Heterogeneous resource partitioning in a generalized individual-based model of multi-species interaction

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Abstract: We describe a parsimonious approach to the problem of a transgenerational individual-based model (IBM) of the interaction between species at different trophic levels. We implement the approach in a model of the interaction of a generalized predator and prey species and compare it with a state variable model of the two species. Similarities and differences between the two models are described. Perhaps the most important finding is the sensitivity of the IBM to the level of individual variation, manifested here by the level of resources carried by each individual. The heterogeneity of resource levels is very important for resilience and the viability of the species in the model. We argue that as individual-based modelling simulates the local interactions between heterogeneous individuals and their environment, interactions which ultimately determine the dynamics of populations, metapopulations, communities and ecosystems, the use of individual-based modelling is important in developing understanding of large-scale ecological patterns.

Keywords: *Individual-based modelling; Lotka-Volterra equations; State variable modelling.*

1. INTRODUCTION

The use of individual-based modelling (IBM) in ecology has grown steadily in the last fifteen years (Grimm, 1999; Judson, 1994; Schmitz & Booth, 1997) since the pioneering work of DeAngelis (1979), Kaiser (1979) and Łomnicki (1978). Individual-based modelling is an alternative to the more traditional state variable approach in which ordinary or partial differential equations are used to predict system outcomes over time. IBM is well-suited to the modelling of systems characterized by large numbers of discrete elements.

An individual-based model consists of a set of heterogeneous discrete objects which change their state over time in a changing environment. Execution of the model is achieved by simulating local interactions between individuals and the time-varying, heterogeneous environment. In contrast, the traditional state variable modelling takes a top-down approach, seeking to express relationships between global outcomes. Global outcomes are modelled directly in a set of equations, and execution consists of evaluating the equations over time, often in discrete time intervals. Populations, rather than individuals, are modelled.

Inherent in state variable models are simplifying assumptions such as homogeneity of individual properties and behaviour. Interactions typically occur randomly in one homogeneous environment space. There are, however, degrees of complexity in ecological systems including temporal and spatial scales, behavioral mechanisms and learning which are not easy to model in differential equations. The mathematics becomes intractable as the details or number of species rises (DeAngelis et al., 2001; Łomnicki, 1999; Schmitz & Booth, 1997).

While the state variable approach has been successful in providing general understanding of system dynamics, it does not address issues of individual heterogeneity, individual learning and behaviour, local interactions or environmental heterogeneity which are important in modelling the complexity of these systems. Our empirical understanding of population dynamics and individual interactions is that these systems cannot easily be modelled using an equation-based state variable approach (DeAngelis et al., 2001; Huston et al., 1988; Łomnicki, 1999; Schmitz & Booth, 1997).

The individual-based approach seeks to address these problems. Individuals in an individual-based model have potentially unique state and behaviour. The behaviour of an individual depends on global rules of engagement and on the state of the individual. The details of the interaction between individuals and the different states of the individuals can have a significant effect on the overall system dynamics and population levels, and begin to address the criticisms of the generalization of these factors in state variable models (DeAngelis et al., 2001; Schmitz & Booth, 1997).

The motivations for building individual-based models include looking for a mechanistic understanding of the complex interactions in ecological systems, the need to build a predictive tool to be used to forecast population levels and an exploration of the effect of adding complexity to a model in order to introduce biological realism.

In this paper we describe two models of the population dynamics of a predator species and a prey species. An individual-based model is compared with a state variable model of the two species. We find that the interaction of the individuals in the individual-based model generates comparable results to the state variable model – the population levels are interdependent and exhibit similar patterns, albeit with characteristics of stochastic and chaotic systems in the IBM. Mean population levels, while not explicitly coded into the IBM, emerge from the heterogeneous individuals and their rules of engagement, and these population levels are quickly resumed after an exogenous shock in the form of population decimation. The state variable model behaves differently in similar experiments.

Perhaps most importantly, we find that the level of variation among the individuals in the IBM has profound implications for the stability of the population levels predicted by the model.

