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Representing the acquisition and use of energy by individuals in agent-based models of animal populations

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Summary

1. Agent-based models (ABMs) are widely used to predict how populations respond to changing environments. As the availability of food varies in space and time, individuals should have their own energy budgets, but there is no consensus as to how these should be modelled. Here, we use knowledge of physiological ecology to identify major issues confronting the modeller and to make recommendations about how energy budgets for use in ABMs should be constructed.

2. Our proposal is that modelled animals forage as necessary to supply their energy needs for maintenance, growth and reproduction. If there is sufficient energy intake, an animal allocates the energy obtained in the order: maintenance, growth, reproduction, energy storage, until its energy stores reach an optimal level. If there is a shortfall, the priorities for maintenance and growth/reproduction remain the same until reserves fall to a critical threshold below which all are allocated to maintenance. Rates of ingestion and allocation depend on body mass and temperature. We make suggestions for how each of these processes should be modelled mathematically.

3. Mortality rates vary with body mass and temperature according to known relationships, and these can be used to obtain estimates of background mortality rate.

4. If parameter values cannot be obtained directly, then values may provisionally be obtained by parameter borrowing, pattern-oriented modelling, artificial evolution or from allometric equations.

5. The development of ABMs incorporating individual energy budgets is essential for realistic modelling of populations affected by food availability. Such ABMs are already being used to guide conservation planning of nature reserves and shell fisheries, to assess environmental impacts of building proposals including wind farms and highways and to assess the effects on nontarget organisms of chemicals for the control of agricultural pests.

Key-words: bioenergetics, energy budget, individual-based models, population dynamics

Introduction

Agent-based models (ABMs; also often referred to as individual-based models) are widely used to predict how populations perform in changing environments. The ways that individuals respond to their individual circumstances in a mapped landscape are modelled in detail, and the emergent dynamics of the population are then studied by computer simulation (e.g. DeAngelis & Mooij 2005; Grimm & Railsback 2005, 2012; Grimm *et al.* 2005; Railsback & Grimm 2012). The availability of food is a key feature of an animal's environment, and the way animals forage depends on their energy budgets, but there is little consensus as to how energy budgets should be modelled in ABMs. Existing approaches include the Wisconsin fish model (Kitchell, Stewart & Weininger 1977; Chipps & Wahl 2008), dynamic energy budget modelling (DEB) (Kooijman 2010), the metabolic theory of ecology (MTE) (Brown *et al.* 2004) and the ontogenetic growth model (West, Brown & Enquist 2001). However, these approaches vary in their assumptions and are not fully compatible with one another.

The scientific study of energy budgets is part of physiological ecology (Sibly & Calow 1986b; Karasov & Martinez del Rio 2007; Chipps & Wahl 2008) and uses insights from evolutionary theory that show how resources should be allocated to maximize Darwinian fitness. Natural selection acts to

maximize reproduction, growth and survival, so that each individual leaves as many descendants as possible, other things being equal (Sibly 2002). However, other things are not equal when trade-offs constrain resource allocation among reproduction, growth and survival. Such trade-offs arise because conservation of matter and energy dictates that resources allocated to one function are not available to others. The principle of fitness maximization subject to resource allocation constraints is central to understanding of physiological ecology and underpins the approach advocated here. However despite diversity in morphology and behaviour, there are many similarities among species in the forms of energy budgets and life histories, and in the ways each of these scales with body mass and temperature (Peters 1983; Schmidt-Nielsen 1984; Reiss 1989; Kooijman 2010; Sibly 2012). These similarities raise the hope that a generic bioenergetic ABM can be constructed that will explain most of the variation in life-history patterns relevant to population dynamics. Indeed, strong moves in this direction have been made by the modelling approaches cited above.

Our goal here is to review the major energetic processes that are relevant to modelling energy budgets for use in ABMs, to identify the major issues confronting the modeller and to make recommendations about how energy budgets for use in ABMs should be constructed. In passing, we note areas of disagreement among the existing approaches and identify areas where more data are needed. We begin with a brief survey of the development of animal bioenergetics and ABMs and then review the scientific literature relevant to modelling energy budgets for use in ABMs. Throughout, we attempt to identify an optimum, minimum specification for energy budgets sufficient for representing individuals in population models. We hope this will be of use to makers of ABMs, allowing them to employ a simple scheme of energy management in their models.

Historical overview of merger of animal bioenergetics and animal ABMs

Modelling of animal bioenergetics as a way to assess responses to the environment began at least as early as the 1960s, building on bioenergetic studies going back decades earlier. Based on a general growth equation (Von Bertalanffy 1957) and an expression for energy balance of Winberg (1956) (cited by Gerking 1994),

$$C = P + R + F + U \qquad \text{eqn 1}$$

where C = food consumption, P = growth and reproduction, R = respiration, F = faecal wastes and U = excretory wastes. The units of this equation are usually given as rates of carbon or energy flux, in g or J per unit time (Peters 1983). A number of bioenergetics models were formulated based on eqn (1) (e.g. Paloheimo & Dickie 1966; Ursin 1967; Kerr 1971) and later refined (see reviews of Weatherley & Gill. 1987; Jobling 1994). Kitchell, Stewart & Weininger (1977) noted that, because body mass responds more quickly to environmental conditions than does population size, the modelling of fish growth, combined with empirical studies on fish size distributions, would be an efficient way to understand environmental effects on a population. Since then, the application of bioenergetics modelling to fish has been especially active. In particular, the 'Wisconsin model' (Kitchell, Stewart & Weininger 1977; Hewett & Johnson 1987) was applied to a number of fish species. A somewhat distinct modelling approach, the DEB model (Kooijman 1993, 2010) was formulated independently. The DEB model takes into account the scaling of metabolic rates with size, is applicable across many taxa and originally was designed to address ecotoxicological problems. A comprehensive review of bioenergetics models is given by Chipps & Wahl (2008).

