

OLM 9.6. The complex dynamics of *Tribolium castaneum*

The discussion of complex population dynamics arising from the interactions of individuals has been discussed to a limited extent in the book (yet, one of the more detailed discussions is the complex dynamics of the *Chlorella* - *Brachionus* system on p.192). This supplementary material presents a brief summary of theory pertaining to the causes of complex dynamics in models of population processes in discrete-time and explicit interactions. Then, relying on the 2005 monograph of Costantino et al., we demonstrate that the main characteristics of the complex dynamics exhibited by a single-species laboratory system can be predicted with a deterministic model. This is also an example of modelling regulation in structured populations, applying the knowledge obtained in ChStruct.

In the continuous-time version of the logistic model population density changes in infinitesimal (infinitely small) steps towards the equilibrium and cannot overshoot it. In fact this is the characteristic of continuous-time, single factor dynamics without delay. If any of these assumptions is not met the dynamics changes. For instance, seasonal reproduction may lead to overshooting the equilibrium, whereas trophic interactions may induce delayed effects on population growth. Discrete models of population growth or explicit models of population interactions (Ch9.3, p.191) may provide better approximation to these features and show complex population dynamics in many cases. If, in a discrete model, we assume that pgr is a monotonically decreasing function of population density, and choose the simplest of such functions, the linear one (in a way analogous to the continuous-time version of the logistic model; Eq. 6.4, p.124), we get the discrete logistic model:

$$N_{t+1} = \lambda_t N_t = (\lambda_0 - aN_t)N_t \quad (9.6.1)$$

The discrete logistic is well known for admitting cyclical and even chaotic dynamics as λ_0 takes higher values (May 1974; Otto and Day 2007); increasing λ_0 ultimately leads to the extinction of the population with increasing overshooting (Figure 9.6.1).

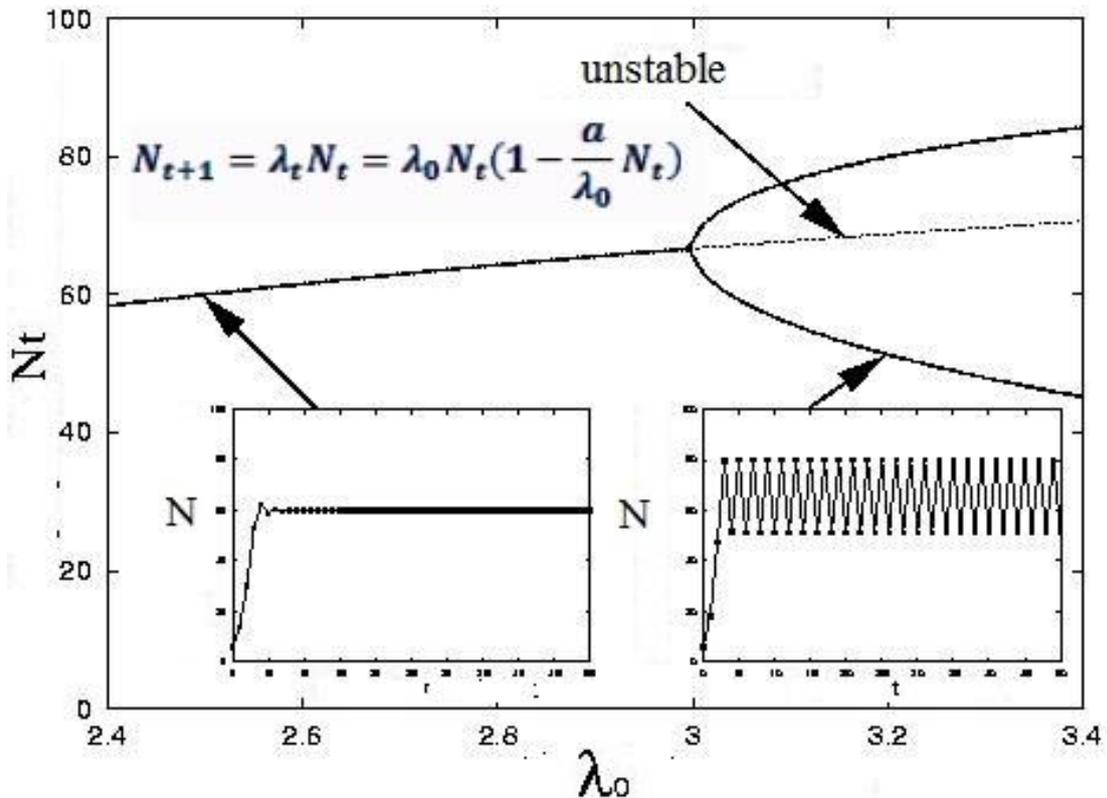


Figure 9.6.1: Behaviour of the discrete logistic model

Bifurcation diagram of the discrete naive logistic model showing the long-term dynamics of a system as a function of the model parameter λ_0 , whose value determines the type of the attractor. Continuous lines are stable, dotted lines are unstable equilibria. The insets show population densities in time for two typical cases. Left inset: $\lambda_0=2.5$, population density approaches a fixed point; right inset: $\lambda_0=3.2$, period 2 cycle. Points represent actual densities, the lines connecting them are drawn for visual clarity (Scheuring 2007).