2. THE INDIVIDUAL-BASED MODEL

The individual-based model described here was built with the goal of parsimony. We have endeavored to keep the number of parameters as low as possible while still including the essential characteristics of the system. As the model involves the interaction of species at different trophic levels the flow of energy resources is an essential characteristic. The IBM creates individual predators and prey which maintain a resource total, a simple analogy of the energy reserves stored by living animals. Resources flow from prey to predators. The concept of using resources as the currency of the model was inspired by the Gecko model of Schmitz and Booth (1997).

Each individual is given a resource level when it is born or created at the beginning of a simulation, and may add to the resource level by eating. Predators acquire the resources of their prey when they are eaten, and prey are given resources during each cycle of the simulation. A cycle is defined here as the basic time-step of the model and may represent different realistic time steps depending on the species being modelled. The individuals reproduce when they have enough resources or they may die of starvation or from being eaten.

The model output is the population levels of the two species each cycle. Statistics may also be calculated and displayed.

The model inputs are:
- Initial numbers of predators and prey (p_n and b_n)
- Predator chances of eating (to be multiplied by the number of prey) (p_η)
- Initial resources of individuals of both species (p_{ir} and b_{ir})
- Reproductive cost for both species (p_{rc} and b_{rc})
- Metabolic tax per cycle for both species (p_{mt} and b_{mt})
- Maximum and minimum resources to be added to each prey individual per cycle (b_{minr} and b_{maxr})

2.1. Description of processing per cycle

During each cycle of the simulator each predator and prey object is processed. One entire population is processed before the other. The order in which the two populations are processed does not affect the model dynamics. Processing the populations involves:

Implementing resource intake. Each predator is given a chance to eat once per cycle. Its chances of eating are proportional to the prey population, as in the Lotka-Volterra equations described below. If the predator is to eat, a prey individual is selected at random and removed from the simulation. The resource total of this prey individual is added to the resource total of the predator. This model operates in one environment space, again like the Lotka-Volterra equations, so the prey eaten can be anywhere in the environment space.

Each prey individual is given resources each cycle to simulate eating. The number of resources given to each prey individual is randomly selected from between an upper and lower bound (two of the model parameters, b_{minr} and b_{maxr}).

Applying metabolic tax. A tax is deducted from the resource total of each individual to simulate the metabolic cost of living for each cycle. If the resource total drops below the metabolic tax per cycle, the individual dies and is removed, as it does not have the resources to live one more cycle. The metabolic tax (p_{mt} and b_{mt}) parameters are global.

Processing reproduction. Each individual may produce one offspring per cycle if it has enough resources to both reproduce and live one more

cycle. If an individual is to reproduce, a reproductive tax is removed from its resource total to represent the energy cost of bearing offspring, and a new individual is added to the simulation. The new individual is not processed until the next cycle. The individuals in this model reproduce by parthenogenesis – mating behaviour and its associated complexity is not modelled. The costs of reproducing are global parameters (p_{rc} and b_{rc}).

2.2. Simulating population dynamics with the IBM

The simulations graphed here were started with 40 predators and 80 prey and were executed for 250 cycles of the model unless otherwise noted. Population levels in Figure 1 have a mean of 70 predators and 110 prey. As Figure 1 illustrates, the model output is similar to that of the Lotka-Volterra equations (Figure 3).

The populations in Figure 1 appear to be dependent on each other as would be expected given the model algorithm. The predator population is dependent on the prey as a source of food, and the prey population is dependent on the predators as their chances of being eaten rises as the predator population rises. No statistical analysis was done to test this dependency.

The input values used to produce Figure 1 are as follows: $p_n = 40$, $b_n = 80$, $p_\eta = 0.0055$, $p_{ir} = 1000$, $b_{ir} = 500$, $p_{rc} = 600$, $b_{rc} = 325$, $p_{mt} = 250$, $b_{mt} = 250$, $b_{minr} = 100$, $b_{maxr} = 490$, $rs[1] = 90$. These values were used for all figures unless otherwise noted.
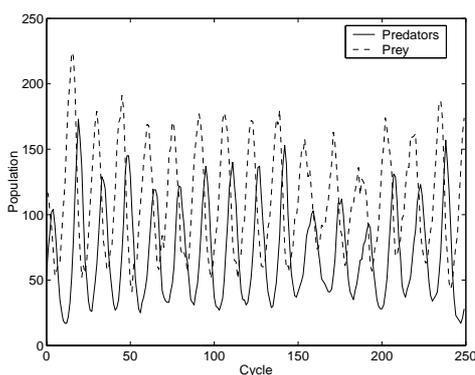

Figure 1. The individual-based model

The set of parameters used to create Figure 1 results in populations which cycle indefinitely.

