Sturdy cycles in the chaotic Tribolium castaneum data series

István Scheuringa,*, Gábor Domokosb

aDepartment of Plant Taxonomy and Ecology, Research Group of Ecology and Theoretical Biology, Eötvös University, The Hungarian Academy of Sciences, Pázmány Péter Sétány 1/c, H-1117 Budapest, Hungary
bDepartment of Mechanics, Materials and Structures, Center for Applied Mathematics and Computational Physics, Budapest University of Technology and Economics, H-1521 Budapest, Hungary

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Abstract

Because of the inherent discreteness of individuals, population dynamical models must be discrete variable systems. In case of strong nonlinearity, such systems interacting with noise can generate a great variety of patterns from nearly periodic behavior through complex combination of nearly periodic and chaotic patterns to noisy chaotic time series. The interaction of a population consisting of discrete individuals and demographic noise has been analyzed in laboratory population data Henson et al. (Science 294 (2001) 602; Proc. Roy. Soc. Ser. B 270 (2003) 1549). In this paper we point out that some of the cycles are fragile, i.e. they are sensitive to the discretization algorithm and to small variation of the model parameters, while others remain “sturdy” against the perturbations. We introduce a statistical algorithm to detect disjoint, nearly-periodic patterns in data series. We show that only the sturdy cycles of the discrete variable models appear in the data series significantly. Our analysis identified the quasiperiodic 11-cycle (emerging in the continuous model) to be present significantly only in one of the three experimental data series. Numerical simulations confirm that cycles can be detected only if noise is smaller than a certain critical level and population dynamics display the largest variety of nearly-periodic patterns if they are on the border of “grey” and “noisy” regions, defined in Domokos and Scheuring (J. Theor. Biol. 227 (2004) 535).

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1. Introduction

Ever since the classical paper by May (1976) appeared, there has been considerable interest in the investigation of chaotic population dynamics. Recent results both in ecology (Henson et al., 2001, 2003; Domokos and Scheuring, 2002; King et al., 2004; Domokos and Scheuring, 2004) and in mathematics (Domokos and Szász, 2003) indicate that due to the extreme sensitivity of chaotic systems, there might be striking differences between predictions based on discrete models applying integers versus continuous models applying continuous variables for population densities.

Continuous models are widespread, however, their validity in case of chaotic dynamics was first questioned in Henson et al. (2001). Continuous models of chaotic population dynamics predict typically aperiodic, random-like fluctuations of population densities. Discrete models, due to the finite number of states, contain always a finite number of finite cycles which can be regarded as stable, in the sense that they are reliably reproduced in each computation. Apparently, neither the purely deterministic discrete (DD) nor the deterministic continuous model offers a full and satisfactory description of the experimental data. Henson et al. (2001, 2003) observed that experimental data of the Tribolium castaneum contained some nearly-periodic
patterns, similar to some of the cycles contained in the 
 discretized version of their continuous population 
dynamical model. This model, named as LPA, is a three 
dimensional nonlinear map describing the dynamics of 
the flour beetle in the larvae (L), pupae (P) and adult (A) 
stages. The authors observed that by adding random 
noise to the discrete LPA model its predictive power was 
radically increased, the time series became more similar 
to experimental data.

These observations prompted a brief discussion on the 
mathematical background (Domokos and Scheuring, 
2002; King et al., 2002) and later a systematic analysis in 
(Domokos and Scheuring, 2004) of discrete (D) and 
continuous (C) population models, both their determi-
nistic (DD, DC) and noisy (ND, NC) versions. One key 
observation in (Domokos and Scheuring, 2002, 2004) is 
that the noise amplitude $\sigma$ can be regarded as a 
transition parameter (or “homotopy parameter”) be-
tween discrete models and their continuous counter-
parts. This heuristic idea is based on rigorous 
mathematical results on expanding maps (cf. Kifer, 
1997; Domokos and Szász, 2003). After defining a 
suitable distance $\delta(X,Y)$ between two noisy models 
$X(\sigma)$ and $Y(\sigma)$ (based on the difference between the 
statistical behavior associated with them), Domokos 
and Scheuring (2004) describes how the $\delta(X(\sigma), Y(\sigma)) = 
\delta(\sigma)$ function behaves typically between different type 
(DD, ND, DC, NC) models. From our current point of 
view, the most interesting relationship is $\delta(ND, NC)$, 
displayed as a schematic plot in Fig. 1 in case of chaotic 
dynamics. The investigations in Domokos and Scheur-
ing (2004) (partly illustrated in Fig. 1) revealed the 
following conclusions:

1. Since individuals are discrete entities, the model 
closest to the physical population is generally a 
discrete model with a certain amount of noise 
originating from the demographic and environmental 
ostochasticity (i.e. a suitable ND model). While it is 
very hard to estimate the noise parameter $\sigma$ 
(originating from biological and environmental fluctua-
tions), we believe that real populations are 
generally in the “noisy zone”.