The difference between the discrete- and the continuous-time logistic vanishes with the time step decreasing. During a short time step the abundance of the population changes very little, and the corresponding λ_0 is close to 1.0, where the discrete logistic model predicts monotonic dynamics as well.

The general conclusion of the discrete-time logistic model is that complex dynamics can be shown by simple systems in constant environments even without environmental stochasticity (May 1974). This can be empirically verified and explained by modelling the interactions between individuals of different developmental stage in a single population.

The deterministic population dynamical model of *Tribolium castaneum*

The flour beetle (*Tribolium castaneum*) is a classic subject of population dynamical lab experiments (Leslie and Park 1949), and it exhibits complex population dynamics (Figure 9.6.2) depending on the experimental conditions.

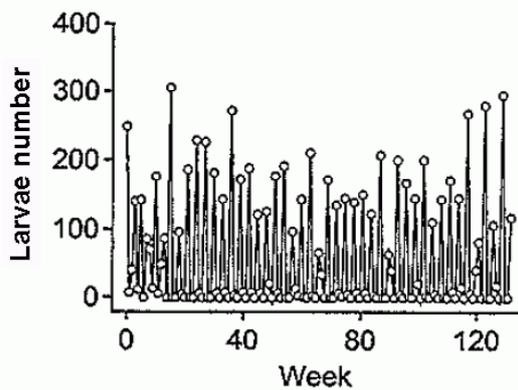


Figure 9.6.2: Population dynamics to be modelled
The abundance fluctuation of larvae in a laboratory population of flour beetle (*Tribolium castaneum*) (Costantino et al. 2005).

Flour beetles pass four stages during their life-cycle: egg, larva, pupa and adult. The growth of a *Tribolium* lab population is regulated by the density-dependent mortality rates of eggs and pupae induced by the cannibalism of larvae and adults. Thus, larvae and adults compose the critical stage groups (p.114) and their densities (L and A) are the regulating variables (Figure 9.6.3).

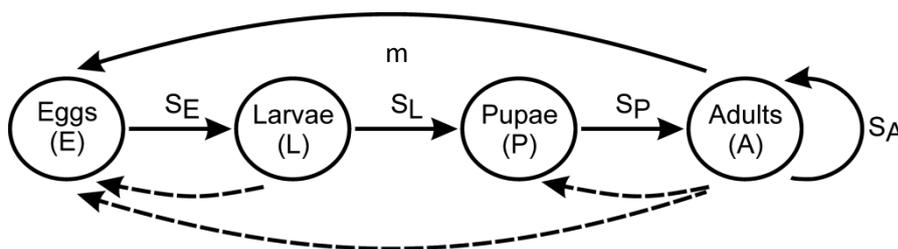


Figure 9.6.3: Life-cycle graph for the population dynamical model of the flour beetle.

Solid arrows are possible stage transitions with the rates of transitions (survival and effective fecundity) indicated on them; dashed arrows represent cannibalistic interactions. L, P and A denote the abundances of the corresponding life cycle stages.

The population is easy to count in all stages, except the egg stage, so the three remaining stages were followed and modelled in the study by Costantino et al. (2005). Censuses were made in two-week periods during which all the larvae have developed into pupae

and all the pupae have become mature adults. Using the life-cycle graph of Figure 9.6.3 one can construct the transition matrix from the stage transition probabilities, as shown in Ch4Struct:

$$\begin{array}{c} \text{L} \quad \text{P} \quad \text{A} \\ \text{L} \begin{pmatrix} 0 & 0 & bs_E \\ s_L & 0 & 0 \\ 0 & s_p & s_A \end{pmatrix} \end{array} \quad (9.6.2)$$

Unlike the PPMs discussed in Ch4Struct, this one has two elements which are not constant but depend on the size and the stage composition of the population, since the growth of the population cannot be exponential; in a closed container with 20 grams of flour it is necessarily regulated. The survival of pupae (s_p) and eggs (s_E) (i.e., the sensitive stage groups, p.112) are density dependent through the cannibalistic interactions from the critical stage groups (adults and larvae).

Thus, the dynamics of the three regularly censused stages are governed by the following equations:

$$L_{t+1} = mA_t s_E \quad (9.6.3)$$

$$P_{t+1} = L_t s_L \quad (9.6.4)$$

$$A_{t+1} = A_t s_A + P_t s_p \quad (9.6.5)$$

In the absence of adults the survival rate of the pupae is 1.0, and it decreases exponentially to 0.0 with the density of adults increasing:

$$s_p = e^{-A_t c_{pa}} \quad (9.6.6)$$

where c_{pa} is the Pupae by Adults coefficient of cannibalism specifying the number of pupae killed by a single adult in a time unit.

A similar formula applies to the survival of the eggs, which are cannibalized by larvae and adults as well, so their survival depends exponentially on the abundance of both larvae and adults, with the corresponding coefficients of cannibalism c_{el} and c_{ea} :

$$s_E = e^{-L_t c_{el} - A_t c_{ea}} \quad (9.6.7)$$

Cannibalism is the only regulating mechanism in the model, so that the effective fecundity (m) and the survival rates of larvae and adults (s_l and s_a) are constants (i.e., independent of population size).

