in different environmental conditions. However, much more complex non-monotonic relationships with U may exist depending on the particularities of the case study whenever the trade-offs of maximising the energy intake and minimising the energy expenditure and ecological risks are considered mechanistically (Scharf 2016). Note that according to the DEB theory, feeding costs are already paid from food intake directly, which implies a reduction of the assimilation efficiency, and costs from routine movements are covered by maintenance (Kooijman 2010). Therefore, movement costs are implicitly considered herein. However, space-use dynamics and optimal movement decisions may be limited in certain contexts at the expense of a higher energy expenditure due to movement costs. Non-monotonic relationships with U should be explored in future applications whenever, for example, experimental data or empirical patterns are available (see Appendix S2 for an example based on a hump-shaped response, Spiegel *et al.* 2013b; Scharf 2016).

Numerical simulations: the mobile-resident and the fast-slow axis of variation

Three sets of numerical simulations were completed to illustrate some relevant properties of our behavioural-bioenergetics model. Aiming to promote generality and a better understanding of the processes involved, simulations were run using a scaled version of the model (see Appendix S1, Table 1). In particular, the simulations focused on two well-contrasted archetypes defining the opposite extremes of a HR behaviour-related gradient (through the *searching rate*) and a second gradient concerning metabolic processes (through the *energy mobilisation rate*).

For the HR behaviour-related gradient, we defined the *resident-mobile* BTs, where a *resident* animal tends to remain closer to its HR centre, and a *mobile* animal can exploit larger HR areas (as introduced in Harrison *et al.* 2015). We specifically focused on the variability of the parameter ε_m , which is individual-specific and underlies consistent, context-independent, between-individual differences in HR behaviour. Therefore, contrasting values of ε_m could give rise to different movement-BTs. To make our numerical simulations more realistic, empirical values for the between-individual variability of HR obtained using acoustic telemetry for the case of pearly razorfish (*Xyrichtys novacula*) were considered, for which estimates of γ and HR_r were obtained for 21 fish by Alós *et al.* (2016a). Provided that both parameters seemed to be gamma-distributed (see Appendix S3), we estimated the parameters of those empirical distributions using the function *fitdistr()* from the library *MASS* (Ripley *et al.* 2017) of the R environment (<https://www.r-project.org/>). By assuming a fixed γ , we defined the *resident-mobile* BTs by the 25 and 75% quantiles of the distribution of the squared root of ε , after scaling them by the median. For simplicity, we assumed that the costs related to different movement-BTs are proportional to the energetic gain (i.e. costs are considered implicitly discounted from the energetics gains derived from each strategy) and does not depend on differences in the routine movement (i.e. which is paid from maintenance). However, this is not a negligible assumption whenever addressing the optimisation of strategies in

different contexts, then its explicit consideration should be required as energetic costs may make a difference in the optimality of different strategies; see discussion and future directions for further details.

Second, we explored the pair *fast-slow* metabolic gradient. In such a case, we focused on the parameter *energy conductance* v . All else being equal, larger values of v imply larger metabolic rates and growth rates, earlier maturation and a higher cumulative reproductive output (Nisbet *et al.* 2012), which is translated into *fast* LHs (Stearns 1992), as opposed to the *slow* ones that will emerge with lower v . Accordingly, v was fixed to 0.04 cm day^{-1} (*fast*) and 0.02 cm day^{-1} (*slow*), as these values are within the empirical range reported at the Add-my-Pet collection (AmP database).

Aiming to capture the model responsiveness to different environments, we characterised three different scenarios with a stationary level of food resources: (1) a food-saturated environment ($x = 50 \text{ s m}^{-2}$), (2) another with a medium level of food resources ($x = 5 \text{ s m}^{-2}$) and (3) a food-scarce environment ($x = 2 \text{ s m}^{-2}$). Finally, seasonal variability was simulated by a fluctuation around a mean value x_m with an amplitude x_a and a period p given by (Muller 2000):

$$x(\tau) = x_m + x_a \cos(2\pi\tau/p), \quad (9)$$

where the above three levels of resource density were considered for x_m , while fluctuation around the mean, x_a , was given by $x_m/3$ and p was fixed at 2.5 scaled time steps τ (see Appendix S3).

Using the set of parameters described above, we ran numerical simulations to explore the ontogenetic trajectories of several state variables (scaled length, reserve density and scaled reproductive output) and the realised ε emerging from the scaled model (Table 1). The coupled system of differential equations (see Appendix S1) were numerically solved using the *ode* function of the *deSolve* library (Soetaert *et al.* 2017) in the R environment (<https://www.r-project.org/>). In the context of the standard-DEB model, an individual will die when U cannot cover the somatic maintenance costs (Muller 2000; Kooijman 2010). Therefore, we considered death to occur when an individual decreases in scaled length (Ledder 2014). Nevertheless, specific rules to survive starvation conditions have been modelled increasing the complexity of the standard-DEB model (e.g. the use of reserve allocated to reproduction, Pecquerie *et al.* 2009; or the energy in the structure and consequently shrinking structure to cover maintenance requirements, Tolla *et al.* 2007). The R script used for running simulations is available as supplementary material (see Appendix S3).

EMERGING LHS FROM THE MECHANISTIC LINKS BETWEEN HR BEHAVIOUR AND DEB

Comparing *mobile* and *resident* animals

In accordance with our expectations, *mobile* animals consistently displayed higher growth rates, a larger scaled length and greater reproductive output than *resident* animals. More interestingly, the strength of the effects of moving with different ε was more conspicuous in scenarios with low resources

(Fig. 2). Despite being resource-density dependent, assimilation is limited to an intrinsic-physiological maximum Q_m . In food-saturated environments, the assimilation rate will be close to this maximum, regardless of how much area the animals cover because f (eqn 7) approaches one, increasing either the resource level or the explored HR area. Accordingly, the growth and reproduction outcomes of different ε became more evident in scenarios with a moderate or low resource density. Hence, animals with higher ε or living in resource-rich environments grew faster and allocated more energy to reproduction across their lifetime (Fig. 2c). Therefore, interestingly, from an ecological perspective, the lower the resource density is, the more important the movement strategy will become.

Comparing metabolically *fast* and *slow* animals

Metabolically *fast* animals showed a higher growth rate (Fig. 3a), which in turn implied a larger length-at-age and faster maturation. All else being equal, given a maturity threshold, sexual maturation (puberty) occurred at a fixed size (e.g. $l = 0.2487$ at $h_p = 0.003$) but at different times depending on the energy mobilisation rate, food density and individual movement (Fig. 3). Consequently, the cumulative reproductive output across the lifetime of a *fast*-type was higher (Fig. 3b), provided no other mortality causes occurred early in life (e.g. predation or starvation; see next section).