2. If $\sigma$ is very small (“clear zone”) and the system is 
chaotic, then the difference between the prediction of 
the noisy discrete (ND) and noisy continuous (NC) 
models is large, so NC models are not applicable in 
this range.

3. If $\sigma$ is very large (“noisy zone”), then the statistical 
behavior predicted by NC and ND models practically 
coincide, so NC models can be applied in this range.

4. For a relatively large, intermediate range of $\sigma$ (“grey 
zone”) neither of the above simple rules can be 

Comparing this theoretical predictions with experi-
mental data series for the $T. castaneum$ and computed 
data from he LPA model cf. (Henson et al., 2001) shows 
that the experimentally observed population is on the 
border of the noisy and the grey zone (Domokos and Scheuring, 
2004). In recent papers (Henson et al., 
2003; King et al., 2004) the authors study the time 
series associated with the discrete and continuous 
LPA model and compare them with the experimental 
data. In the time series from the experiments they 
identify periodic patterns which correspond partly to 
cycles of the discrete model, partly to an unstable, 
quasi-periodic attractor in the continuous model. The 
same patterns are detected in the time series produced by 
the ND model. Their conclusion is that “it is the 
transient but recurrent cyclic patterns generated by 
chaotic attractors and their discrete state analogies, 
woven together by stochasticity, that distinguish 
chaos as manifested in noisy, discrete state population 
systems” (King et al., 2004). This conclusion 
implies that both the continuous and the discrete models 
are needed to understand the behavior of a real 

Although these conclusions are certainly interesting, 
some questions remain open. The most important ones 
are associated with the applied aspects, i.e. how to find a 
proper model with reliable predictions for a given 
population? Assuming that an adequate continuous 
model is available, the following natural questions may 
be asked:

(a) How to find the proper discrete model, i.e. how to 
choose between several possible rounding algorithms?

(b) How to identify those cycles in the discrete model 
which will persist as nearly-periodic patterns in the 
presence of noise?

(c) How to identify the nearly periodic patterns in 
experimental or model-predicted time series?
In this paper we address these issues. In particular, Section 2 describes the behavior of cycles in DD models. Based on simple examples we will show that discrete cycles may or may not be sturdy with respect to small perturbations of the model parameters and different choices of the rounding algorithm (questions (a), (b)). From the point of view of applications the sturdy DD cycles are important, because these are the ones which we expect to see as recurrent nearly-identical patterns in ND models, in particular if the noise level is in the grey zone. Section 3 describes a systematic statistical approach to the identification of nearly-periodic patterns (question (c)) in noisy, discrete systems which can be either ND models or experimental data sets. Section 4 is devoted to the discussion of the results on the LPA models and on experimental data, obtained by the aforementioned statistical method. On one hand, these findings confirm some of the observations in (Henson et al., 2001, 2003; Domokos and Scheuring, 2002; King et al., 2004; Domokos and Scheuring, 2004) however, they also offer new clues.

We will point out that whenever “mixing” of discrete and continuous model occurs, it can be observed on the border of the grey and noisy zones. We discuss and summarize our results in Section 5.

2. Cycles in deterministic discrete (DD) models

2.1. Discretization algorithms

We assume that the continuous model is given by an iterated map of the form
\[ x_{i+1} = f(x_i), \]  
where \( x_i \) denotes the number of individuals (size of the population). Such models describe population dynamics in discrete time, however, the size of the population \( x_i \) can be any real number. When dealing with DD models, only integer values of the population size \( x_i \) are admitted (which will be denoted by \( X_i \)), so \( f \) needs to be discretized and this can be performed in various ways. The function \( \text{int}(x) \) will describe the largest integer that is smaller than \( x \). Throughout the paper we will refer to the following discretization strategies:

1. **Floor model**: \( X_{i+1} = \text{floor}(f(X_i)) = \text{int}(f(X_i)) \).
2. **Ceiling model**: \( X_{i+1} = \text{ceiling}(f(X_i)) = \text{int}(f(X_i)) + 1 \).
3. **Round model**: \( X_{i+1} = \text{floor}(f(X_i)) \) if \( f(X_i) - \text{int}(f(X_i)) < 0.5 \), otherwise \( X_{i+1} = \text{ceiling}(f(X_i)) \).

One could also use a probabilistic discretization algorithm where the probability \( p_1 \) of rounding down is given by \( p_1 = (x - \text{int}(x)) \) (so the probability of rounding up is of course \( p_2 = (1 - x + \text{int}(x)) \) and \( p_1 + p_2 = 1 \)). Although this latter method appears to be rather natural, it is rarely applied. Discretized models produced by this algorithm would fall even without added environmental noise into the “noisy, discrete” (ND) category, defined in (Domokos and Scheuring, 2004). In previous works on discrete population dynamics (Henson et al., 2001, 2003; Domokos and Scheuring, 2002; King et al., 2004; Domokos and Scheuring, 2004) the Floor and Round models have been investigated.