Due to the negative feedback a stationary composition can be achieved only if there exists a p -state the leading eigenvalue of whose transition matrix is 1. Such a p -state is an equilibrium state, but not necessarily a stable one. If a stable equilibrium is not attained and the population does not go extinct, then the size and the composition of the population may oscillate or be chaotic. For cyclic dynamics the PPM pertaining to a complete cycle is the product of the PPMs of the time units within a complete cycle (cf. p.62). The leading eigenvalue of the product matrix will be 1. If the dynamics is chaotic, then it is the asymptotic growth rate determined by the “random” series of transition matrices along the chaotic attractor that will have a value of 1.

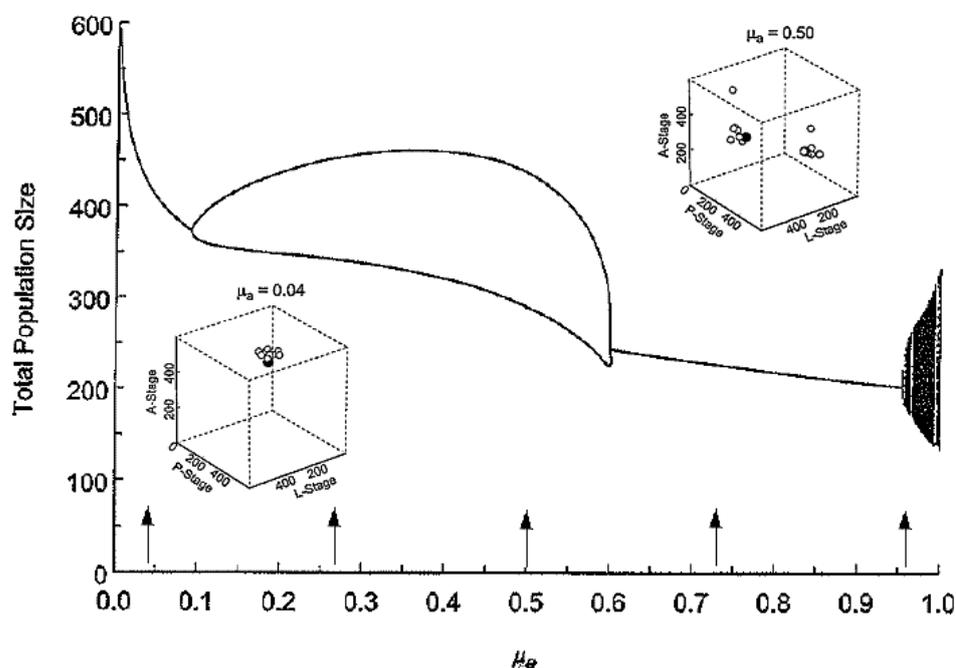


Figure 9.6.4 Behaviour of the flour beetle model

Bifurcation diagram of the deterministic model, with adult mortality ($\mu_A=1-s_A$) as the bifurcation parameter. The parameters of the model were estimated from data of the laboratory population: $m = 7.48$, $c_{ea}=0.0091$, $c_{pa}=0.0041$, $c_{el}=0.0120$, $s_L=0.7330$. Arrows indicate s_A values at which the predictions of the model were tested experimentally. The panels inserted show the experimental data (open circles) and the equilibrium values predicted by the model (black dots) at $s_A = 0.04$ and $s_A = 0.5$ after Costantino et. al. 2005.

Each of the three possible dynamical behaviours (stable fixed point, cycles, chaos) can be produced empirically, by changing the survival probability of the adult stage. Systematically changing the parameters of the model yields predictions for the expected asymptotic dynamics of the experimental population. For example, at low adult mortality ($\mu_A = 1-s_A$) we expect that increasing μ_A will decrease the equilibrium size of the population (Figure 9.6.4). Increasing μ_A further will result in periodic oscillations between two different population sizes. At even larger adult mortalities the system – surprisingly – admits a single stable equilibrium state again, and at very high values of μ_A we expect instability and quasiperiodic asymptotic dynamics. Since it is easy to decrease s_A by

removing a certain fraction of the adults at censuses, the predictions of the model could be validated experimentally at adult mortalities labelled with arrows on Figure 9.6.4. The population showed the dynamics predicted by the deterministic model.

Parameter estimations in this experimental situation can be accomplished using nonlinear regression, which is easiest to do if the fluctuations around the expected value follow the Gaussian distribution. Since this requirement was not met for the raw abundance data, (Dennis et al. 1995; Dennis et al. 2001) used logarithmic and square root transformed data as dependent variables.

The deterministic model presented here predicts the expected values of population size, not the actual numbers of individuals, and it could not reproduce all the qualitative features of the experimental system, because at the small abundances characteristic of the experiment the effect of demographic stochasticity was substantial. It was the stochastic version of the model that could account for this effect (Costantino et. al. 2005).

References

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