Agent-based models and bioenergetics were first merged in the modelling of fish populations. A major stimulus to the merger was the practical question of how resilient fish populations are to increases in mortality during early life stages. Many fish populations were thought to have strong compensatory mechanisms, by which additional mortality to fish in the larval and other early life-history stages could be offset by more food and faster growth of survivors. But classical state variable models of populations were not able to simulate the resulting complex size-dependent relationships. The merger of ABMs with bioenergetics models allowed for detailed modelling of the dynamics of size-structured populations, and many of those models were applied to young-of-the-year populations, focusing on the growth and survival of juveniles (Madenjian & Carpenter 1991; DeAngelis *et al.* 1993; Scheffer *et al.* 1995; Rose *et al.* 1999). From those beginnings, the use of bioenergetic ABMs expanded in many directions and energy budget ABMs are now well established in modelling fish populations and are used to make important management decisions, though more work is still needed on model evaluation to improve the fit between model predictions and field and laboratory data (Chipps & Wahl 2008; Petersen, DeAngelis and Paukert 2008a).

The number of ABMs of terrestrial animals that include bioenergetics is still small; though, the numbers are growing. Reuter & Breckling (1999) developed an ABM for nesting robins to estimate the energetic needs during the critical reproductive phase. Wolff (1994) modelled the foraging and energetics of a colonial wading bird, the wood stork. Reuter (2005) modelled the bioenergetics of populations of small mammals both in northern Germany and Scandinavia, showing cycling as an emergent behaviour in the latter case. A number of models in the ALMaSS system (Topping *et al.* 2003) include individual energy budgets. The skylark, hare and partridge models (Topping & Odderskær 2004; Topping, Hoye & Olesen 2010b; Topping *et al.* 2010a) use foraging by adults in heterogeneous environments to determine the energetic intake, growth and survival of young. Parrott & Kok (2002) developed a generic model of a terrestrial animal, which can be used to describe interactions between animal species in a landscape with autotrophic resources. Stillman & Goss-Custard (2010) accurately simulated the foraging behaviour and overwinter mortality of several shorebird and wildfowl species to inform a number of real-world management decisions, and their methodology may have wider

application (Stillman 2008). DEB has been applied within an ABM to earthworms (Baveco & DeRoos 1996) and oysters (Bacher & Gangnery 2006).

The energy budget ABMs cited above span a wide range of complexity, from relatively simple to highly complex. Because the costs in terms of time and data of developing ABMs can be high, unnecessary complexity should be avoided, but this raises the question as to how much complexity is necessary for adequate modelling of energy budgets. In the next section, we review the scientific literature relevant to modelling energy budgets for use in ABMs.

Elements of energy budget models: an overview

Our aim is to identify a generic specification for energy budgets that is both sufficiently complex and as simple as possible for representing individuals in population models (Fig. 1/Table 1). Our proposal is that the modelled animal forages as necessary to supply its energy needs for maintenance, growth and reproduction. If there is sufficient energy intake, the animal allocates the energy obtained in the following order: maintenance, growth, reproduction, energy storage, until its energy stores reach an optimal level. If there is a shortfall, the priorities for maintenance and growth/reproduction remain the same until reserves fall to a critical threshold below which all are allocated to maintenance. The maximum rates of ingestion and allocation depend on body mass and temperature. We make suggestions for how each of these processes should be modelled mathematically.

THE ENERGY BUDGET

The resources acquired by an organism are generally considered to be allocated separately to maintenance, growth, reproduction or storage, as shown in Fig. 1 (Peters 1983; Sibly & Calow 1986b; Stearns 1992; Karasov & Martinez del Rio 2007). This is a diagrammatic representation of eqn (1), omitting faecal and excretory waste. The total available for allocation is limited by the amount the animal eats, so if more is allocated to one function, less is available for others. This follows from conservation of mass and energy (eqn 1).

There is little information as to how priorities change when there is not enough food, but it is generally thought that until reproduction the first priority after maintenance is growth (see, e.g. Sibly & Calow 1986a). DEB and the MTE make different assumptions. DEB assumes that throughout life, a constant fraction of input is allocated to maintenance and growth, with the rest going in juveniles to maturation and in
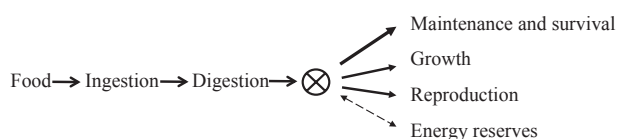
adults to reproduction, the 'kappa rule' (Kooijman 2010). MTE assumes that resources are allocated in fixed proportions to maintenance, growth and reproduction, the same in all species (Sibly 2012). Calculations are generally in units of energy per unit time, for example watts, even though acquisition and allocation of many specific nutrients subscribe to the same principles (see, e.g Kaspari 2012).