2.2. Dynamics of the discrete map: sturdy and fragile cycles

After one of the listed three discretizations has been performed, the model is discrete and deterministic, i.e., it has a finite number of different states, each corresponding to possible (integer) values of the population’s size. The dynamical behavior of such a finite state model may be best visualized via an oriented graph, the vertices of which correspond to the different population sizes, the oriented edges describe the action of the discrete map. Each vertex has exactly one outgoing edge (defined by the map) and zero or more incoming edges. Such a finite, oriented graph has necessarily a finite number of cycles. (One, trivial example is a tree graph with a single root, edges oriented towards the root. Such a graph has one cycle of length one.) The structure of the graph (i.e., number and length of cycles and paths leading into the cycles) is characteristic for the dynamical behavior of the modeled population. For example, the above mentioned tree graph describes a population that will have constant size after a finite number of time-steps, regardless of the initial (starting) size.

We will investigate the simple example of the well-known logistic map
\[ x_{i+1} = f_{\text{logistic}}(x_i) = \frac{\mu}{N} x_i(N - x_i) \]  
and its discretized floor, ceiling, and round versions. Our goal is to show how the structure of the graph (and thus the global dynamics) depends on the maximal size \( N \) of the population (carrying capacity of the environment), the discretization strategy and the control parameter \( \mu \). The map (2) is known to be chaotic for a range of the control parameter \( \mu \), in particular, for \( \mu = 4 \) the statistical behavior is characterized by a unique, absolutely continuous probability density function and no stable periodic orbit exists. One would expect that as \( N \) is increased, the statistical density associated with the DD model converges to the continuous function. However, this is not the case. As we pointed out before the discrete model always possesses a finite number of (stable) cycles. For discretized ergodic maps, little is known about the length and distribution of these cycles which appear in rather irregular patterns as \( N \) is varied.

Random map models and computer simulations indicate that the cycle length of the logistic map is characteristic for the dynamical behavior of the DD models, in particular if the noise level is in the grey zone. From the point of view of applications the sturdy DD cycles are important, because these are the ones which we expect to see as recurrent nearly-identical patterns in ND models, in particular if the noise level is in the grey zone.
implies the presence of very few (≈ log N) cycles. Although these rules seem to be correct on average for discrete maps, large irregular fluctuations can be observed. Since the statistical behavior of the discrete map is mainly determined by the cycles, it is hard to predict anything definite.

Although there is no mathematical evidence at hand, one can observe that some of these cycles appear to be rather sturdy, while others are extremely fragile with respect to variations of the control parameter and rounding algorithm. On the other hand, changing the population maximum N almost always leads to a radical transformation of the cycle pattern. Fig. 2 shows the complete graph associated with different versions of the logistic map (2). The columns correspond to different values of the control parameter μ, the rows show different discretization strategies. The first three rows correspond to N = 22, the last row to N = 21. As we can observe, the 3-cycle ≈ [4] → [13] → [21] and the fixed point at [0] proves to be sturdy with respect to variation of μ and the discretization strategy, other cycles appear only locally. The same pattern can be clearly observed for much larger values of N and for more complicated, higher dimensional maps as well;

![Fig. 2. The complete graph appearing in the floor-, ceiling and round-discretization of the logistic map at N = 22 and 21. Observe sturdy (grey and bold) and fragile cycles (bold).](image-url)
some cycles are sturdy, others are rather fragile. These concepts could be made more precise by introducing suitable norms both for the parameters and the discrete trajectory, however, rigorous analysis is beyond the scope of the present paper.

It is well understood mathematically (Domokos and Szász, 2003; Kifer, 1997) that certain random perturbations added to the DD map not only destroy the just described exotic cyclic structure but also restore the original invariant density function. From the point of view of biology the crucial question is whether the existing environmental and biological noise have this view of biology the crucial question is whether the original invariant density function. From the point of described exotic cyclic structure but also restore the Sza´ sz, 2003; Kifer, 1997) that certain random perturba-
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patterns
sequences is

\[ X^{(p)}(t) = (x(t), x(t+1), \ldots, x(t+p-1)) \]

and the sample sequence \( S^{(p)} = (s(0), s(1), \ldots, s(p-1)) \) with period \( p \) (that is \( s(p) = s(0) \)), as

\[
D(X^{(p)}(t), S^{(p)}) = \sum_{j=1}^{d} \left( \frac{1}{p} \left[ \frac{1}{2} \sqrt{ \sum_{i=0}^{p-1} [x_j(i + t) - s_j(i)]^2} \right]^2 \right),
\]

where \( x_j(i + t) \) and \( s_j(i) \) are the \( j \)-th coordinate of the data and sample vectors in the \( d \)-dimensional space. The expression in the big parenthesis measures the relative Euclidean distance of sequences \( \{x_j(i + t)\}_{i=0}^{p-1} \) and \( \{s_j(i)\}_{i=0}^{p-1} \) in the \( j \)-th subspace. (The absolute Euclidean distance of the sequences is divided by the period \( p \) of the sample. It is also divided by the average obtained from the total lengths of data and the total lengths of the sample sequences in the \( j \)-th subspace.) The total distance of \( X^{(p)}(t) \) and \( S^{(p)} \) is the sum of these subspace distances. A related distance function was defined for similar analysis earlier (King et al., 2004), however application of relative distance provides direct comparison between the different pieces of sequences.