Regarding HR behaviour, several relevant patterns emerged from the dichotomy of *fast-slow* PTs (Fig. 4). A high v actually implies a quick energy mobilisation and, consequently, a low level of U (i.e. lower steady *reserve energy density* U^{st} , Table 1), thus impelling the animal to increase ε , and consequently, to explore larger HR areas, allowing the exploitation of greater resources. When comparing different scenarios, the effect of having a higher v (leading to larger ε with respect to the *slow*-type) will be larger in food-scarce environments. Consequently, HR sizes differed less between different environments when the mobilisation rate was high; and, all else being equal, the scarcity of food led to a larger HR.

Responsiveness to changing resource densities and state-dependent space-use

The higher growth rate characterising metabolically *fast* animals (Fig. 3) implies a larger length-at-age and, consequently, higher maintenance costs, with consequences for the responsiveness to fluctuating environments. As shown in Fig. 4, increasing v implies lower U . Increasing ε in a way that the assimilation rate approaches its maximum can compensate for this quick mobilisation to obtain enough energy to cover higher maintenance costs. However, this increase in ε is not always sufficient given that it is bounded by an intrinsic-behavioural maximum ε_m .

Consequently, metabolically *fast* animals were more prone to die earlier in life when a decrease in resource density occurred. Conversely, a *slow*-type animal was more resilient to the same variations in resource dynamics (Fig. 5). Interestingly, assuming the absence of any other mortality causes (e.g. predation; see discussion for more details), the cumulated reproductive

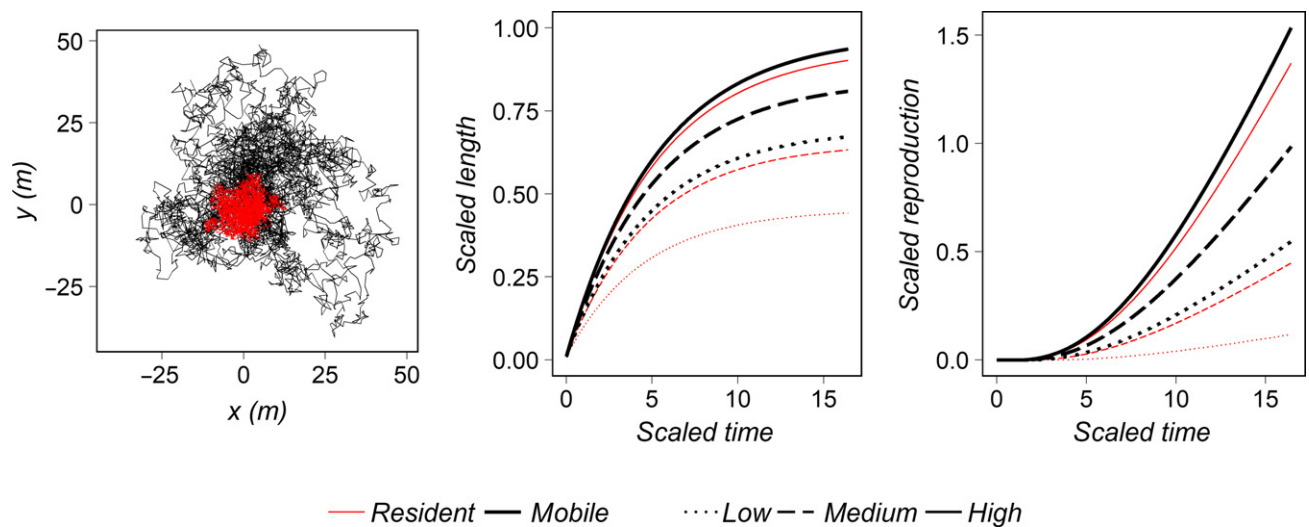


Figure 2 Expected life history-trajectories for home range (HR)-behavioural *resident*- and *mobile*-types. (a) Simulated discrete 1-week-long HR trajectories in a 2D scenario (eqn 1) (time steps of 15 min). Dynamics of the (b) scaled length and (c) scaled reproduction output in scenarios with low, medium and high levels of food resources. (See Appendix S3 for R-script and parameter values).

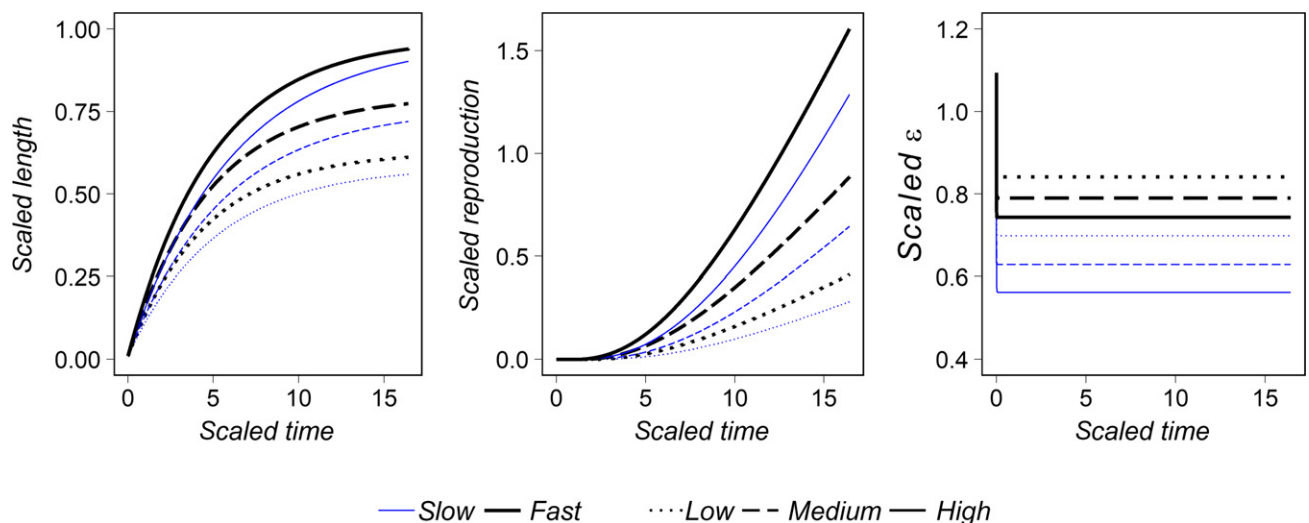


Figure 3 Expected life history trajectories and home range performance for metabolically *slow*- and *fast*-types. Dynamics of the (a) scaled length, (b) scaled reproduction output and (c) scaled- ϵ in scenarios with low, medium and high levels of food resources. (See Appendix S3 for R-script and parameter values).

output across all the lifespan of such a *slow*-growing animal was larger despite delayed sexual maturation, with respect to the *fast*-type. However, if we assume variability in BTs between individuals within the same metabolically related type (Fig. 6), *mobile* animals, characterised by a higher intrinsic-behavioural maximum ϵ_m , show higher fitness with respect to the *resident* ones in those environments. Additionally, under severe starvation conditions, energy allocated to reproduction ($1 - \kappa$) could have been redirected to cover maintenance requirements (Pecquerie *et al.* 2009), which requires more complex development of the model proposed herein.