SCALING OF THE ENERGY BUDGET WITH BODY MASS AND TEMPERATURE BETWEEN AND WITHIN SPECIES

Food acquisition, maintenance, growth and reproduction all require energy, and all scale in similar ways with body mass and body temperature (Brown *et al.* 2004). These scaling relationships underlie most of the processes in Fig. 1 and can be used in extrapolation between species when data for modelled species are not available directly. Fundamental to these scaling relationships is the way that animals' power consumption varies with body mass and body temperature.

The total power consumption of an organism is referred to as its metabolic rate. Technically, it is best measured as heat production by calorimetry in watts, but often is measured as rate of O_2 consumption or CO_2 production in animals. Animal physiologists distinguish basal or resting metabolic rate (BMR), the rate of metabolism of an inactive, starving animal measured over a relatively short period of time, typically minutes (McNab 1997), from the rate of metabolism in the field (FMR), which is of the order of three times BMR (Peterson, Nagy & Diamond 1990; Brown & Sibly 2012). Most but not all measurements of metabolic rate have been of BMR.

It has been known for at least a century that BMR varies with body mass and within limits with temperature. Although details are still debated, there is a large and long-standing literature showing that, across the diversity of living things and ecological settings, BMR scales with body mass as a power law and with temperature as an exponential (summarized by Peters 1983). More recently, the equation has been derived from first principles and biological mechanisms as the central equation of the MTE. The equation relates body mass M and body temperature T, measured in kelvins ($=°C + 273 \cdot 15$), to metabolic rate B:

$$B = B_0\, M^{\gamma} e^{-E/\kappa T} \qquad \text{eqn 2a}$$

where B_0 is a normalization constant that is independent of body mass and temperature, M^{γ} is how metabolic rate scales with M to a power γ, an allometric scaling exponent, and $e^{-E/\kappa T}$ is the exponential Arrhenius function, where E is an 'activation energy' and κ is Boltzmann's constant ($8 \cdot 62 \times 10^{-5}$ eV K^{-1}) (Gillooly *et al.* 2001; Brown *et al.* 2004; Brown & Sibly 2012). Experimental studies have shown that the allometric exponent, γ, is usually between 2/3 and 1. Since the pioneering work of Kleiber (1932) and Brody & Proctor (1932), many empirical studies have obtained a value for γ close to 3/4, and $M^{3/4}$ scaling of metabolic rate has often been referred to as Kleiber's law. Values for E have been reported in the range 0·41–0·74 eV, clustering around 0·65 eV (Gillooly *et al.* 2001; Brown *et al.* 2004). These considerations suggest the equation

Fig. 1. The processes of food acquisition and the allocation of energy. Width of allocation arrows indicates priority.

Table 1. The principal parameters required in a minimum model of the energy budget. Approaches to estimating parameter values are described in the text

Sections	Equations	Symbol	Parameter
Food acquisition and digestion	3	IG_{max}	Maximum ingestion rate
Food acquisition and digestion			Assimilation efficiency
Energy reserves			Optimal energy reserves
Scaling of the energy budget with body mass and temperature between and within species	2	B_0	Normalization constant for BMR
Growth at constant body temperature	4e	m_0	Neonate mass
Growth at constant body temperature	4f	m_∞	Maximum body mass
Growth at constant body temperature	4f	b	Growth time constant
Growth at constant body temperature			Energy cost of synthesizing 1 g somatic tissue
Reproduction			Age at first reproduction
Reproduction			Body mass at first reproduction
Reproduction			Maximum number of offspring/litter
Reproduction			Energy cost of synthesizing 1 g reproductive tissue
Reproduction			Time required to synthesize 1 g reproductive tissue

BMR, basal metabolic rate.

can be given in a more specific form in which $\gamma = 3/4$ and $E = 0.65$ eV for processes governed by respiration, so that:

$$B = B_0 M^{3/4} e^{-0.65/\kappa T} \qquad \text{eqn 2b}$$

In this form, variation between animal groups is only expected in the value of the normalization constant, B_0. For homoeotherms, the Arrhenius term $e^{-E/\kappa T}$ is unnecessary because body temperature is to first-order invariant and its value can be subsumed into the normalization constant. Values of γ and the normalization constant (taken as the intercept in a log–log plot) are given for 32 lineages of homoeotherms and 48 lineages of poikilotherm in Appendix III of Peters (1983). Some more recent estimates may be found in Glazier (2005).

So far we have considered the interspecific scaling of metabolic rate. There has been some debate as to whether the same scaling rules apply intraspecifically. This is expected if metabolic rate is determined by mechanistic constraints as many believe, and we suggest this be assumed in a minimum model. However, there is a suggestion that juveniles of large species have higher metabolic rates than same-size adults of smaller species (Makarieva, Gorshkov & Li 2009). Intraspecific scaling relationships of 218 species are tabulated in the study by Glazier (2005).

The importance of eqn (2) is that it represents how an animal's power consumption – measured as metabolic rate – scales with body mass and body temperature. Because power is needed for food acquisition, maintenance, growth and reproduction, these processes scale in similar ways with body mass and body temperature (Brown *et al.* 2004).