The distance \( D(X^{(p)}(t), S^{(p)}) \) can be computed for every \( t = 1, 2, \ldots, T - p + 1 \), where \( T \) is the length of the data series. A sequence \( X^{(p)}(t) \) is said to be \( \varepsilon \)-similar to \( S^{(p)} \) at \( t^* \) if \( D(X^{(p)}(t^*), S^{(p)}) < \varepsilon \), where \( \varepsilon \) is set to be a small positive number. The sum of events where the data sequence is \( \varepsilon \)-similar to the sample is denoted by \( N^{(p)}(\varepsilon) \). As we have seen in the previous section, different cyclic patterns can be found in the same DD model, so the above mentioned procedure has to repeated for all \( S^{(p)} \) sample sequences with period \( p \), emerging in the studied DD-model. Consequently, it might occur that a piece of data sequence is assigned to more than one sample sequence, that is, \( X^{(p)}(t_1) \) is \( \varepsilon \)-similar to \( S^{(p)} \), and \( X^{(p)}(t_2) \) is \( \varepsilon \)-similar to \( S^{(p)} \), and \( X^{(p)}(t_1) \cap X^{(p)}(t_2) \neq 0 \). Then the assignment is skipped which is valid only at the higher \( \varepsilon \) level. For example, assuming \( X^{(p)}(t_1) \cap X^{(p)}(t_2) \neq 0 \) and \( \varepsilon > D(X^{(p)}(t_1), S^{(p)}) \geq D(X^{(p)}(t_2), S^{(p)}) \), then \( X^{(p)}(t_2) \) is \( \varepsilon \)-similar to \( S^{(p)} \), but \( X^{(p)}(t_1) \) is not considered to be \( \varepsilon \)-similar to \( S^{(p)} \). (Naturally, the same procedure is applied if \( S^{(p)} = S^{(p)} \).) After excluding these overlaps there will be \( N^{(p)}(\varepsilon) \) number of \( \varepsilon \)-similar sequences in the data series for every \( S^{(p)} \). In this analysis, at any \( \varepsilon \) level, one data point is assigned either to one (and only one) sample sequence or to no sample sequence at all.

To determine whether the presence of \( \varepsilon \)-similar patterns are significant in the \( T \)-length sequence, we use a standard randomization test (Manly, 1991). We produce \( K - 1 \) random permutations of the original data sequence, and compute \( N^{(p)}(\varepsilon) \) again for every

3. A systematic approach to detecting nearly-periodic patterns

It is a common task in many different fields to seek intermittently periodic patterns, trends or anomalies in data series. Applications include in stock data, alarms of telecommunications and event logs of computer networks (Han et al., 1998, 1999; Ozden et al., 1998). The general aim is to find characteristic patterns with unknown periods by an effective algorithm in these huge data series (Han et al., 1999; Ma and Hellerstein, 2001).

Although we are also looking for nearly-periodic patterns, the emphasis is completely different. Our main question is, whether there exist patterns in a given data series (produced either by experiments or by numerical simulation of the model with added noise) which are significantly similar to one of the periodic cycles present in the associated deterministic DD model. Thus, in contrast to the aforementioned applications, we are looking for a priori given sample patterns, and the numerical efficiency of analysis is not a central issue because the biological time series are relatively short.
permuted case. If \( N_{\text{perm}}^{(p)}(e)<N_{1}^{(p)}(e) \) for every \( K-1 \) permuted sequence, then the \( \varepsilon \)-similar patterns are considered to be significantly present in the original sequence at \( 1/K \) significance level, in the opposite case the result is said to be non-significant at this level. We set henceforth \( K = 999 \), i.e., the significance level is 0.001. (Because of the small statistical strength of the randomization tests we use a rather low significance level.)