Overall, HR behaviour reflected temporal resource variability given the links between environmental and internal states introduced by the assimilation rate and the state-dependent regulation of ϵ . Accordingly, temporal fluctuations in HR

plasticity were more evident in food-scarce environments (Figs 5d and 6d), but less in food-saturated environments, where in addition, the functional response was less affected by resource variability (Fig. 5e). Furthermore, both *fast* (Fig. 5) and *mobile* (Fig. 6) animals showed less differences in LHs between different resource-level scenarios than the opposite types, *slow* and *resident* respectively.

MAIN INSIGHTS FROM OUR BEHAVIOURAL-BIOENERGETICS MODEL AND POTENTIAL IMPROVEMENTS

Our behavioural-bioenergetics model predicts that animals increase their HR area in environments with lower food resources and adjust their performance to environmental

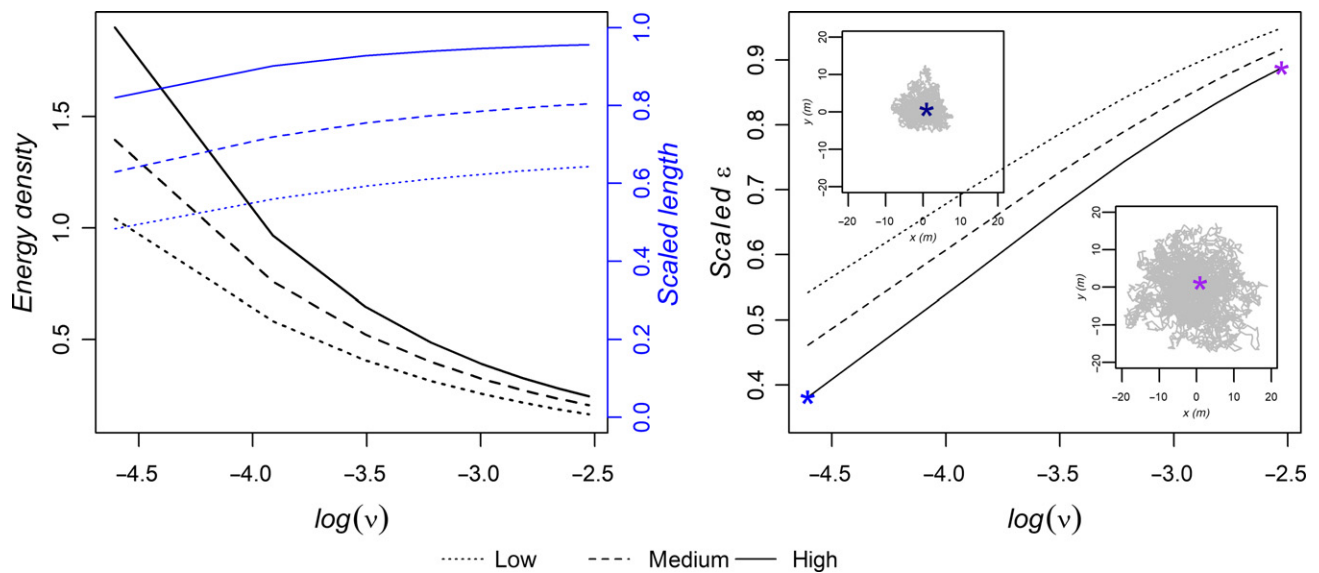


Figure 4 (a) Steady states of energy density and scaled length and b) steady scaled- ϵ for a range of energy conductance values (from 0.01 to 0.08 cm day^{-1}) in scenarios with low, medium and high levels of food resources. In the right panel, from left to right, path representations in a 2D scenario for the extreme scaled- ϵ , from the lowest to the highest (blue and purple stars respectively), are represented. (See Appendix S3 for R-script and parameter values).

fluctuations. Furthermore, metabolically *fast* animals increase their HR area to cope with higher energy needs but the environment-related HR plasticity is less evident in comparison to *slow* animals. However, *fast* animals are more vulnerable to changing environments due to their higher energy requirements with respect to the actually available resources (Muller 2000; Ricklefs & Wikelski 2002). Food density has empirically supported effects on movement, foraging and energy dynamics (Shepard *et al.* 2013; van Gils *et al.* 2015; Rizzuto *et al.* 2017). Lower food densities require animals to forage over larger areas to acquire a given amount of energy (South 1999; Tamburello *et al.* 2015; Grant *et al.* 2017). Additionally, the seasonal varying and spatial-heterogeneous distribution of food translates into space-use variation when compared with constant and homogeneous food levels (Gallagher *et al.* 2017; Scott *et al.* 2017). Moreover, responsiveness to resource abundance can differ between PTs and BTs, as it has been reported empirically [e.g. aggressive lizards (i.e. *fast* individuals) were less responsive to habitat quality and local food abundance (Spiegel *et al.* 2015)] and predicted by our model (Figs 5 and 6). Growth rate correlates with activity (e.g. Martin-Smith & Armstrong 2002) and higher energy requirements lead to an increase of movement (e.g. Strople *et al.* 2018). In addition to food, temperature is another forcing variable that deserves attention in future research. Temperature modulates all metabolic rates (Nisbet *et al.* 2012; Agüera *et al.* 2015) and, consequently, the dynamics of internal state variables. In ectothermic organisms, this relationship is more evident (Pecquerie *et al.* 2009; Scott *et al.* 2017). Thereby, temperature effects on metabolic processes should be scaled up to animal behaviour (Gibert *et al.* 2016; Holtmann *et al.* 2017a). The combined effects of variability in food resources and temperature on movement behavioural plasticity have been previously reported in nature (e.g. Börger *et al.* 2006; Teal *et al.* 2012; Nakayama *et al.* 2016, 2018; Strople *et al.* 2018), and our

model can easily accommodate temperature dependencies as well.

Home range size and space-use patterns emerge from a complex network of interactions between different factors (internal and external) and scales (temporal and spatial). Here, we only focused on the roles of the internal energy needs in shaping HR behaviour at the individual level. Such an explicit dependence revealed reciprocal interactions between the internal state of the individual, the external availability of resources and movement-BTs. Here, we assumed a monotonic functional response for the dependence of HR behaviour on internal energy-related state (eqn 8), and costs of movements were implicitly considered as a fixed part of maintenance (Kooijman 2010). However, when available energy reaches some minimum value, the response could be a movement reduction, which is against the monotonic increase predicted by our model. Other plausible functional forms may better (or differently) explain this connection. For instance, empirical support has been found for a hump-shaped movement pattern over food deprivation (Spiegel *et al.* 2013b; Scharf 2016), as a conservative response that minimises the risk of physiological collapse at starvation. The selected functional response will certainly influence the predictions obtained, depending, for instance, on the environmental factors we are testing (see Appendix S2). Importantly, once the basis of the obtained predictions is understood, we will be able to explore new predictions when changing the assumptions of our model (Box 1) or by including other functional forms relating HR behaviour with bioenergetic constraints (e.g. movement costs) and ecological factors.