FOOD ACQUISITION AND DIGESTION

Food resources are generally chosen from those available according to the principles of optimal foraging, that is, according to the net rate at which they provide energy per unit time (Davies, Krebs & West 2012). Thus, when foods vary in energy yield per unit time after allowing for energy costs of foraging, the animal selects the most profitable.

Generally, food resources vary both temporally and spatially. Variation in food density affects the rate of ingestion of food up to an asymptote, the form of this relationship being known as a 'functional response' (Fig. 2). Many functional responses have been proposed, all of which are at best approximations of reality. We will mention only one, the two-parameter Holling type 2 response (Holling 1959) (Fig. 2), which may be suitable for most purposes, as this response often approximates that observed in nature (Ricklefs & Miller 2000; Begon, Townsend & Harper 2006; Krebs 2009). The Holling type 2 functional response may be written as:

$$\text{Ingestion rate} = IG_{max} \times (\text{food density})/(\text{food density} + k)$$
$$\text{eqn 3}$$

where IG_{max} is the maximum ingestion rate in g or J per unit time, and k is a constant, inversely related to searching efficiency, which shows how quickly the response curve reaches its maximum as density increases.

Maximum ingestion rates generally scale allometrically with body mass and temperature according to equations of the form of eqn (2). Values of normalization constants and body mass exponents are given for 10 lineages of homoeotherms and six of poikilotherms in Appendix VIIa of Peters (1983) (see also Clauss *et al.* 2007, for mammalian herbivores), but to our knowledge, no comparable data are available for temperature dependence.

The acquisition of food has energy costs, for example through locomotion, and these will sometimes be important (e.g. Bernstein, Kacelnik & Krebs 1991). An idea of their magnitude can be gained from a recent study of greylag geese, which swim at $2.2 \times$ BMR, walk at $1.7 \times$ BMR but fly at $10 \times$ BMR (Kahlert, 2006). Useful allometries of the energy costs of running, flying and swimming are given in the study by Schmidt-Nielsen (1984) and discussed in Alexander (2005).
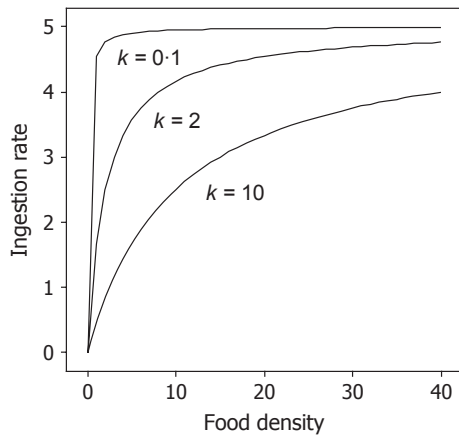
Fig. 2. The relationship between ingestion rate and food availability. The curves shown are Holling type 2 functional responses as specified by eqn (3), with $IG_{max} = 5$.

After ingestion, food is processed by the digestive system and a proportion becomes available for allocation to the various functions shown in Fig. 1. This proportion is called assimilation efficiency, defined as (energy obtained by digestion)/(energy ingested as food). Assimilation efficiency depends on diet and averages around 50–60% (Peters 1983) and appears not to vary with body mass (Hendriks 1999). Whereas flesh and seeds may be upwards of 80% assimilated, this falls to 40–70% for young vegetation and lower for mature vegetation and wood (Peters 1983). Hendriks (1999) gives the assimilation efficiencies of detritivores, herbivores and granivores/carnivores as around 20%, 40% and 80%, respectively.

Assimilated energy is available for distribution between the four destinations shown on the right of Fig. 1, described in detail in the next sections. We consider energy storage first because maintenance, growth and reproduction all draw on energy reserves when food is in short supply.

ENERGY RESERVES

Energy reserves in terrestrial vertebrates are stored mainly as fat in adipose tissue or as carbohydrates in the liver. These reserves allow the animal to maintain its functions during temporary periods of starvation. If energy input from food exceeds the requirements of maintenance, growth and reproduction, then any excess is stored in the animal's energy reserves, the rate of storage being limited by ingestion or digestion rate. Conversely, reserves are used to supply energy requirements if the supply from feeding is inadequate.

Fat rather than carbohydrate is generally used for long-term energy storage because of its higher energy density: fat yields more than twice as much energy as carbohydrate (39·3 vs. 17·6 kJ g^{-1} dry weight) (Schmidt-Nielsen 1997); though there can be variation in the energy density of lipid stores between species that can be up to 40%, depending on the specific constituent triacylglycerides (McCue 2010). There are costs to energy storage, and the total cost of synthesizing and storing one gram of fat is about 54 kJ (Pullar & Webster 1977;

Emmans 1994). Despite the attractions of fat, some animals use other fuels, for example sessile marine animals, for which carrying extra weight is not costly, use glycogen, while earthworms and flatworms use protein and degrow when starving.