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[1] The seed supplied to the Java pseudorandom number generator, explained in section 2.2.

Figure 2 illustrates the model output over 5000 cycles: we have run the simulator for over 100 000 cycles with similar results. Figure 2 is typical of the output over thousands of cycles using different sets of stable parameter values. The population levels of the two species demonstrate oscillating levels as do the population levels generated by the Lotka-Volterra equations, but the stochastic and possibly chaotic nature of the model is evident in the varying overall population levels over many cycles and in the occasional extreme values.
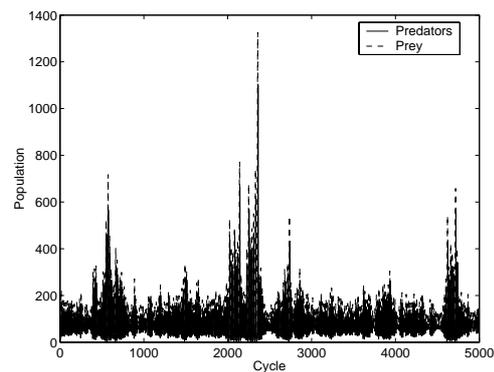
Figure 2. The IBM over 5000 cycles

Because of the stochastic nature of the model, and because the model was sensitive to parameter values, a statistical analysis of population levels to accurately determine trends was not pursued. The figures presented in this paper are representative of the parameter space explored. The model is not deterministic, but it is worth noting here an implementation detail: the computer programming language used generates pseudorandom numbers using the linear congruential method (Java language documentation). If the same seed is used to generate the pseudorandom numbers in different executions of the model, an identical sequence of pseudorandom numbers will result. This means that while the model has a stochastic element, an individual execution of the model may be exactly repeated.
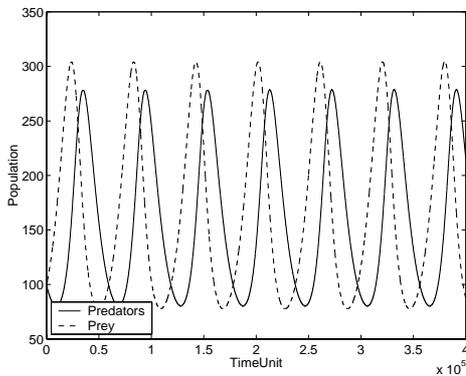
3. THE STATE VARIABLE MODEL

The equations developed by Lotka and Volterra in the 1920's (see, for example, Adler, 1998) are used here to implement a state variable approach to the predator-prey problem. The equations are as follows:

$$\frac{db\,(t)}{dt} = [\,\lambda\, -\, \varepsilon p\,(t)]\,b\,(t) \quad (1)$$

$$\frac{dp\,(t)}{dt} = [-\delta\, +\, \eta b(t)]\,p(t) \quad (2)$$

Where b represents the population of prey, p the population of predators, λ the prey growth rate in the absence of predators, ε the chances of a prey object being eaten, δ the predator growth rate in the absence of prey and η the chances of a predator eating. The initial population levels are known. We use the Euler method to implement an ODE solver.
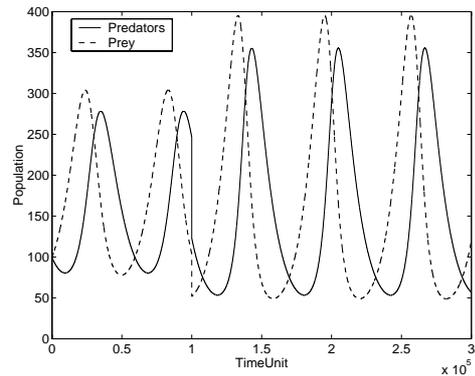

Figure 3. The state variable model

Figure 3 is a graph of the population levels produced by a computational implementation of the ODE solver. The model is calibrated with the following parameter values: $\eta = 0.006$, $\varepsilon = 0.0075$, $\delta = 1.0$ and $\lambda = 1.2$, and initial values: $b_0 = p_0 = 100$. The simulation was run for 40 time units with a time step of 0.0001.