Other multiple, diverse, behavioural and ecological factors independent of (or in addition to) energy requirements can lead to consistent between-individual differences in HR behaviour and mediate in its dynamics. Our model could be extended to any behaviour (others than movement-related

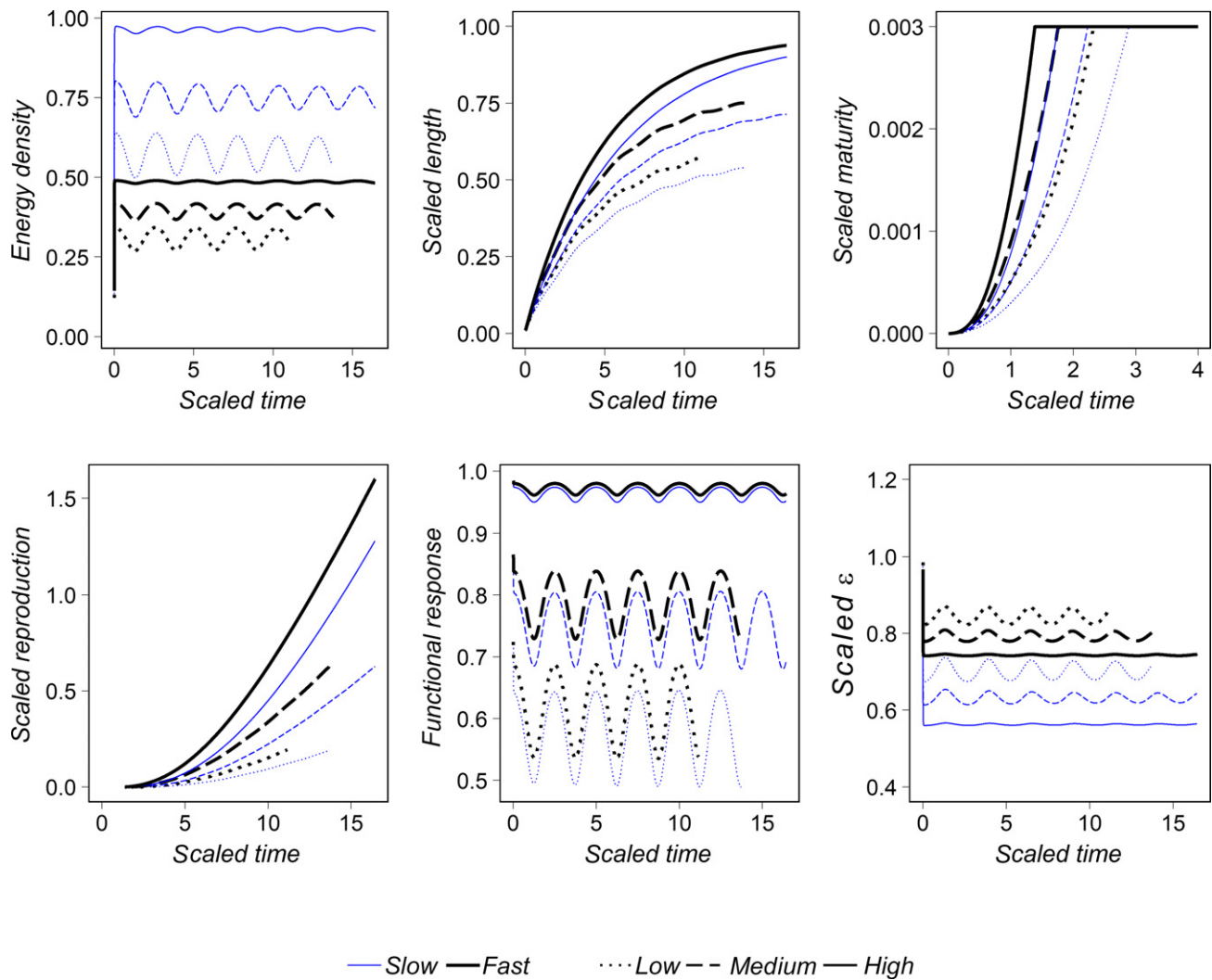


Figure 5 Expected life history-trajectories and life history performance for metabolically *slow*- and *fast*-types in fluctuating environments. Dynamics of the dimensionless state variables, functional response and the emergent scaled- ϵ in scenarios with low, medium and high levels of food resources, where fluctuation is given by $1/3$ around the average value with a period set up to 2.5 scaled time steps, τ . Lines end at individual death (when the energy density cannot compensate for the structural maintenance costs). (See Appendix S3 for R-script and parameter values).

BTs, i.e. exploration or activity) playing a role in food acquisition (e.g. aggressiveness or boldness, Andersen *et al.* 2017) or mediating social agonistic interactions with conspecifics (Moorcroft *et al.* 2006; Spiegel *et al.* 2016), and that may be associated with consistent space-use differences. For instance, empirical work suggest that more aggressive individuals might be spending more time for social agonistic interactions that may affect their overall space-use in lizards, spider and fish (Wilson & McLaughlin 2007; Pruitt & Riechert 2012; Spiegel *et al.* 2015). Moreover, consistent between-individual differences in habitat preference (Leclerc *et al.* 2016; Holtmann *et al.* 2017b) and the way an individual faces risks of predation (Bonnot *et al.* 2015) can lead to consistent differences in HR behaviour among BTs. Additionally, careful attention must be paid to density-dependent space-use behaviour that may mediate competition for resources (Travis *et al.* 1999; Matthysen 2005). Abundance may affect prey availability and competitiveness for resources, but it may enhance social interactions as well, such as those described above. A potentially

fruitful avenue of future improvement of our model is to provide an extension to more complex behavioural interactions, density-dependent processes and habitat characteristics (e.g. landscape heterogeneity, environmental disturbances) shaping the dynamics of HR behaviour.