4. Nearly-periodic patterns in the noisy LPA models and the \( T. \) castaneum data series

4.1. Introduction of the LPA model

There exist only a very limited number of field and experimental data series in ecology which are of sufficiently high quality to check theoretical hypothesis about the existence sturdy nearly-periodic patterns present in Nature. The \( T. \) castaneum data series from the experiments of Costantino et his co-workers (Costantino et al., 1997; King et al., 2004) are certainly among these few, making theoretical predictions and experimental data comparable. They grew 24 cultures of flour beetles for more than 8 years in a controlled environment. Knowing the life-history of this species they suggested the following deterministic map for the dynamics of the beetle \( Tribolium \) (Costantino et al., 1997)

\[
\begin{aligned}
L_t &= bA_{t-1} \exp(-\varphi A_{t-1} - \varphi L_{t-1}), \\
P_t &= (1-\mu_t)L_{t-1}, \\
A_t &= P_{t-1} \exp(-\varphi A_{t-1}) + (1-\mu_t)A_{t-1},
\end{aligned}
\]  

(4)

where \( L_t \) denotes the number of larvae, \( P_t \) denotes the number of pupae and \( A_t \) denotes the number of adults at time \( t \). The unit of time is 2 weeks to fit the model to the experiment, \( b \) is the average number of larvae recruited per adult per unit time. Eggs are eaten by adults and larvae while pupae are eaten by adults at the same time, so exponentials represent the fractions of individuals surviving this cannibalism within the unit time with coefficients \( c_{\text{ea}}/V \), \( c_{\text{el}}/V \) and \( c_{\text{pa}}/V \), respectively. \( V \) denotes the size of habitat, the unit of which is 20 g flour, the amount of medium used in the laboratory experiments. This DC (deterministic-continuous) version of the LPA model describes successfully a wide variety of nonlinear phenomena, including chaos observed in laboratory data series (Costantino et al., 1997; Cushing et al., 2001). However, there are weaknesses of this model: the noise present in all populations is neglected. Thus, rather some NC-LPA models including environmental (Costantino et al., 1997) and/or demographic noise (Dennis et al., 2001) have to be studied. Even more elaborate ND-LPA models take the role of discreteness of variables \( L \), \( P \) and \( A \) into account as well (Henson et al., 2001, 2003; King et al., 2004; Domokos and Scheuring, 2004). Assuming that the main source of stochasticity is demographic noise, the generally used ND-LPA equations are

\[
\begin{aligned}
L_t &= \text{discr} \left( \sqrt{bA_{t-1}} \exp(-\varphi A_{t-1} - \varphi L_{t-1}) + E_{1}\right)^2, \\
P_t &= \text{discr} \left( \sqrt{(1-\mu_t)L_{t-1} + E_{2}} \right)^2, \\
A_t &= \text{discr} \left[ P_{t-1} \exp(-\varphi A_{t-1}) \right] + \text{discr} [(1-\mu_t)A_{t-1}],
\end{aligned}
\]

(5)

where \( \text{discr}[\cdot] \) denotes an operation creating integer values on the right side of the map. This could be any of the three alternative algorithms described in Section 2.1, however because of direct manipulation of adult numbers in the experiment the round operation is the most adequate in the last equation. The symbols \( E_{1t}, E_{2t} \) denote normal random variables with mean zero and variance–covariance matrix \( \Theta \) (Henson et al., 2001, 2003; King et al., 2004).

The adult mortality rate \( \mu_a \) is experimentally set to be 0.96. The parameter \( c_{\text{pa}} \) was manipulated to be 0.00, 0.05, 0.10, 0.25, 0.35, 0.50, 1.00 in the different treatments. It is important to note that \( \mu_a \) and \( c_{\text{pa}} \) are set by adding or removing adults in the experimental protocol (Costantino et al., 1997), thus any of the described discretization methods can be only regarded as valid as far as it agrees with the experimental procedures. The other parameters were estimated from the first 80 weeks of data: \( b = 10.45, \mu_t = 0.2000, c_{\text{ea}} = 0.1310 \) and \( c_{\text{el}} = 0.01731 \) (Dennis et al., 2001). The variance \( \Theta_{11} \) and \( \Theta_{22} \) of \( E_{1t} \) and \( E_{2t} \) was estimated as 2.332 and 0.2374 respectively and \( \Theta_{12} = \Theta_{21} \approx 0 \) (Dennis et al., 2001). The experiments were initiated with 250 L-stage, 5 P-stage and 100 A-stage individuals, and the numbers of L, P and A stage animals were counted biweekly. This experiment resulted in three data series containing more than 200 points for every treatment. It was demonstrated that the data series behaves chaotically under the \( c_{\text{pa}} = 0.35 \) treatment in concordance with the dynamics of the DC-LPA model (Costantino et al., 1997; Dennis et al., 2001). Thus, our analysis utilize data series under this treatment, as other related studies have done earlier (Henson et al., 2003; King et al., 2004). The only difference is that we analyzed all the three time series, while earlier works used only one replicate at this treatment.

