

Process algebra models of population dynamics

Chris McCaig, Rachel Norman, and Carron Shankland

Department of Computing Science and Mathematics, University of
Stirling, {cmc,ran,ces}@cs.stir.ac.uk

1 Introduction

The idea that populations cannot grow without bound has been of interest to modellers for centuries. Malthus, in 1798, [Mal98] proposed a simple exponential growth model based on compound interest, but noted that this was unrealistic, since when a population becomes very large, access to resources will become restricted, restricting further growth in the population.

In this paper we present WSCCS models of population dynamics and compare the MFE that can be derived to the population level equations traditionally used to describe population dynamics. To do this we must capture births and deaths in our model and this is done by the same method used by Sumpter [Sum00]. Birth is modelled by having individuals become a parallel agent, which includes one agent to represent the parent and one agent to represent the offspring. Death is captured by allowing individuals to become the null agent 0.

To capture realistic population growth, which has some upper limit determined by the environment, we require density dependent behaviour, with the likelihood of either giving birth or dying, dependent on the current size of the population. In the models presented here we add density dependence to the death rate, although similar models can be developed with density dependent birth [McC07]. Biologically there are many systems where the death rate will increase as the density increases. In this case food and shelter become scarce and individuals become weaker and are more likely to die.

Brännström and Sumpter [BS05] made use of a site-based framework to develop derivations of several different single species population models. They were able to derive several well known models (including the models proposed by Beverton and Holt [BH57], Hassell [Has75] and Ricker [Ric54]) but notably not Verhulst's logistic equation [Ver38], which is the most commonly used equation to describe population dynamics [AM81, GH92]. In this chapter we develop WSCCS models of population dynamics that introduce density dependence both explicitly and implicitly and compare the resulting MFE to models from the literature.

$$\begin{aligned}
Rep &\stackrel{\text{def}}{=} N \times N \\
N &\stackrel{\text{def}}{=} p_d \cdot \surd : 0 + p_b \cdot \surd : Rep + (1 - p_d - p_b) \cdot \surd : N \\
Population &\stackrel{\text{def}}{=} N\{n\}[\{\surd\}]
\end{aligned}$$

Figure 1: Density dependence without food

2 Implicit competition

In the simplistic model given in Fig. 1 the N agents die with probability p_d , becoming the null agent 0, or give birth with probability p_b , becoming the agent Rep , which consists of two N agents in parallel. This model leads to a single MFE,

$$N_{t+1} = N_t(1 + p_b - p_d). \quad (1)$$

With fixed probabilities p_b and p_d the average behaviour of this model would be similar to that of the simple exponential growth model described by Malthus [Mal98], $N_{t+1} = \lambda N_t$, with $0 \leq \lambda \leq 2$. With $p_b > p_d$ the population will become infinitely large; $p_b < p_d$ will lead to the population dying out, while $p_b = p_d$ will lead to an equilibrium state for any initial population size, $N_0 = n$. This model does not capture the reality of population growth but density dependent growth can be achieved by making use of functional probabilities as described in [McC07].

Density dependent death can be added to Fig. 1 by adding functional p_d directly proportional to N :

$$p_d \stackrel{\text{prob}}{=} \min(\max(0, p_{d0} + k * \lfloor N \rfloor), p_L),$$

where p_{d0} is the probability of death in the absence of crowding. This is added to the MFE by substituting for

$$p_d = p_{d0} + kN_t,$$

which gives us the MFE

$$N_{t+1} = N_t(1 + p_b - p_{d0} + kN_t).$$

this can be rearranged to give

$$N_{t+1} = N_t + r \left(1 - \frac{N_t}{K}\right) N_t,$$

which is the discrete time version of Verhulst's logistic equation [Ver38] with $r = p_b - p_{d0}$ and $K = (p_b - p_{d0})/k$.

3 Explicit competition

The model in Section 2 assumed that we understand how the size of the population affects the growth of the population. The advantage of individual-based modelling techniques is that we can avoid such population level assumptions, with the population level behaviours arising from the individual interactions. To achieve this in models of population dynamics we use agents to represent a resource for which the individuals compete. Access to the resource can be used to determine the likelihood of either birth or death.