Foraging behaviour is known to switch between intensive and extensive modes of search (Bartumeus *et al.* 2014; van Gils *et al.* 2015; Spiegel *et al.* 2017) to produce complex movement patterns (Börger *et al.* 2006, 2008). Several statistical models have been proposed to describe the spatial and temporal dynamics of movement (Bartumeus *et al.* 2002, 2005; Marthaler *et al.* 2004; James *et al.* 2011; Watkins 2012; Spiegel *et al.* 2013a; Auger-Méthé *et al.* 2015) that ultimately determine searching efficiency (e.g. Visser 2007; Bartumeus *et al.* 2008a,b, 2014). Different mechanisms have been proposed as the main drivers of the statistical properties of those mechanistic models; for example, the responsiveness to conspecifics and landscape heterogeneities (Moorcroft & Lewis 1999; Moorcroft *et al.* 2006; Mueller &

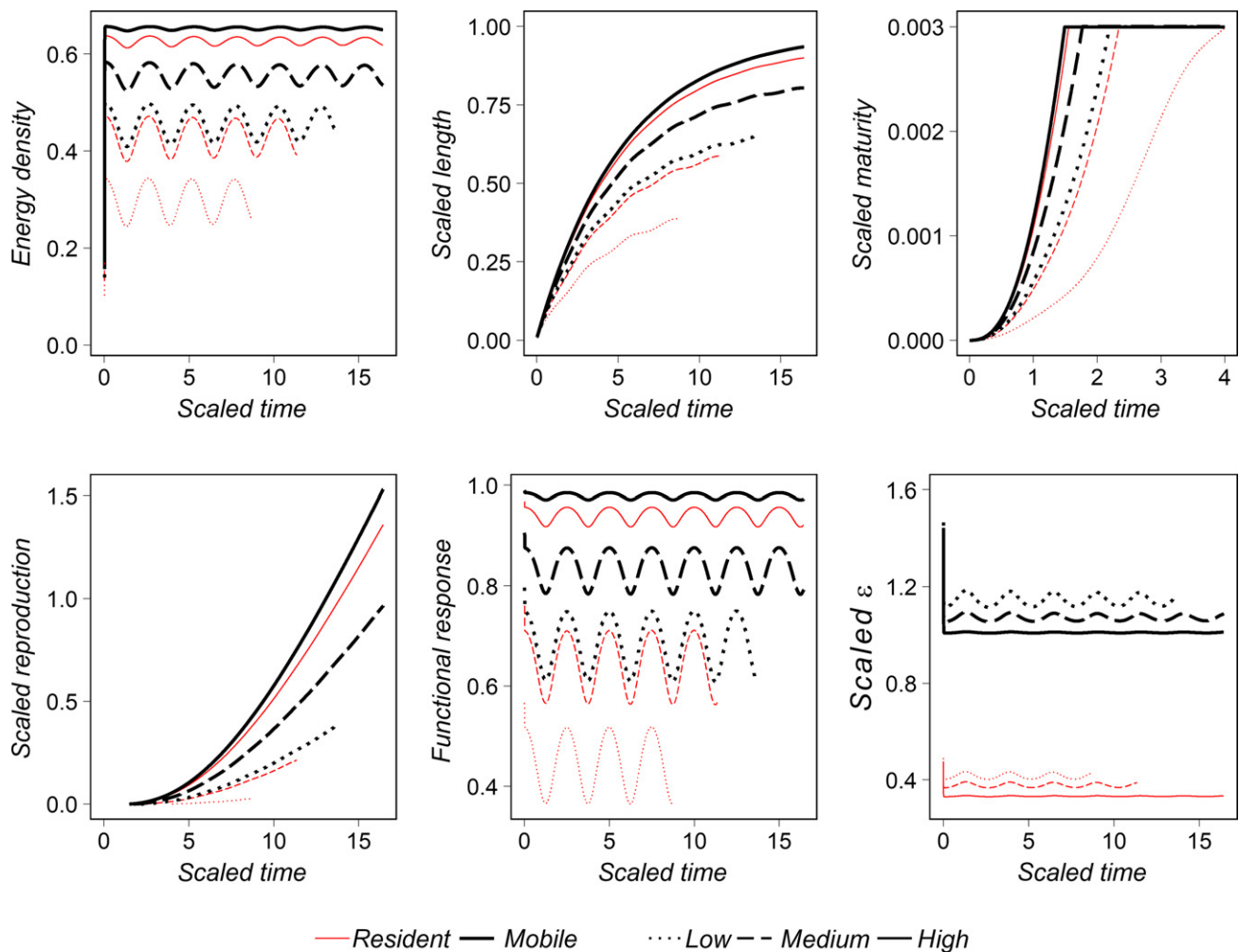


Figure 6 Expected life history-trajectories and life history (HR) performance for HR-behavioural *resident*- and *mobile*-types in fluctuating environments. Dynamics of the dimensionless state variables, functional response and the emergent scaled- ε in scenarios with low, medium and high levels of food resources, where fluctuation is given by 1/3 around the average value with a period set up to 2.5 scaled time steps, τ . Lines end at individual death (when the energy density cannot compensate for the structural maintenance costs). (See Appendix S3 for R-script and parameter values).

Fagan 2008) or memory in area restricted searches (Van Moorter *et al.* 2009; Fronhofer *et al.* 2013). Here, for convenience and simplicity, we used a BRW to describe HR movement and defined movement-BTs as proxy of the activity levels given in eqn 2. This simple description has been applied in multiple works referring to HR behaviour (e.g. Alós *et al.* 2016a,b; Breed *et al.* 2017; Campos-Candela *et al.* 2018). Within our proposed model, disentangling ε and γ will allow one to explore different dimensions of the HR behaviour. Here, we only focused on the interplay of ε with LHs. However, γ parameter may play through different mechanisms an important role in shaping HR and LHs as well. For instance, the tendency to keep closer to the HR centre may affect the probability of finding food or predators and γ dynamics may co-vary with external factors such as predators or conspecific densities (Spiegel *et al.* 2015). Furthermore, the quality of the habitat can be related to the variability in scaled resource density x in eqn 7, and it can relate to certain BTs through different functional responses as well. Thus, future developments should increase the

complexity of HR models and include other drivers in addition to energetic requirements.

TESTABLE PREDICTIONS AT THE INDIVIDUAL LEVEL: STRENGTHENING LINKS BETWEEN THEORETICIANS AND EMPIRICISTS

Overall, empirical support for the associations among BTs, PTs and LH traits theoretically predicted by the POLS hypothesis are weak and ambiguous (Niemelä & Dingemanse 2018; Royauté *et al.* 2018). Instead, they open the debate on which factors determine or not the emergence of POLS, focusing mainly on the influence of the ecological context (Montiglio *et al.* 2018). The existence of correlational patterns between space-use and risk-related behaviours with physiological or LH traits, or between HR size and environmental conditions are successfully predicted by our model (empirical evidence supporting the assumptions, hypotheses and predictions of our behavioural-bioenergetics model, Box 1, are listed in Table 2). However, most of our model's predictions are not

Table 2 Overview of some empirical, qualitative or theoretical conclusions from different works that provide partial evidences either in support or against the assumptions, hypotheses and predictions addressed in our mechanistic theoretical model.