Surplus energy from food is not added to reserves indefinitely. Instead, animals stop eating once reserves reach a certain level, presumably corresponding to an optimum compromise between the benefits of being able to survive a hunger gap and the costs of carrying extra weight, for example reduced ability to escape from predators (Witter & Cuthill 1993; Gosler, Greenwood & Perrins 1995; Lind, Jakobsson & Kullberg 2010). The optimum will vary with time and place, and prior to migration, animals may accumulate a fat store of 25–50% of body mass (Pond 1978; Peters 1983). While optimum values cannot be predicted a priori, information on natural fat content exists for many species (see, e.g. Pond 1978). Relative to energy expenditure, larger mammals carry more body fat than smaller ones [fat = 75 M$^{1.19}$, fat in g and M in kg (Lindstedt & Schaeffer 2002, Table 3)] and so can survive substantially longer periods of starvation.

A more detailed model might divide biomass into irreversible mass, including compounds like bones and organs that cannot be starved away by the animal in time of need, and reversible mass, which includes energy reserves such as fat, muscle tissue and gonads (Persson *et al.* 1998). Persson *et al.* (1998) constrained the ratio of reversible mass to irreversible mass to be below a specified maximum, which differs between juveniles and adults, as the latter also allocate mass to gonads.

MAINTENANCE AND SURVIVAL

Energy for maintenance is roughly equivalent to BMR, so its dependence on body mass and temperature is given by eqn (2). Energy allocated to maintenance fuels the basic processes of life essential for survival, and these have first call on energy obtained from feeding and on an animal's energy reserves when food is short. Energy is allocated to maintenance as long as energy is left in the reserves. For modelling purposes, the animal may be considered dead when the reserves are exhausted. After this point, muscle protein is consumed, but it is unlikely the animal could then recover if fed. Starvation refers to the process during which an animal requiring food is unable to eat for lack of food and should be distinguished from hibernation and aestivation, which are not considered here but have been reviewed elsewhere (see references in McCue 2010). There have been reports that metabolic rate decreases with prolonged fasting, but this may be simply a result of decreased body mass (McCue 2010).

GROWTH AT CONSTANT BODY TEMPERATURE

If energy is available after the costs of maintenance have been paid, juveniles allocate energy to somatic growth. The energy content of wet flesh is about 7 kJ g^{-1} (Peters 1983), and to this is added the costs of synthesizing flesh, which are of the order of 6 kJ g^{-1} for mammal embryos and 2 kJ g^{-1} for embryos of birds and fish developing in eggs (Moses *et al.* 2008). After

hatching/birth, the costs of synthesis are of the order of 6 kJ g^{-1} for all three taxa (Moses *et al.* 2008). Taking a different approach, Sibly & Calow (1986b, pp. 54–55) estimate the efficiency of synthesis in juveniles (J flesh/(J flesh + J synthesis)) as 40–50% for homoeotherms and somewhat higher for poikilotherms (the mean of 26 species was 66%, range 30–89%). As 1 g wet flesh contains 7 kJ, this gives the energy cost of synthesis as a little over 7 kJ g^{-1} for homoeotherms and around 3·6 kJ g^{-1} for poikilotherms.

Growth is, however, not just a matter of supplying energy. Molecules have to be precisely assembled in appropriate order, and so there are limits to the rate at which new flesh can be synthesized. These limits are implicit in the relationship of maximum growth rate with juvenile body mass, *m*. A frequently used relationship for maximum growth rate has the form:

$$dm/dt = a\,m^g - b\,m \qquad \text{eqn 4a}$$

where *a*, *b* and *g* are parameters and dm/dt denotes growth rate at body mass *m* (Reiss 1989; Kerkhoff 2012). If body mass can be assumed proportional to the third power of body length, *l*, then eqn (4a) can also be written as:

$$dl/dt = (a'\,l^{(3g-2)} - b\,l)/3 \qquad \text{eqn 4b}$$

where a' is a new parameter. MTE suggests an exponent of $g = \frac{3}{4}$ (Moses *et al.* 2008; Kerkhoff 2012), which perhaps fits the data a little better than the exponent of 2/3 suggested by Von Bertalanffy (1957). However, in describing growth curves, it makes little difference which exponent is used (Kerkhoff 2012). An additional consideration is that a 2/3 exponent allows eqn (4b) to be rewritten in the simple form:

$$dl/dt = b\,(l_\infty - l)/3 \qquad \text{eqn 4c}$$

where l_∞ denotes maximum body length. Equation (4c) can be integrated and expressed as:

$$l = l_\infty \left\{ 1 - \left(1 - \frac{l_0}{l_\infty} \right) e^{-bt/3} \right\} \qquad \text{eqn 4d}$$

or

$$m = m_\infty \left\{ 1 - \left(1 - \left(\frac{m_0}{m_\infty} \right)^{1/3} \right) e^{-bt/3} \right\}^3 \qquad \text{eqn 4e}$$

where l_0 and m_0 are neonate length and mass at $t = 0$ and m_∞ denotes maximum body mass. Equation 4e is commonly referred to as the von Bertalanffy equation. The parameter *b* can be obtained by fitting eqn (4d) or eqn (4e) to data recording increase in body length or mass with age in ideal conditions. Equation 4a can now be written as:

$$dm/dt = b(m_\infty^{1/3} m^{2/3} - m) \qquad \text{eqn 4f}$$

Equation (4) shows how the maximum rate at which resources can be allocated to growth changes as the juvenile increases in mass. If more is available from digestion than can be consumed by maintenance and growth, then any surplus goes into energy reserves.