The assumptions on which the Lotka-Volterra model is based include the homogeneity of individual organisms and the homogeneity of the environment. The individual-based model built here makes some of these assumptions, including the homogenous distribution of the species. The significant feature of the IBM, however, is the heterogeneity of the individuals.

## 4. BEHAVIOUR OF THE MODELS AFTER POPULATION DECIMATION

The stability of both models and the tendency towards stable population means in the individual-based model are illustrated when the models are subjected to an exogenous shock. In the graphs below the two populations are halved at a given time during the simulation. This is at

cycle 100 in the IBM and at time unit 1 in the state variable model.

Figure 4. Artificial reduction of population numbers in the state variable model

After the shock the state variable model resumes stable cycling population levels, but the minima and maxima are permanently altered (Figure 4). The population reduction can be seen at time unit 1 where the two population lines are vertical. In contrast the IBM resumes the same mean minima and maxima after reacting to the shock over cycles 100 to 140 (approximately) in Figure 5. A vertical line has been added to the graph to indicate where the populations are halved.
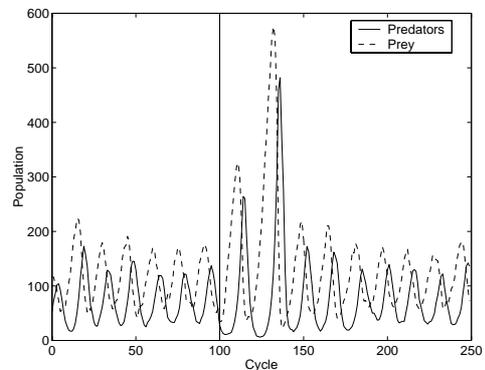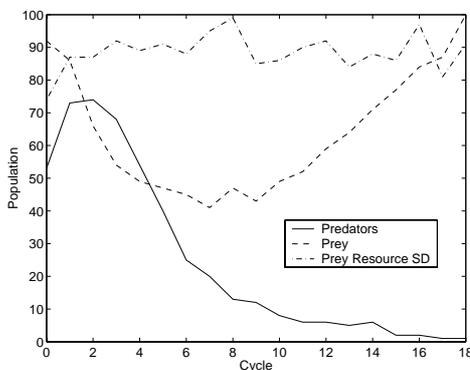

Figure 5. Artificial reduction of population numbers in the IBM
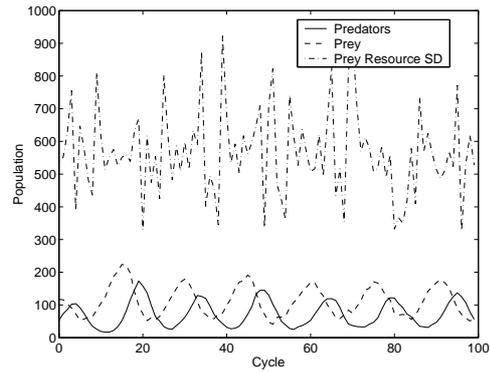
5. INDIVIDUAL HETEROGENEITY

The resources carried by each individual in the IBM are the only source of individual variation in this model. Preliminary results indicate that this variation is important to the stability of the population numbers. If the simulator is started with little or no variation in the resource levels of the individuals, the population levels are very unstable and one of the populations usually drops to zero. Figure 6 illustrates the two populations and the standard deviation of the prey resources

for each cycle when the resource standard deviation is low at the start of the simulation. The simulation lasts less than 20 cycles and stops when the predator population drops to zero. Figure 7 illustrates the simulation started with higher resource standard deviations and is in fact the first 100 cycles of the simulation illustrated in Figure 1 with the standard deviation of the prey resources for each cycle added to the figure. There is no parameter used to directly set the resource levels of individuals. The simulation in Figure 7 is achieved by re-starting the simulator after producing Figure 6 using the individuals which are left in the computer memory when the simulation that produced Figure 6 was halted. These individuals have a higher level of resource variation than those at the start of a clean simulation.