Assumption, hypothesis or prediction (in Box 1).	Type of work and case species	Pace Life traits	Intrinsic variables	Extrinsic variables	HR- or movement-related behavioural variables	Main observations	Ref.
[P1] <i>Weak support</i>	Fieldwork Bird species	–	Metabolic rate	–	Migrating movement	Higher metabolic rate in migrating (temperate) populations <i>vs.</i> lower metabolic rate in resident/sedentary (tropical) populations	Wikelski <i>et al.</i> (2003)
[A1] <i>In support</i> [P5] <i>Weak support</i>	Fieldwork Mammal species	–	Age and sex	Distribution of habitats, special heterogeneity	HR size	Most of the variability in HR size was due to interindividual variability (but not associated with age nor sex). The effects varied between timescales and the distribution of habitats The time scale is an important factor to detect different patterns of variability	Börger <i>et al.</i> (2006)
[P1] <i>Weak support</i>	Fieldwork Laboratory Bird species	–	Reproductive parameters: net success, fledging size and condition (repeated measures during 4 years)	Territory quality	Exploratory behaviour in a novel environment	Slow-exploring females had a higher nest success and largest fledgling Fast-exploring males occupied better quality habitats and fast-fast pairs produced offspring in best condition Opposite pairs (slow-slow and fast-fast-exploring individuals) produced more recruiting offspring, which suggests that the foraging strategy may compensate for the lower quality of territories in slow explorers pairs	Both <i>et al.</i> (2005)
[H3a] <i>Weak support</i> [P2] <i>Weak support</i> [P3] <i>Weak support</i> [P5] <i>Weak support</i>	Modelling	–	Age	Value of resources	HR size	Positive correlation between age and quality of the habitat predicts shrinking HR size during the lifespan Large resource heterogeneity may be behind HR size instability	Tao <i>et al.</i> (2016)
[H3] <i>Weak support</i>	Meta-analysis	–	Metabolic rate, hormone levels, body weight and structural length	–	Aggressiveness, exploration and pro-activity	Intrinsic state explained significant variation in behaviour among individuals Intrinsic state and behaviour are on average integrated among individuals Tagged individuals revealed repeatable HR-behavioural traits (spatial extent or radius and intensity or exploration rate), thus demonstrating the existence of movement-BTs	Niemelä & Dingemans (2018)
[A1] <i>In support</i>	Fieldwork Marine fish	–	–	–	HR radius and exploration rate		Alós <i>et al.</i> (2016a,b)

(continued)

Table 2. (continued)

Assumption, hypothesis or prediction (in Box 1).	Type of work and case species	Pace Life traits	Intrinsic variables	Extrinsic variables	HR- or movement-related behavioural variables	Main observations	Ref.
[H2] <i>In support</i> [P1] <i>In support</i> [P3] <i>In support</i> [A1] <i>In support</i> [P1] <i>Against</i>	Fieldwork Freshwater fish	Growth rate	Sex	Food density	HR space-use: location and portion of time spent in that location Dominance Activity and boldness	Positive relationships between rates of movement and growth of both sexes High degree of unpredictability in food supply results in correlation between growth and movement Strong evidence for consistent among-individual differences in activity and risk-taking behaviour Negative correlation between activity and risk-taking behaviour with body length. No correlation with routine metabolic rate and body condition Evidence of interindividual repeatable differences in SMR, MMR and AS Repeatability in metabolic rate declines with changes in environmental conditions or the physiological state, or with an increase of the period between measurements Correlations among SMR, MMR and AS across individuals have been found but with different directions Some works show positive correlations between measures of resting metabolic rate, SMR and boldness or activity level among individuals The environment may affect the degree of co-variation between metabolic traits and behaviour	Martin-Smith & Armstrong (2002) Polverino <i>et al.</i> (2016)
[A1] <i>In support</i> [P3] <i>Weak support</i> [P5] <i>Weak support</i>	Review Laboratory Fish	–	Standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS)	Different conditions of food availability, temperature, oxygen availability	Activity, dispersal, boldness	Repeatability in metabolic rate declines with changes in environmental conditions or the physiological state, or with an increase of the period between measurements Correlations among SMR, MMR and AS across individuals have been found but with different directions Some works show positive correlations between measures of resting metabolic rate, SMR and boldness or activity level among individuals The environment may affect the degree of co-variation between metabolic traits and behaviour	Metcalf <i>et al.</i> (2016)
[A1] <i>In support</i> [H2] <i>Weak support</i> [H3] <i>Weak support</i> [P1] <i>In support</i>	Fieldwork Freshwater fish	Juvenile growth rate, reproductive effort and age at the onset of maturation.	Condition factor, body length	Environmental isotopes in diet	Movement traits, Prey selection	Strong repeatability in movement traits across months Correlation tests revealed a link between movement traits, prey selection and LH traits in the wild Juvenile higher growth rate correlated with higher activity Higher reproductive effort and sooner maturation correlated with higher switches between active and inactive mode	Nakayama <i>et al.</i> (2017)

