



# Predicting how many animals will be where: How to build, calibrate and evaluate individual-based models



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## ABSTRACT

Individual-based models (IBMs) can simulate the actions of individual animals as they interact with one another and the landscape in which they live. When used in spatially-explicit landscapes IBMs can show how populations change over time in response to management actions. For instance, IBMs are being used to design strategies of conservation and of the exploitation of fisheries, and for assessing the effects on populations of major construction projects and of novel agricultural chemicals. In such real world contexts, it becomes especially important to build IBMs in a principled fashion, and to approach calibration and evaluation systematically. We argue that insights from physiological and behavioural ecology offer a recipe for building realistic models, and that Approximate Bayesian Computation (ABC) is a promising technique for the calibration and evaluation of IBMs.

IBMs are constructed primarily from knowledge about individuals. In ecological applications the relevant knowledge is found in physiological and behavioural ecology, and we approach these from an evolutionary perspective by taking into account how physiological and behavioural processes contribute to life histories, and how those life histories evolve. Evolutionary life history theory shows that, *other things being equal*, organisms should grow to sexual maturity as fast as possible, and then reproduce as fast as possible, while minimising *per capita* death rate. Physiological and behavioural ecology are largely built on these principles together with the laws of conservation of matter and energy. To complete construction of an IBM information is also needed on the effects of competitors, conspecifics and food scarcity; the maximum rates of ingestion, growth and reproduction, and life-history parameters.

Using this knowledge about physiological and behavioural processes provides a principled way to build IBMs, but model parameters vary between species and are often difficult to measure. A common solution is to manually compare model outputs with observations from real landscapes and so to obtain parameters which produce acceptable fits of model to data. However, this procedure can be convoluted and lead to over-calibrated and thus inflexible models. Many formal statistical techniques are unsuitable for use with IBMs, but we argue that ABC offers a potential way forward. It can be used to calibrate and compare complex stochastic models and to assess the uncertainty in their predictions. We describe methods used to implement ABC in an accessible way and illustrate them with examples and discussion of recent studies. Although much progress has been made, theoretical issues remain, and some of these are outlined and discussed.

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## 1. Introduction

A major challenge in ecological modelling is to make reliable predictions about what will happen to real populations in real landscapes. In some ways this may seem a simple task—Newton solved similar problems in mechanics over 300 years ago. But

animals and plants are not identical particles obeying simple mathematical laws, they make complex decisions based on their needs and perceived opportunities in their environments. Only with the advent of computing power has it become possible to simulate these processes with any degree of realism, and so to link the levels from individual organisms to populations of individuals. In this approach what happens to the population emerges from complex interactions between autonomous individuals and their environments, in the computer simulations as in life.

Models are always simplified representations of the real system, and so a trade-off is necessary between model complexity and realism (Evans et al., 2013). The different degrees of this

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trade-off are characterised by the different model types available. Differential equation models are typically used in simple assessments of unstructured population growth, whilst matrix models are essentially sets of linear difference equations which separate the population into classes (e.g. life-cycle stage) with class-specific life-history parameters (e.g. juvenile survival). Both approaches provide insight into general patterns of population growth in specified environmental conditions. They have the advantage that they can accept population-level data on birth and death rates, and they are often tractable using analytical methods. However they cannot easily accommodate autonomously acting individuals, and it is difficult to characterise the effects of location and habitat.

These high levels of detail can readily be incorporated into individual-based models (IBMs; also called agent-based models (ABMs)). In IBMs, the actions of unique individuals are simulated as they interact with one another and the landscape in which they live (DeAngelis and Mooij, 2005). Individuals can vary according to their state variables (e.g. age, sex, mass) whilst patches of mapped landscapes can be characterised by key ecological drivers (e.g. temperature, food, exposure to chemicals). The dynamics of populations in different environmental conditions then emerge from simulations of individuals' behaviours (Grimm and Railsback, 2005). Thus, where prediction is required about the fate of populations in different landscape scenarios, one way ahead is through IBMs (Stillman et al., 2015). Accordingly, IBMs are currently being used to design strategies of conservation and of the exploitation of fisheries, and for assessing the effects on populations of major construction projects and of novel agricultural chemicals (see, e.g., Galic and Forbes, 2014; Hartman and Kitchell, 2008; Nabe-Nielsen et al., 2014; Stillman and Goss-Custard, 2010).