4.2. Qualitatively different cycles in different DD-LPA models

In this section, we will provide a complete list of all qualitatively different cycles appearing in the
deterministic, discretized LPA modes. As we mentioned beforehand, two of the different discretization algorithms, which we denote by 3a and one 1-cycle at the given parameter values. Two among the three 6-cycles are very similar to each other, so we can consider them as one type (6a), the third will be referred to as 6b. The round-LPA contains six different 6-cycles, one 8- and one 3-cycle, the latter will be denoted by 3b. Similarly to the floor-LPA model, the six different 6-cycles form two groups. Five cycles are very similar not only to each other, but also to the 6a type of the floor model, so we denote them by the same symbol. The sixth cycle is extremely close to the 6b type of the floor model, so we denote it by the same symbol. So we have one 1-cycle (unstable fixed point), one 3-cycle (3a) and two qualitatively different 6-cycles (6a and 6b) in the floor-LPA and one 3-cycle, two 6-cycles (6a and 6b) and one 8-cycle in the round-LPA model (Fig. 3). We remark that the 6b-cycle is very similar to the duplicated 3b-cycle of the round-LPA model. This reduces the number of effectively different cycles in the two discretization methods to 6: the 1-cycle, the 3a- and 3b-cycles, the 6a- and 6b-cycles and the 8-cycle. Similar classification is used by King et al. (2004), here we only refined it by compartmentalizing the 3b-cycle and 6b-cycles into different classes, and we classified the floor model in a similar way.

In Fig. 3 we can observe that the 1-cycle, the 3a-cycle and the 8-cycle are fragile, since their presence depends on the discretization procedure. The remaining three cycles (3b, 6a, 6b) are present in both (Floor and Round) models, so they appear to be sturdy. (Although 3b only appears in the Round model, it is extremely close to the first 3 elements of the sturdy 6b, so it can also be regarded as sturdy.) To check further the sturdiness of the latter three cycles we varied the estimated dynamical parameters (sturdiness of the latter three cycles we varied the parameters (Cushing et al., 2001; King et al., 2004). Unless the experimental protocol is exactly known there are no strong biological or mathematical reasons to apply one or the other discretization procedure and, as pointed out in Section 2.1, other methods can be defined as well. As we pointed out in Section 2.2, the applicability of models depend on the robustness of the emerging cycles against the structural and parameter perturbations.

Below we will list all co-existing cycles belonging to two different DD-LPA models (floor and round, differing in the discretization algorithm) and we will identify the sturdy ones. The floor-LPA has three different 6-cycles, one 3-cycle (which will be denoted by 3a) and one 1-cycle at the given parameter values. Two among the three 6-cycles are very similar to each other, so we can consider them as one type (6a), the third will be referred to as 6b. The round-LPA contains six different 6-cycles, one 8- and one 3-cycle, the latter will be denoted by 3b. Similarly to the floor-LPA model, the six different 6-cycles form two groups. Five cycles are very similar not only to each other, but also to the 6a type of the floor model, so we denote them by the same symbol. The sixth cycle is extremely close to the 6b type of the floor model, so we denote it by the same symbol. So we have one 1-cycle (unstable fixed point), one 3-cycle (3a) and two qualitatively different 6-cycles (6a and 6b) in the floor-LPA and one 3-cycle, two 6-cycles (6a and 6b) and one 8-cycle in the round-LPA model (Fig. 3). We remark that the 6b-cycle is very similar to the duplicated 3b-cycle of the round-LPA model. This reduces the number of effectively different cycles in the two discretization methods to 6: the 1-cycle, the 3a- and 3b-cycles, the 6a- and 6b-cycles and the 8-cycle. Similar classification is used by King et al. (2004), here we only refined it by compartmentalizing the 3b-cycle and 6b-cycles into different classes, and we classified the floor model in a similar way.

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Although the DC-LPA model is chaotic at \( c_{pl} = 0.35 \), it has an Arnold tongue with a 11-cycle at the estimated parameters (Cushing et al., 2001; King et al., 2004). Consequently, nearly-periodic patterns of length 11 are present in finite regions of the time series of the DC-LPA model (Fig. 4). We expect similar patterns in the noisy NC-LPA model, for moderate noise levels. This pattern is not exhibited in the DD-LPA models, however as the noise level increases, we enter the grey zone and the ND-LPA model becomes more and more similar to NC-LPA model (cf. Fig. 1, for more details see Domokos and Scheuring, 2004)), thus the emergence of the 11-cycle in ND-LPA models can be also expected at some noise level in the grey zone. (The noise should be sufficiently large to make the discrete model appear similar to the continuous, however, sufficiently small to leave the 11-patterns partially intact.) As a consequence, together with the 6 cycles appearing in the DD models we also have to look for the 11-cycle of the DC model in the studied data series. Besides the experimental data, we generated data series from the model equations (3), using the estimated parameters.

4.3. Identification of nearly-periodic patterns in experimental and simulated data series

In this section, we will apply the statistical technique of Section 3 to identify nearly-periodic patterns belonging to the cycles listed in Section 4.2. According to the method introduced in Section 3, we measured the number \( N_{\text{pl}}(\epsilon) \) of hits for nearly-periodic patterns in the real and simulated data series for all the 7 qualitatively different cycles (6 of them present in the deterministic floor-LPA and round-LPA models plus the 11-cycle of the NC-LPA).