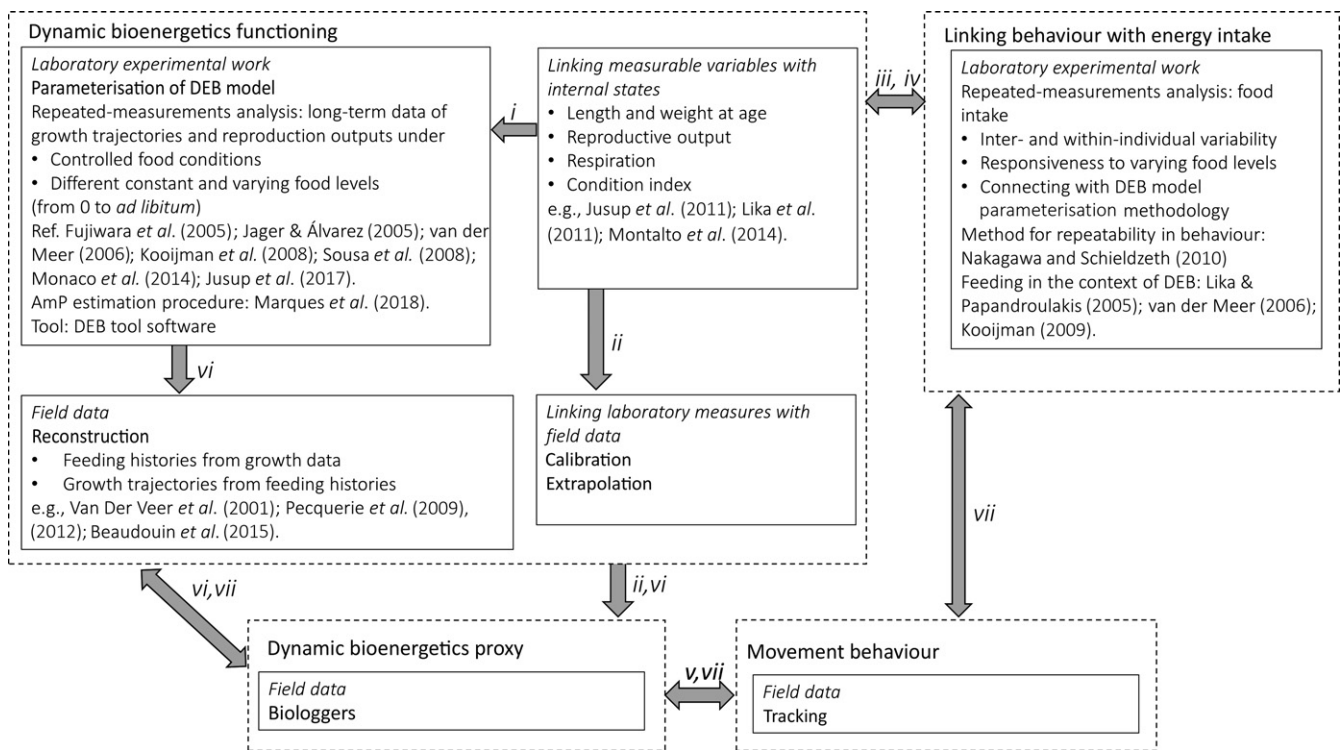


Figure 7 To design proper experiments and fieldwork to explicitly test personality-dependent movement syndromes remains an open challenge. Combining individual biological and physiological long-term repeated data from free-ranging animals and laboratory-controlled experiments will allow the reconstruction of feeding histories in the wild, extrapolation of field data into bioenergetic processes, understanding of environmental effects in the repeatability of traits and internal state dynamics and, eventually, provide support to the processes that favour or hinder the development of personality-dependent movement syndromes. In the figure, numbers represent a feasible sequence of steps; see main text for more details.

linear and are environmentally dependent; thus, the existence of simple, linear correlations between BTs, PTs and LH is an oversimplified, naïve expectation. Additionally, the use of sub-optimal proxies to intrinsic variables or physiological measurements or inappropriate choice of LH metrics could be also behind the weak empirical support for some POLS predictions (Araya-Ajoy *et al.* 2018; Niemelä & Dingemans 2018).

Certainly, to provide evidence supporting the behavioural state dependences defined by our behavioural-bioenergetics model (Fig. 1) is challenging but it is feasible with a combination of properly designed laboratory-based assays and the recent development of animal biotelemetry. Thus, we propose to connect (Fig. 7) the experimental approaches of DEB theory (Kooijman *et al.* 2008), personality-related behavioural ecology (Réale *et al.* 2007; Nakagawa & Schielzeth 2010; Sih *et al.* 2012) and movement tracking ecology (Hussey *et al.* 2015; Kays *et al.* 2015; Lennox *et al.* 2017). First, repeated measurements for intrinsic states, physiological variables and behavioural traits at the individual level along the lifetime should be produced (Mathot & Frankenhuys 2018). Moreover, most physiological variables are inherently difficult to observe and measure. Thus, proper, well-sustained methods should be selected (Sousa *et al.* 2008; Nisbet *et al.* 2012). Parameters, state variables (i.e. energy, structure, maturation and reproduction) and processes in DEB theory cannot be directly observed (Kooijman *et al.* 2008; Sousa *et al.* 2008; Jusup *et al.* 2017). Nevertheless, some shortcuts have been proposed

(see Table 11.1 in Kooijman 2010), and, recently, the procedures for estimating DEB parameters have been substantially improved (Marques *et al.* 2018). Moreover, estimating the full range of DEB parameters from empirical data is not always required, and many bioenergetics parameters can be extrapolated from one species to another (Kooijman *et al.* 2008), or even from the population level to the individual level. Once DEB parameters are available, environmental-forcing variables can be used to reconstruct the feeding history of a given individual or, in the opposite way, growth data can be used to reconstruct environmental-forcing variables (Pecquerie *et al.* 2009, 2012). Eventually, from feeding histories, movement-related behaviour can be indirectly reconstructed. Some recent empirical work is already moving in this direction to better understand salmon migrations (Strople *et al.* 2018). Aiming to relate individual metabolic functioning to BTs, experiments under controlled laboratory conditions should combine monitoring of long-term growth trajectories, cumulative reproduction, personality assays and feeding-related behaviour. However, although experimental arenas provide a good opportunity to assess metabolic-related parameters and animal behaviour in controlled environments, they may not be representative of how animals spatially behave in the wild (e.g. Klefoth *et al.* 2012; Závorka *et al.* 2015; Laskowski *et al.* 2016). Generally, captivity experiments represent a tiny fraction of the spatially unconstrained behaviour in the wild and provide a very short-term representation of the behavioural performance in relation to the LH variation.

Box 1 A mechanistic theory for personality-dependent movement behaviour based on dynamic energy budgets: assumptions, hypotheses and predictions.

Naming assumptions and predictions of a novel model may help in the challenge of looking for empirical evidence of the underlying theory. It is common to neglect the evaluation of assumptions of models (whether conceptual or theoretical) before testing their predictions when studying the relationships between variability in behavioural traits, physiological traits and LHs (Mathot & Dingemanse 2015; Sih *et al.* 2015; Mathot & Frankenhuis 2018; Niemelä & Dingemanse 2018). Aiming to overcome this weakness and to guide future research through such challenges, we specify here the core assumptions, hypotheses and predictions of our behavioural-bioenergetics model.

Core assumption of the model*

[A1] Between- and within-individual differences across time and ecological contexts exist for life histories, physiological and behavioural traits.

Testable hypothesis

[H1] Interindividual variability in physiological traits mediate the emergence of between- and within-individual differences in LH dynamics through mass/energy fluxes.

[H2] Interindividual variability in movement-related behavioural traits mediate the emergence of different life histories through mass/energy fluxes at the individual level.

[H3] Movement-related behaviour directly links to internal states through the intake rate and accommodates energy needs through a feedback link with the dynamics of the internal energy, which connects the individual internal energy needs with the environmental foraging opportunities.

[H3a] Within-individual variability in HR includes two sources of variation: internal state-dependent ontogenetic patterns and the effects of environmental variation at the individual level (i.e. plasticity).

[H3b] Physiological traits links mechanistically to HR size dynamics through the dynamic of the energy-related internal state.

[H3c] Mechanistic relationships between physiological and behavioural traits lead to between-individual variability in HR size.

[H3d] Physiological traits mediate the within-individual variability in HR size responsiveness to environmental fluctuating changes.

Predictions:

[P1] *mobile*-behavioural and *fast*-physiological/metabolic types lead to faster growth and earlier sexual maturation.

[P2] Changes in the individual realised HR size depend on the amount of environmental resources in the ecological context.

[P3] Under limiting, unpredictable or fluctuating resource densities:

- HR size increases.
- the correlation between interindividual variability in HR behaviour, LH traits and physiological features (e.g. metabolic rates) are more conspicuous.
- environmental-related effects on HR plasticity, LH and fitness are more evident.
- slower growers and/or mobile individuals show higher fitness.

