

Single generation cycles and delayed feedback cycles are not separate phenomena



T. Pfaff^a, A. Brechtel^a, B. Drossel^a, C. Guill^{b,*}

^a Institute of Condensed Matter Physics, Hochschulstraße 6, 64289 Darmstadt, Germany

^b Institute for Biodiversity and Ecosystem Dynamics, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

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ABSTRACT

We study a simple model for generation cycles, which are oscillations with a period of one or a few generation times of the species. The model is formulated in terms of a single delay-differential equation for the population density of an adult stage, with recruitment to the adult stage depending on the intensity of competition during the juvenile phase. This model is a simplified version of a group of models proposed by Gurney and Nisbet, who were the first to distinguish between single-generation cycles and delayed-feedback cycles. According to these authors, the two oscillation types are caused by different mechanisms and have periods in different intervals, which are one to two generation times for single-generation cycles and two to four generation times for delayed-feedback cycles. By abolishing the strict coupling between the maturation time and the time delay between competition and its effect on the population dynamics, we find that single-generation cycles and delayed-feedback cycles occur in the same model version, with a gradual transition between the two as the model parameters are varied over a sufficiently large range. Furthermore, cycle periods are not bounded to lie within single octaves. This implies that a clear distinction between different types of generation cycles is not possible. Cycles of all periods and even chaos can be generated by varying the parameters that determine the time during which individuals from different cohorts compete with each other. This suggests that life-cycle features in the juvenile stage and during the transition to the adult stage are important determinants of the dynamics of density limited populations.

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1. Introduction

Ecological models which involve the age or size structure of a population have been studied for almost one century now (Kermack and McKendrick, 1927). It is known that the detailed age or size structure of populations can have a major influence on the dynamics of ecological systems. Vital rates, such as growth rate, death rate and fecundity are in general dependent on the age of an individual (de Roos et al., 2003a). The structure of a population is important for effects such as generation cycles (Gurney and Nisbet, 1985; Knell, 1998; Ruxton and Gurney, 1992), juvenile bottle necks (Neill, 1988), life boat mechanisms (Bosch et al., 1988), host–parasite interaction (Godfray and Hassell, 1989; Gordon et al., 1991; Godfray, 1987) or emergent Allee effects (Courchamp et al., 1999; de Roos et al., 2003b), as well as for the effects of environ-

mental stochasticity (Bjørnstad et al., 2004). A population can either be structured by age or size. In the first case the development of an individual always follows the same time course, while in the second case development depends on food intake and metabolism. Mathematical models can capture the population structure in different ways, the three most prominent being stage structured models that divide a population into several stages in which the vital rates are uniform among all individuals (Gurney et al., 1980, 1983), matrix models that use discrete time steps and a matrix as the update function of a state vector (Caswell, 2001), and finally physiologically structured models that define the vital rates as functions of the continuous structure parameter (de Roos, 1996).

In this paper, we focus on generation cycles and investigate age-structured stage models. Generation cycles are a consequence of population structure that has been observed in a wide spectrum of field and laboratory populations. Even a single species in a constant laboratory environment can exhibit population density oscillations, as has been shown by Nicholson in the famous blow-fly experiments (Nicholson, 1954, 1957). A population of blow flies was kept under constant conditions with a constant daily amount of resource and it was observed that the population fluctuated with

* Corresponding author.

E-mail addresses: pfaff@fkp.tu-darmstadt.de (T. Pfaff), andreasbrechtel@googlemail.com (A. Brechtel), drossel@fkp.tu-darmstadt.de (B. Drossel), c.p.guill@uva.nl (C. Guill).

a period slightly larger than the generation time. Such an oscillation period of the order of the generation time is the indicator of generation cycles. In contrast to this, other types of population cycles, like predator–prey cycles, have larger periods depending on the life cycle of predator and prey (Murdoch et al., 2002). Generation cycles are frequently observed in natural populations (NERC, 2010) and they can occur in isolated species as well as in generalist species that are likely to have a stable resource basis, whereas predator–prey cycles are more common for specialist predators (Murdoch et al., 2002).

Gurney and Nisbet (Gurney and Nisbet, 1985; Gurney et al., 1983) investigated generation cycles by a comprehensive stage structured population model and identified mechanisms behind these cycles. The model was inspired by the laboratory situation of constant food supply. The population was divided into a juvenile and an adult stage. The cycles were found to be driven by density dependent competition of juveniles. According to the model, this competition can be due to four different effects: a direct death of juveniles (*Larval Death LD*), increased development time of juveniles (*Maturation Time MT*), decreased survival of pupae (*Pupal Survival PS*), or a decreased fecundity in the adult stage (*Adult Fecundity AF*). Gurney and Nisbet studied 4 different versions of their model, each of which contained one of these effects. They evaluated these models in the vicinity of the Hopf bifurcation that marks the onset of oscillations in parameter space. The main findings were that a competition that has a direct influence on the population dynamics (LD and MT) leads to cycles of 1–2 times the maturation time τ , while competition that has a delayed influence on the dynamics (PS and AF) leads to cycles of 2–4 times the maturation time. These two disjoint intervals of one octave led to a classification of generation cycles into *single generation cycles* for cycles with periods between τ and 2τ , and *delayed feedback cycles* for periods from 2τ to 4τ . This theory has been considered to be among the “most important advancements in the theory about the life history–population dynamic interplay” (de Roos et al., 2003a).