Fig. 5 depicts the number \( N_{\text{pl}}(\epsilon) \) of non-overlapping segments of sequences similar to one of the 7 sample cycles as functions of the similarity level \( \epsilon \). Significant appearance of the observed patterns is denoted by a plus mark in the center. The 1-cycle of the floor-model was never observed. It can be seen from Fig. 5 that none of the 7 cycles appear exactly in the data series, the best fitting patterns are at \( \approx 0.05 \) relative distance from the exact cycles. The fragile cycles either do not appear at all, or rather sparsely, such as the 3a-cycle in the Floor and the 8-cycle of the Round models. These cycles are generally present in a non-significant manner in the experimental data (except the 3a-cycle in the second data series at some \( \epsilon \) level) (Figs. 5 and 6).

The first and the second data series behave very similarly: the 6a-cycle like patterns dominate the data followed by low numbers of the other cycles. There are
less 6a-cycles and more 6b-cycles in the third data series. Since the 6b-cycle is very similar to two subsequent 3b-cycles (Fig. 3), it is clear that the 3b-cycle like patterns can appear in the same region in the Round model analysis where the 6b-cycle is detected in the floor model. Since longer cycles are destroyed by noise more effectively, the 3b-cycle patterns can be found with smaller distances at the same region of the sequence where the similar 6b-cycle would be detected only at higher $\varepsilon$ level. This is the reason why the 3b-cycle is more pronounced in the Round-model analysis than in the floor-model one. It is interesting to observe that the 11-cycle pattern is present only in the second data series in a significant manner. We remark that earlier analysis (Henson et al., 2003; King et al., 2004) applied only this second data series.
Fig. 4. 11-cycle patterns in the data generated by the DC-LPA model: (a) The number of larvae as function of time. The points and intervals indicate positions in the data where the 11-cycle is detected according to the distance function (3) at $\epsilon = 0.125$. (b) The 11-cycle of Eq. (5) in the L, P, A space at parameters defined in the text.

Fig. 5. The number $N_C(\epsilon)$ of non-overlapping intervals similar to one of the cycles of the floor- (left column) and the round-model (right column) as functions of similarity level $\epsilon$. Circles denote the 6a-cycle, squares the 3a- or 3b-cycle respectively, diamond is the mark of 11-cycle, pentagons denote the 6b-cycle and triangles mean the 8-cycle in the round model. Significant appearance of the patterns is denoted by the plus mark. Some marks are shifted along the $y$-axis for the better visualization.
Naturally, there is no a priori given level for the similarity measure $\varepsilon$. Too low $\varepsilon$ excludes all correspondence, while too high $\varepsilon$ level indicates poor correspondence between the data and sample sequence. However, the number of hits saturates at about $0.1$–$0.13$ for all data series (Fig. 5), which suggests to choose for practical purposes $\varepsilon$ from this interval.

We generated data series by the noisy floor-LPA and round-LPA models at different noise levels, while the other parameters took the estimated values. Omitting the initial transients we recorded 213 time-steps. (In order to analyze longer time series we included the initial transient in the experimental data. Since the transient is short (about ten time steps) to include or omit the transition causes only small difference in the analysis.) The same pattern-detecting analysis was applied as before. If noise was set to be weak (i.e., the model was in the “clear zone”), then the 6a-cycle dominates the series (Fig. 7, $\alpha = 0.1$). The other cycles emerge in the “grey zone”, similarly as we observed in the experimental data (Fig. 7, $\alpha = 0.4, 1$). Few patterns, (typically the 11-cycle) are detected in the “noisy zone” only at high levels of epsilon (Fig. 7, $\alpha = 3$).

5. Summary and conclusions

Since experimental and field population data are generally missing or too weak to confirm a given model with its details, population dynamical equations are based often on somewhat arbitrary assumptions. One strong counter-example is the T. castaneum, where the family of LPA models of population dynamics have been widely tested by experimental data (Costantino et al., 1997; Dennis et al., 2001; Henson et al., 2001). The most recent question in this field is whether the deterministic or noisy continuous-models (DC, NC) or their corresponding discrete-state (DD, ND) counterparts provide better fit to the population data (Henson et al., 2001; Domokos and Scheuring, 2004). Ambiguity in the discretization procedure makes the situation more complex.

In this paper we investigated two types of DD models, the floor-LPA, and the round-LPA, which have been applied earlier as well.

Recent studies argue that if population is chaotic then characteristics of DC- and DD-LPA-models emerge in mixed manner in the data: there are patterns in the data similar to both the 11-cycle of the DC and to the cycles of the DD model. Consequently, for the mathematical description of the dynamics both type of models have to be considered (Henson et al., 2003; King et al., 2004).