[P4] Individual resilience to resources environmental fluctuations decreases with faster mobilisation rates.

[P5] Responses at the within-individual level are expected from both, ontogenetic dynamics or environmental fluctuations, but they will be apparent at different temporal scales.

***Model vs. simulation assumptions.** Note that simulation assumptions have been conducted to explore the model performance but are not core assumptions of the model itself. To limit the model complexity we consider that:

- resources are homogeneously distributed and stationary (i.e. no density-dependence resource dynamics occur).
- individuals move independently one from others and no social interactions (e.g. competitiveness, agonistic interactions, and mating) are considered.
- variation among BTs in habitat quality and/or ecological risks is not considered.
- variation among BTs in movement costs are negligible for the total lifetime budget. Energetic-related BTs costs are proportional to the energy gain and discounted implicitly from feeding rate.

Note also that ecological trade-offs are excluded in simulations, no optimisation of the strategies is analysed and no other causes of mortality than the risk of starvation are considered. Further exploration of the model should overcome these assumptions and assess its performance when they are not met, considering the complexity of the ecological contexts and including trade-offs others than starvation within eco-evolutionary frameworks, which is one potential utility of this theory.

Fortunately, several biotelemetry devices (Hussey *et al.* 2015; Kays *et al.* 2015), biologgers, accelerometers and sensors (Cooke *et al.* 2008; Hays *et al.* 2016; McGowan *et al.* 2017) are currently available for simultaneously measuring spatial behavioural traits (Hussey *et al.* 2015) along with environmental-forcing variables such as temperature in free-living animals for long-term periods. Taken together, these provide powerful tools to study the physiology of free-ranging animals while their positions are known (Brownscombe *et al.* 2017; Jeanniard-du-Dot *et al.* 2017; Grénillet *et al.* 2018) and to link behaviours with energy intake or expenditure (Härtel *et al.* 2011; Nathan *et al.* 2012; Louzao *et al.* 2014). Combining long-term data from free-ranging animals along with laboratory-controlled experiments in different manipulated environments will enable us to reconstruct feeding histories and to understand the role of environmental effects in the behavioural predictability and plasticity at the individual level. Accordingly, a feasible sequence of steps to provide empirical support to our behavioural-bioenergetics model could be as follows (Fig. 7): (1) estimate bioenergetics parameters by linking measurable variables with non-observable state variable (i.e. internal states or physiological processes); (2) develop methods for extrapolating the patterns and processes from the laboratory to field conditions; (3) describe (repeated measurements) and validate the links between feeding-related behaviour and intake rate with DEB processes; (4) manipulate forcing variables for testing the links between behavioural traits and internal state dynamics in different conditions; (5) monitor the wild movement and the internal measurable variables previously calibrated (step 2) in the lab; (6) reconstruct the feeding histories and the growth/energy dynamics from field data; and finally, (7) assess the interconnecting links between the physiological and behavioural patterns of variability.

FUTURE DIRECTIONS WITHIN AN OPTIMALITY APPROACH

Within an eco-evolutionary perspective, our behavioural-bioenergetics model may help in the understanding of whether (and when) different mechanisms lead to the same observable pattern, or different patterns arise from the same mechanism depending on ecological factors (i.e. equifinality *vs* multifinality as introduced by Mathot & Frankenhuys 2018), which remains a cornerstone within POLS theory. However, the emergence of context-specific optimal strategies (e.g. current *vs* future reproduction, Houston & McNamara 1999; Ricklefs & Wikelski 2002) should be assessed by using optimisation theory. This procedure will require explicit attention to different causes of context-related mortality (e.g. predation, harvesting activities) and energy-related constraints that compromise survival (Both *et al.* 2005; Biro *et al.* 2006; Holt & Jørgensen 2015; Jørgensen *et al.* 2016). Therefore, the eco-evolutionary outcomes of our behavioural-bioenergetics model's predictions must be considered with caution. First, movement costs are certainly important in terms of optimising strategies where trade-offs between energy assimilation and energy expenses due to the movement for finding food may play together in the final energetic balance at the individual

level (Shepard *et al.* 2013; Louzao *et al.* 2014; Wilson *et al.* 2015), thus they should be explicitly considered. Second, trade-offs of different combinations of BTs and PTs should be assessed within a broader ecological scenario and not only from the bioenergetics rules (Dall & Griffith 2014), since the emerging trends may become relevant in nature under specific selection pressures (Jørgensen & Holt 2013; Jørgensen *et al.* 2016; Killen *et al.* 2016) and risk-averse strategies may evolve (Harel *et al.* 2016; Teckentrup *et al.* 2018). For example, HR size may determine the encounter rate with predators (van Gils *et al.* 2015; Vander Vennen *et al.* 2016) or anthropogenic threats (Alós *et al.* 2012, 2016b), and many LH traits related with vulnerability to be killed may correlate (Biro & Stamps 2008; Polverino *et al.* 2016; Nakayama *et al.* 2017). In such a context, the knowledge that DEB theory emphasises mechanisms rather than correlational patterns implies a relevant step forward in relation to other conventional energy models (e.g. the metabolic theory of ecology (Brown *et al.* 2004) or the Wisconsin bioenergetics model (Deslauriers *et al.* 2017), mainly based in allometric relationships. This shift (from correlations to mechanisms) in modelling may help in generating specific testable predictions.

CONCLUDING REMARKS

Insights from the analytical exploration of our behavioural-bioenergetics model at the individual level reveal that the proposed mechanism connecting movement-BTs, PTs, internal states and LH (Fig. 1), when assuming a prevalent foraging role for movement behaviour (Box 1), predicts patterns that have support either theoretically or empirically (Table 2) and agree with the conceptual POLS expectations. Additionally, our behavioural-bioenergetics model offers a new window of opportunity for mechanistically studying the establishment of HR behaviour from a bioenergetics side in interaction with internal states and LH. It opens a promising roadmap to assess and reinforce the hypothesis that the HR behaviour displayed in a given ecological context may be, at least in part, an emergent property of the individual internal metabolic functioning (Dingemanse *et al.* 2010; Killen *et al.* 2016; Metcalfe *et al.* 2016).

Finally, within a behavioural optimisation framework (Houston & McNamara 1999), a thoughtful exploration of the full space of our behavioural-bioenergetics model parameters through state-dependent dynamic models will allow the assessment of the ecological processes that may favour or hinder the expected associations within POLS. Overall, we provide an unifying theoretical model to test the adaptive value of POLS and shed light on the processes underlying the emergence of optimal movement behavioural strategies and/or personality-dependent movement syndromes (Harrison *et al.* 2015; Spiegel *et al.* 2017).

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AUTHORSHIP

ACC, MP and JA initiated the research. SB and AA contributed to the mathematical derivation of the ideas presented in the manuscript. ACC conducted the research, facilitated by discussions with all co-authors. ACC, MP and JA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY STATEMENT

There are no data to include.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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