Figure 7. Higher initial resource variation

6. DISCUSSION

In this paper we have presented preliminary results obtained from the IBM described. We have not yet performed any structured and exhaustive analysis of the stability of the model, its robustness to parameter values or the dependence of the populations on each other. This will form the basis of future work, and is necessary before the generality of the results can be asserted. The comments made in this discussion should be read with this in mind.

The individual-based model of predator-prey interaction described here is based on a simple set of rules governing resource flow in the system. It produces cycling predator-prey population dynamics similar to those of the Lotka-Volterra model. There are significant differences between the two models, however, and one difference is revealed when the models are subjected to an exogenous shock in the form of population decimation. While this permanently affects the population levels in the state variable model, the IBM returns to the original population levels after reacting to the shock. Initial results indicate that the behaviour of the IBM after the shock appears to be highly dependent on which individuals are left, their resource means and resource variance. In Figure 5 the drop in predator numbers evident immediately after this shock could perhaps be explained if many of those predators *not* removed by the shock would not have survived the next few cycles anyway (due to their resource levels), and the resulting disproportionate drop in predator numbers results in an unusually high prey population, dragging the predator population up as well. These new population peaks are unsustainable given the resources entering the system, and the population means and variances move back to the stable levels inherent in the system. This is contrasted with the simple adjustment in the state variable model after the

Figure 6. Low initial resource variation

The importance of the level of variation in resources to the stability of the model over many cycles is consistently observed. The initial prey resource variance is more important than the initial predator resource variance. It is difficult to make conclusions about the importance of this finding as the model is of two generalized species and the parameter values are therefore not derived from empirical data. We add this finding, however, to the growing evidence in the literature that individual variation is important to the long-term viability of species in individual-based models of ecological systems (DeAngelis et al., 2001; Huston et al., 1988; Łomnicki, 1999; Schmitz & Booth, 1997). The significance and importance of individual variation, and the correlation between the prey numbers and the prey resource standard deviations will be the subject of future research.

shock, and illustrates the inherent stable population levels in the IBM.

Perhaps the most important finding of the work described here is the sensitivity of the model to individual variation. In this model the variance of the resource total in the population is critical to the stability of the population levels. A low resource variance almost always leads to the extinction of one of the species. The dynamics involved in the model which produce this effect will be explored in future research, but the parallels with real populations are interesting. The importance of variation, both genetic and phenotypic, to population viability is emphasized by many researchers, for example Meffe and Carroll (1997). The importance of individual-based modelling to ecology *because* of the possibility that individual variation may be built into the model is of central importance to the work of researchers including DeAngelis et al. (2001), Huston et al. (1988) and Schmitz & Booth (1997). Emerging themes in the literature include the importance of individual variation in both real and simulated populations, and that the modelling of individual variation and heterogeneous local interactions in IBMs leads to different system level outcomes compared with state variable models of the same system.

7. CONCLUDING REMARKS

The state variable approach to ecological system modelling has been to generalize and simplify system parameters to build parsimonious and deterministic models. These models have been useful in classical population ecology in helping to understand broad system dynamics. The approach in an individual-based model, in contrast, is to simulate local interactions between heterogeneous individuals, interactions which ultimately determine the dynamics of populations, metapopulations, communities and ecosystems.

This paper describes an individual-based model of the interaction between two species. The model was built by using the energy flow in a predator-prey system as its currency. The model exhibits inherent mean population levels, levels to which the model returns after artificial adjustment. It also exhibits an intriguing sensitivity to the level of individual variation. Sensitivity to individual heterogeneity is consistently cited in the literature as important to individual-based models of ecosystems and to the ecosystems themselves. In future work we will explore these characteristics and in doing so may possibly take a step towards understanding large-scale ecological patterns by investigation of generalized individual interactions.

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