Although IBMs are powerful tools for ecological management, they also face major challenges. There may not be sufficient data available to build a realistic model, running IBMs may be computationally expensive, and run times may be prohibitively long. Furthermore attempts to represent multiple processes and interactions in IBMs can lead to models being over-parameterised, leading to reduced realism and an inability to extrapolate to other sites and/or time periods. Their predictions are then imposed rather than emergent (Grimm and Railsback, 2005; Martin et al., 2013). Because models are needed to forecast what happens in novel conditions, it is desirable that they be mechanistic in the sense that they accurately capture the underlying relationships between biological processes and environmental conditions.

In this paper we consider two particular problems: How to build ecological IBMs from first principles, and how to calibrate and evaluate them. When IBMs are built to predict the numbers and spatial distributions of animals, as is often the case in applied studies, we argue that insights from physiological and behavioural ecology offer a sound recipe for building realistic models. We also argue that model calibration and evaluation can be achieved using the new technique of Approximate Bayesian Computation (Beaumont, 2010). Thus the paper has two foci, which run in parallel but are not necessarily related to each other. Together they give our vision of "next generation ecological modelling", which is the focus of the special issue in which this paper appears. We try to produce concrete suggestions, but hope our readers will forgive us for not being able to fully describe the pros and cons of alternative approaches. This is partly for lack of space, but also in part because the new techniques we envisage are not yet fully developed or compared with alternatives, so informed comparisons and discussion are not yet possible. Our overarching aim is to be able to link the levels from individuals to populations in a transparent and credible fashion that is firmly rooted in biological knowledge.

## 2. Building IBMs from first principles

In this section we identify principles which may be used to build ecological IBMs and consider how to build such models using available biological knowledge. Our approach is partly based on Sibly et al. (2013) and is similar to the Dynamic Energy Budget approach (Kooijman, 2010; Martin et al., 2012). We then consider how population dynamics emerge from the simultaneous behaviours and interactions of individuals. At the end of the section we discuss some of the complications that arise in linking the levels from individuals to populations.

IBMs are based on knowledge about individuals, and the subdisciplines of biology that deal with individuals are physiological and behavioural ecology. These consider how physiological processes within individuals, and decisions made by individuals, contribute to life histories. Natural selection acts on life histories, favouring some at the expense of others, and this has ramifications for the evolution of physiologies and behaviour. So it is sensible to start by considering how life histories evolve.

The theory of life-history evolution is well established (see e.g., Sibly, 2002; Stearns, 1992) and explains why organisms are expected to maximise Darwinian fitness and so to win out in the struggle for existence in the environment in which they evolved. In particular *other things being equal* organisms are expected to:

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|---|-----------|
| • Grow to sexual maturity as fast as possible | (Axiom 1) |
| • Reproduce as fast as possible               | (Axiom 2) |
| • Minimise <i>per capita</i> death rate       | (Axiom 3) |

The phrase 'other things being equal' means that growth, reproduction and death rate are independent, *i.e.*, they do not trade off against each other. However this is not always the case, e.g., growing faster may only be possible by taking risks, which may mean the death of the individual. In such cases organisms may trade off risk of death to increase their growth rate. Much attention has been given to the evolution of life histories that are subject to constraints imposed by life-history trade-offs (Sibly, 2002; Stearns, 1992). The predicted outcome of the evolutionary process in a constant environment is referred to as an *optimal strategy*, meaning the strategy that maximises Darwinian fitness subject to the imposed constraints. Constraints and opportunities differ among species, and this is one reason why species differ from each other. Incorporating trade-offs into IBMs can be straightforward; for instance, the increased mortality that comes with foraging in dangerous but rewarding places may be a direct result of encountering predators more often. Provided the different situations of different species are well-modelled, their different trade-offs should emerge automatically.

One major constraint to increasing Darwinian fitness stems from the availability of resources. The energy and nutrients needed to build animal bodies are derived from food, but food may be in limited supply. This imposes major constraints on behaviour and physiology as follows:

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| • Energy is conserved within individual bodies | (Axiom 4) |
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This means that the only energy available to power organisms is that which they derive from food or sunlight. Allocation of resources within bodies is similarly constrained:

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| • Matter is conserved within individual bodies | (Axiom 5) |
|--|-----------|

This means that the only chemicals available to build organism bodies are those they derive from food.

Life-history theory is the foundation on which physiological and behavioural ecology are built. We now consider their relevant findings at the level of the individual.

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