In this section, we have considered the maximum rate of allocation of resources to growth in juveniles. It has been implicitly assumed that body temperature is constant, but this is not necessarily true in ectotherms; the effects of rearing temperature on growth in ectotherms are considered in the next section. The case of growth continuing after first reproduction is more complicated and is considered below in Indeterminate growth: where growth continues after the age of first reproduction.

COMPLICATIONS OF TEMPERATURE-DEPENDENT GROWTH IN ECTOTHERMS

Ectotherm metabolic and juvenile growth rates depend not only on body mass but also on body temperature, and ectotherm body temperatures are affected by ambient temperature. It is known that many ectotherms emerge smaller at higher temperatures [the temperature–size rule (Atkinson 1994)]; though, the adaptive reasons for this are not well understood (Atkinson & Sibly 1997; Kingsolver & Huey 2008). Phenomenologically, it seems ectotherms initially develop faster if it is warmer but then mature at a smaller final mass. In at least some species, the process can be described by a negative linear relationship between the logarithms of parameters l_∞ and *b* in eqn (4c) (Charnov 1993; Pauly, Moreau & Gayanilo 1996; Atkinson & Sibly 1997). For example, in the fish *Merlangius merlangus*, the relationship has been estimated as $\ln l_\infty = -\frac{1}{2} \ln b + 3$ with l_∞ in cm and *b* in y^{-1}. Using this, eqn (4c) can be rewritten as:

$$dl/dt = l_\infty^{-2} e^6 (l_\infty - l)/3 \qquad \text{eqn 5}$$

Initial growth rate is proportional to the Arrhenius function (Gillooly *et al.* 2002, using data from terrestrial invertebrates and zooplankton), and this corresponds approximately to the first term in eqn (5) when *l* is small, that is $dl/dt \approx 1/3\, l_\infty^{-1} e^6$, giving:

$$l_\infty \approx c\, e^{0.65/\kappa T}, \qquad \text{eqn 6}$$

where *c* is a constant that has to be determined. Equations (5,6) together represent a first attempt to show how the maximum rate at which resources can be allocated to growth varies with body size and temperature.

REPRODUCTION

Reproduction does not occur until the animal has attained a certain size and assembled the bodily structures necessary for reproduction. These structures (e.g. gonads, oviduct and uterus) themselves require resources and some models account for this explicitly (e.g. Kooijman 2010). We suggest that this is not necessary provided a minimum size (or age) of reproduction is included. Allometric coefficients for age at maturity are given for seven vertebrate lineages in Peters (1983) Appendix VIIIb, and further information is available for mammals and birds in the study by Calder (1984) and for mammals in Ernest (2003).

Reproduction, like growth, requires that molecules be precisely assembled in appropriate order, and this imposes limits

on the rate at which new flesh can be synthesized. Several off-spring may be synthesized simultaneously as a 'litter' or 'clutch'. The maximum rates of production are implicit in the allometric coefficients for numbers and sizes of offspring given for a number of lineages in Appendix VIIIa of Peters (1983). Data on the timing of the phases of reproduction in some vertebrate lineages are given in Appendix VIIIb of Peters (1983). The energy cost of synthesizing flesh for reproduction is the same as for growth, see section Growth at constant body temperature.

Food supply and in some species temperature affect when an animal reaches the size required for reproduction. For determinate growers, that size would be adult size. However, while this approach may suffice for many vertebrates, some invertebrates respond to food shortage/stress in more complex ways, by decreasing size of first reproduction and clutch size, and in some species by increasing neonate mass. Some of these invertebrates are indeterminate growers, and these are dealt with in the next section.

INDETERMINATE GROWTH: WHERE GROWTH CONTINUES AFTER THE AGE OF FIRST REPRODUCTION

Although in some species, somatic growth stops when reproduction starts, as in most birds and mammals, in other species, it continues, as in some fishes, reptiles and invertebrates. These strategies are referred to as 'determinate' and 'indeterminate' growth, respectively. In general, allocation follows the rules indicated in Fig. 1, but there is a complication: How should resources be partitioned between growth and reproduction in the case of indeterminate growth? Evolutionary theory provides only limited insight (Perrin, Sibly & Nichols 1993; Ejsmond *et al*. 2010), and the process is generally modelled phenomenologically using von Bertalanffy's eqn (4e) with modification if temperature varies (see, e.g. Fontoura & Agostinho 1996; Jager, Reinecke & Reinecke 2006; Kooijman 2010). Equation 4f shows as before how the maximum rate at which resources can be allocated to growth changes with body mass and ambient temperature. When food is abundant, then energy is allocated to reproduction and growth as fast as it can be used, and any surplus goes to reserves. When there is not enough food, reproduction likely has priority over growth, because early reproduction is in general strongly favoured by natural selection (Sibly & Calow 1986a).

Other approaches to modelling indeterminate growth are possible. Many DEB models assume the animal allocates throughout life a fixed fraction of energy to somatic maintenance plus growth, the rest being allocated to reproduction and the bodily structures necessary for reproduction and their maintenance (Kooijman 2010). Quince *et al*. (2008a,b) developed a fitness-maximizing model of biphasic somatic growth in fish, in which they distinguished between pre- and postmaturation growth with an explicit description of energy allocation within a growing season, and tested predictions against growth data from lake trout (*Salvelinus namaycush*).