Sumpter [Sum00] developed a mechanism for describing density dependent growth in a population, which made use of food as an agent. Individuals in the population compete for the available food resource, giving birth after eating, and die probabilistically. Eating is a prioritised activity, so if an individual can eat they must. This means that every member of the population will give birth at each step of time until the size of the population is larger than the number of food agents, after which the number of births will be equal to the number of food agents. By intuitive reasoning Sumpter derived the following MFE for his model:

$$N_{t+1} = (1 - p_d)N_t + \min[(1 - p_d)N_t, f] ,$$

where p_d is the probability of death in any timestep and f is the number of food agents. Sumpter found that this MFE has a stable steady state of

$$N^* = \frac{f}{p_d} ,$$

when $p_d \leq 0.5$.

The model in Fig. 2 instead makes use of non-prioritised communication between the population and food. This allows for a situation where some individuals fail to find food when foraging, even if food is available. The other difference with Sumpter's model is that the density dependence here is on the death rate, rather than birth. In Fig. 2 the N_1 agents can eat, becoming the agent N_2 , but if they do not eat they die, becoming the null agent 0. The N_2 agents then give birth probabilistically and to be realistic, N_2 agents can also die probabilistically. This means that in each step of time a proportion of the population die, for instance, due to age and some die due to a lack of food.

The MFE for this model is

$$N_{t+1} = (1 + p_b - p_d) \frac{f N_t}{f + N_t}, \quad (2)$$

where $f N_t / (f + N_t)$ represents the proportion of the population that eat and therefore survive the competition for food, with the factor $(1 + p_b - p_d)$

$$\begin{aligned}
Rep &\stackrel{\text{def}}{=} N1 \times N1 \\
N1 &\stackrel{\text{def}}{=} 1.eat : N2 + 1.\sqrt : 0 \\
F1 &\stackrel{\text{def}}{=} 1.\overline{eat} : F2 + 1.\sqrt : F2 \\
\\
N2 &\stackrel{\text{def}}{=} p_b.\sqrt : Rep + p_d.\sqrt : 0 + (1 - p_b - p_d).\sqrt : N1 \\
F2 &\stackrel{\text{def}}{=} 1.\sqrt : F1 \\
\\
Population &\stackrel{\text{def}}{=} N1\{n\} \times F1\{f\}[\{\sqrt\}]
\end{aligned}$$

Figure 2: Density dependence on deaths with non-prioritised communication

representing the increase in the population due to births and the decrease due to probabilistic death. Equation (2) can be rearranged to give

$$N_{t+1} = \frac{aN_t}{1 + cN_t}, \quad (3)$$

where $a = (1 + p_b - p_d)$ and $c = 1/f$. Equation 3 is the Beverton-Holt model [BH57], which was originally proposed as a model of salmon populations displaying density dependent birth; however we have derived this equation from a model that features density dependent death. Although this model has previously been described it is not commonly used for describing density dependent populations so it is interesting that this term has naturally arisen from our WSCCS model that explicitly includes the population interacting with a resource.

4 Summary

In this chapter we have introduced several different models that seek to capture realistic growth. The model in Fig. 1 and make use of functional probabilities to introduce density dependent behaviour into the population. From this model the resulting MFE is a discrete time version of the logistic growth model.

The fact that we have achieved the logistic equation from our model may seem to contradict the findings of Brännström and Sumpter [BS05] who did not find the logistic equation for any of their models. It should be noted that we are effectively choosing our probabilities using the same assumptions that lead to the logistic equation in the traditional population level models by making the probabilities linearly proportional to the population size; however, Brännström and Sumpter did try to get the logistic equation and

couldn't, so even though we have “forced it” it is still significant that we can get it. Other methods of choosing these probabilities, such as non-linear proportionality, would lead to different MFE. A major difference is that Brännström and Sumpter's site-based framework is inherently spatial whereas the models presented here assume random mixing of the population.

An alternative model was presented that made use of agents to represent food as a resource for the population. This mechanistic model more closely represent behaviour in a population with density dependence arising naturally from competition for resources. From this model we obtain the Beverton-Holt equation [BH57], which was proposed to describe the dynamics of fish populations.

Although the model that explicitly captures competition for resources has a greater degree of biological realism, it also introduces a greater degree of mathematical complexity into the MFE.

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