The findings of Gurney and Nisbet thus suggest that the oscillation period does not depend on all details of the model but essentially on the time period during which density-dependent competition affects a population. In this respect their results appear to be very general. On the other hand, their investigation is constrained by the strict coupling between the maturation time and the time delay between competition and its effect on the population. This delay is either zero (LD and MT models) or one generation (PS and AF models). However, the effect of competition is usually a combination of several of the above-mentioned phenomena. Additionally, competition can have effects over time periods other than zero and the maturation time, if, for instance, the food consumption of one cohort affects the food available to another cohort, or if the duration of the non-competing egg and pupal stages cannot be neglected.

In this paper, we present and investigate a model that fills these gaps. Our model considers the time period over which competition is felt by a cohort as a separate parameter, different from the maturation time, and variable within realistic limits. The model has the same general form as the PS model, but includes a simpler expression for the density-dependent probability to survive from birth into the adult stage. It contains the situations described by the PS and LD models as special cases, and we find in these cases a dynamical behavior similar to that of the LD and PS models, thus confirming again that the main determinant of the oscillation period is the relation between the maturation time and the time delay over which competition is felt. We corroborate this finding further by briefly studying two additional model versions that have a complexity intermediate between our simple model and the LD and PS models by Gurney and Nisbet and display a similar dynamical behavior. Due to the greater computer power and new

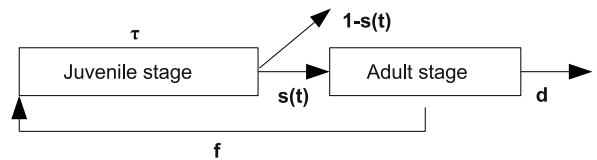


Fig. 1. Sketch of the model.

numerical solvers, we were able to investigate the original LD and PS models beyond the parameter range originally studied by Gurney and Nisbet, revealing oscillation periods much larger than four times the maturation time in the PS model and even chaos. We also study our model for general values of the competition time, confirming and complementing all these results. Typically, the periods of generation cycles cover a broad range of values and can be continuously changed by changing the competition time. It follows that periods do not lie in disjoint intervals of one octave, which makes a clear distinction between single-generation cycles and delayed-feedback cycles impossible. Furthermore, we find chaotic behavior in almost all model versions.

Our general model is described in detail in the next section. Section 3.1 presents the results for the two parameter sets that show a similar behavior to the LD and PS models by Gurney and Nisbet, which are also studied. Section 3.2 discusses the model dynamics for general values of the parameters. The conclusions are drawn in Section 4.

2. Model

The model is of the same form as the PS model by Gurney and Nisbet (1985). A sketch of the model is given in Fig. 1. The population is divided into two stages, the juvenile stage, which is not explicitly modeled, and the adult stage with a population density $A(t)$. Our fundamental equation for the population dynamics is

$$\frac{dA(t)}{dt} = s(t) \cdot f \cdot A(t - \tau) - d \cdot A(t). \tag{1}$$

New individuals are born with a rate f (“fecundity”) that is proportional to the number of adults. The newborn juveniles need a time τ to mature to adults. Only a proportion $s(t)$ of the juveniles survive maturation. The survival function $s(t)$ depends on competition for food during the competitive part of the juvenile stage. The adults die with a constant death rate d . As we show in Appendix A, the general model described by Eq. (1) is identical to the PS model by Gurney and Nisbet (1985). Other model versions by Gurney and Nisbet are obtained by introducing a density dependent death rate for the juvenile stage, or by making the maturation time τ or the fecundity f density dependent. These versions however are not considered in the following.

In the PS model, the survival function $s(t)$ depends via a double integral on the population densities between time $t - 2\tau$ and t . In general, the survival function is a decreasing function of the strength of competition that an individual has experienced during the juvenile stage, as indicated in Fig. 2(a). In order to make the model more transparent, while preserving its most important features, we use a simpler form for $s(t)$ with less parameters than in the PS model. We assume a linear dependence of the survival function $s(t)$ on the birth rate of competitors $C(t)$ (to be specified below) of the cohort that matures at time t , see also Fig. 2(a):

$$s(t) = \max \left(r_{\max} \cdot \left(1 - \frac{C(t)}{C_{\max}} \right), 0 \right). \tag{2}$$

The survival function is r_{\max} without competitors and 0 for $C(t) \geq C_{\max}$. A linear form is a good approximation if the system is close to a fixed point. In fact, we will see that even far away from the fixed

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