ALLOMETRY OF MORTALITY RATE

Some ABMs require specification of the background mortality rate. If this is not known directly for the modelled species, an estimate can be obtained from the allometric relationships governing energy budgets (eqn 2). Mortality rate is strongly linked to the energy budget because mortality rates must equal birth rates long term, so that populations do not indefinitely increase or decrease (Peters 1983; Sutherland, Grafen & Harvey 1986; Sibly & Calow 1987). Equalizing of birth and death rates comes about through ecological density-dependent processes that regulate the population (Sinclair 1989). The processes that produce density dependence may be direct (animals interfering with each other) or indirect (mediated by a factor such as food availability) and should be part of the ABM, but an estimate of background mortality rate may be obtained if necessary from MTE's suggestion that per capita mortality rates should, like birth rates, be proportional to $M^{-1/4}e^{-E/kT}$ (Brown *et al*. 2004; Brown & Sibly 2006). Allometric coefficients for mortality rates overall follow MTE predictions: values are given for mammals, birds, fish, invertebrates and phytoplankton in the study by McCoy & Gillooly (2008, 2009).

Approaches to parameterizing bioenergetics models

Bioenergetics models may be difficult to parameterize, especially for rare species or in cases where funding is not sufficient to study the organisms in detail. The set of parameters needed in a minimum model is shown in Table 1. Where data are available for modelled species, these should be used, though the energetics of relatively few species have been studied in sufficient detail to determine all relevant parameters (but see Kitchell, Stewart & Weininger 1977; Rice *et al*. 1983; Stewart *et al*. 1983). Where data are lacking, it may be possible to estimate parameter values using other approaches (Petersen, DeAngelis & Paukert 2008b). The main approaches are the following.

ALLOMETRIC EQUATIONS

Parameter values can often be estimated to order of magnitude using the allometric relationships emphasized throughout this review (e.g. eqn 2). Allometric equations themselves may need parameterization (e.g. values of normalization constants or scaling exponents), and we have cited sources for these where available.

PARAMETER BORROWING

A common approach to building bioenergetics models for fish species is to borrow parameters and model equations from related species, or from species with similar life histories (e.g. Beauchamp & Van Tassell 2001). The parameter sets available in the literature are reviewed, and parameters are then selected based on understanding of behaviour, taxonomic relationship,

physiology and range of habitats occupied (e.g. Hanson *et al.* 1997) (see Chipps & Wahl 2008, for a discussion of problems associated with borrowing parameter values).

MONTE CARLO FILTERING AND PATTERN-ORIENTED MODELLING

Monte Carlo filtering involves randomly sampling model parameter values from a set of plausible values, then running the model with these parameter values to produce output. The output is statistically compared with a test criterion, which may be from field or laboratory studies (Rose *et al.* 1991). If model output is not different from the test criteria, then the sampled parameter value(s) are assumed to be acceptable. Petersen & Paukert (2005) used this approach to develop a set of bioenergetic model parameters for humpback chub *Gila cypha* in the lower Colorado River. They first assumed that taxonomic relationships could be used to set the upper and lower bounds on parameters for consumption and respiration in a bioenergetics model. Once the bounds for critical parameters were determined through a literature review, a Monte Carlo simulation was constructed to sample parameters from a uniform distribution within the bounds and grow simulated fish at different temperatures. The model fish were tested against fish grown in laboratory experiments (Gorman & Van Hoosen 2000).

Monte Carlo filtering is used in pattern-oriented modelling (POM, Grimm *et al.* 2005) which is a general strategy to make models realistic across different levels of organization and scales. POM has been defined as the 'multi-criteria design, selection, and calibration of models of complex systems' (Grimm & Railsback 2012, p. 300). By designing models to simultaneously reproduce multiple patterns, they are more likely to capture the internal organization of the real system sufficiently well to understand emergent properties and cross-level and cross-scale interactions, and to make robust predictions. POM may include so-called weak patterns, which are not particularly striking or hard to simulate, for example, differences in size distributions between spatial areas or seasons, or patterns of size-selective mortality. Comparisons of patterns with model outputs may eliminate many competing model structures and parameterizations (Wiegand *et al.* 2003; Wiegand, Revilla & Knauer 2004; Railsback & Grimm 2012). Thus, even weak patterns contain information that can be utilized to inversely parameterize energy budget models. The POM approach is designed to reduce model uncertainty as much as possible. We cannot go here into the issue of uncertainty, which is a problem in all models, but refer the reader to the study by Grimm *et al.* (2005) for detailed discussion.

Growth of roach *Rutilus rutilus* in a heterogeneous lake environment has been modelled using this type of approach (Hölker & Breckling 2002). The authors' particular objective was to estimate the energy cost of swimming. They developed a spatially explicit individual-based model for roach in a lake, which included bioenergetics and rules for activity and habitat choice. The activity rules included three modes of swimming: high cost, low cost and spawning. The mode of swimming depended on physiological status, light conditions and habitat choice (pelagic or littoral). These behavioural rules were tested and modified by comparing the movement patterns produced in the model with observed patterns of individual fish obtained by telemetry, as well as the density patterns of roach in the lake averaged over time.

Sophisticated approaches derived from Monte Carlo filtering are being developed and applied to obtain best-fit estimates of parameters whose values cannot be otherwise established (Piou, Berger & Grimm 2009; Beaumont 2010; Csillery *et al.* 2010). These approaches also allow statistical comparison of models to ascertain which model fits the data best.

ARTIFICIAL EVOLUTION

In this approach, models are used to infer unknown behaviours and life-history strategies of the organism by assuming that the species will be optimally suited for the conditions of the environment in which it lives. Therefore, the relevant environmental conditions, such as resource availability, temperature, spatial heterogeneity of suitable habitat and temporal variability of conditions, are modelled. Whatever information is available relative to a species' bioenergetics and life history is used to set constraints. Other aspects of energetics and life history, such as an individual's behaviours, which may not be well known, are included as variables in a simulation of evolution. An agent-based model of the species' population is developed using environmental conditions, bioenergetic constraints and behaviours. Simulations start with an initial set of individuals with a wide range of genotypes and continue through many generations, during which genotypes undergo mutation, natural selection and recombination. Strand, Huse & Giske (2002) used this approach to determine optimal energy allocation, fat reserves, age and month of spawning, diurnal pattern, and vertical distributions of juvenile and adult Mueller's pearlside *Maurolicus muelleri* (see also Huse, Strand & Giske 1999).

Conclusion

Including energy budgets in ABMs is essential if populations are affected by their food supplies. This allows deaths from starvation and opportunities for reproduction, to be properly related to the availability of food, which typically varies over the modelled landscape. While reviewing relevant scientific literature, we have here tried to identify the minimum requirements for energy budget models, utilizing the parameters shown in Table 1. We hope this will enable development of a general model, which will facilitate modelling of new species, and allow ready comparison of modelled species, which would differ only in parameter values and not in structure.

Models of the type discussed here specify what happens in all modelled situations and so take an overview of animal biology. This approach allows identification of gaps in scientific knowledge. One of the main weaknesses in the literature is that there is very little information on what happens when food supplies are suboptimal. What happens when input cannot

supply growth/reproduction at the maximum rate? Does the animal use reserves to fuel growth at maximum rate until reserves reach some critical low threshold after which all go to maintenance as suggested here? Or is a constant fraction of input allocated to maintenance and growth, the rest going to reproduction, as assumed by DEB, the 'kappa rule' (Kooijman 2010)? We also have only limited understanding of the adaptive reasons for observed patterns of temperature-dependent growth (see section Complications of temperature-dependent growth in ectotherms) and indeterminate growth (see section Indeterminate growth: where growth continues after the age of first reproduction). Further work by evolutionary biologists is needed; meanwhile, modellers must rely on phenomenological descriptions of growth patterns. Additional identification of gaps in knowledge can come from sensitivity analyses to identify model parameters with marked effects on population statistics. Such parameters need to be estimated precisely, and this may require further work by ecologists. We hope that by calling attention to gaps in knowledge, our review will elicit experimental work that will add to understanding of physiological ecology.

Clearly, many variants of the minimal model are possible and may be essential, for example to model species that hibernate or aestivate or disperse in some seasons or circumstances. The minimal model is the basic structure on which greater complexity to approximate real systems can be built. Additional realism, though, always comes at a cost in terms of added complexity. We hope that makers of ABMs will consider alternative versions of their models to see which best fit existing data. The general approach to model evaluation is POM (Grimm & Railsback 2005; Grimm *et al.* 2005). Energy-based ABMs offer the possibility of matching patterns of individual energy use and change in body mass over time, and so to discriminate between, for example, DEB's kappa rule and the approach to energy allocation advocated here (see, for example, Nisbet *et al.* 2004). To evaluate competing generic energy budget theories, comparison of predictions with 'stylized facts' may be worthwhile. 'Stylized facts' (Kaldor 1961) are broad, though not necessarily universal, generalizations of empirical observations and describe essential characteristics of a phenomenon that require an explanation (Heine, Meyer & Strangfeld 2005). Sousa, Domingos & Kooijman (2008) present stylized facts reproduced, or hardwired, into DEB models, but they are all restricted to the individual level. Similar evaluations, including population-level stylized facts, may be possible once energy budget models are more routinely used in ABMs. Ideally, evaluation of models using the pattern-oriented approach would be supplemented by statistical comparisons to ascertain which model fits the data best, while discounting models of greater complexity. Methods are available for achieving this (e.g. Piou, Berger & Grimm 2009; Beaumont 2010; Csillery *et al.* 2010; Hartig *et al.* 2011); though, implementation may not be without problems (Robert *et al.* 2011).

The development of ABMs incorporating individual energy budgets is essential for the realistic modelling of populations subject to variation in food availability. Such models may be used to assess the effects of proposals for landscape management (e.g. Jepsen & Topping 2004; Topping *et al.* 2005; Stillman & Goss-Custard 2010; Topping 2011). Examples include conservation management of nature reserves and shell fisheries, assessment of environmental impacts of building proposals including wind farms and highways, and assessment of the effects on nontarget organisms of new chemicals for the control of agricultural pests.

Acknowledegments

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