In this paper we re-analyzed the experimental data with a different method. We looked for disjoint intervals being similar to one of the cyclic patterns present in the Floor-LPA, Round-LPA and the DC-LPA models. We checked the significance of the results at different similarity levels. The same analysis has been carried out on the data generated by the noisy Floor-LPA and Round-LPA models at different noise levels.

Since real population dynamical processes are built up by complex stochastic steps (Dennis et al., 2001), any discretized, noisy LPA model is rough and contains more-or-less arbitrary approximations. For example, how to discretize the continuous LPA is such an arbitrary step. If small structural and parameter changes cause only small differences in the behavior of these models, they can be considered as equivalently good and robust approximations of the real processes. This is the case when the dynamics of DC models (DC-LPA in our case) is regular. However, if the DC model is chaotic, then the DD models are structurally unstable: any small perturbation in the structure and parameters of the model can generate new and annihilate existing cycles (Domokos and Scheuring, 2002; Domokos and Szász, 2003). However, there are “sturdy” cycles in the DD models as well, which resist small perturbations. We pointed out that in the statistical analysis for nearly-periodic patterns these sturdy cycles of the Floor- and Round-LPA models dominate the results, nearly-periodic patterns corresponding to fragile cycles are identified very rarely. Moreover, the fragile cycles are found only in a non-significant manner (Fig. 6). This result corroborates the hypothesis that because of inner stochasticity of dynamical processes only the sturdy cycles can be significantly present in real population time series.

The 11-cycle of the DC-LPA was found in a much less pronounced manner in our analysis than an earlier study has suggested (King et al., 2004). There are three reasons

![Fig. 6. The number of cyclic patterns averaged on the three data series at $\varepsilon = 0.125$. Non-significant results are denoted by ns on the top of the bars.](image)
of this discrepancy: first, and most importantly King et al. (2004) seek the cyclic patterns in a “non-disjoint” manner in their analysis, that is, some intervals are frequently assigned to more than one cycle (see e.g. their Figs. 2, 5 and 6), while we introduced here a “disjoint” method. (There is rationality in both analyses: since the cycles, or part of them, are very similar to each other it is probable that a segment of data lies close to more than one cycle. The “non-disjoint” method solves this problem by assigning a pattern to different cycles. The “disjoint” method is based on the numerical observation that time series are composed by the noisy but disjoint...
periodic orbits in the grey zone, so it concentrates on finding them.) Second, they use only one fixed (and relatively high) similarity level, so the fact that the 11-cycle is fitted only at higher similarity level than any sturdy cycles of the DD models cannot be explicitly realized in their analysis. (A careful study of the figures reveals this fact.) Third, they studied only the second data series, where we also found the 11-cycle to be present significantly, but according to our method, the 11-cycle was not present in a significant manner in the other two data series. So, our results hardly support the view that characteristics of DD and DC models typically appear hand-in-hand in real data, however they apparently confirm this as a real possibility. This possibility is, in fact, realized in the current problem: the 11-cycle is the consequence of Arnold-tongue being present of DC-LPA model nearby the determined parameters (Cushing et al., 2001). Frequency locking, and consequently Arnold-tongues emerge typically in systems where two (or more) oscillators are coupled nonlinearly, and the ratio of oscillator’s frequencies are rational numbers (Ott, 2002). We do not know whether population dynamical models generally satisfy these conditions, nevertheless there exist other population dynamical models where Arnold tongues are present (Greenman and Benton, 2004). External periodic environmental forcing can cause the presence of Arnold tongues as well (King and Schaffer, 1999). The cycles present in the tongue (like 11-cycle in the LPA model) determine the basic frequency of the attractor close to the Arnold tongue even when the system is chaotic (King and Schaffer, 1999; Cushing et al., 2001). So, as it was shown earlier and also in this analysis, this periodicity can be detected even in noisy systems. This cycle is unstable, but it is “much less” unstable than any other periodic orbit. However, in other chaotic systems (e.g. the logistic map, $\mu = 4$) there is no such strong periodicity. The infinite number of unstable periodic orbits have almost the same weight in creating the time series. These unstable orbits can be detected by an algorithm similar to the one described here (Lathrop and Kostelich, 1989; Dhamala et al., 2000), however, because these cycles are unstable in a “similar strength”, the probability to detect a periodic orbit depends on its length, and decreases exponentially with the noise and with the length of the cycle (Dhamala et al., 2000).

It is highly probable that demographic and environmental noises are inherently high in every real population, thus it seems unlikely that the unstable cycles of DC systems (especially if they are long) could be detected in field data series. Furthermore, we concluded that even the characteristics of Arnold-tongues can be important merely at specific noise levels. If a small noise keeps the NC system in the “clear” zone, the data series will be practically periodic with periods determined by the applied DD model and the initial conditions (Fig. 7, $\alpha = 0.1$). The time series produce the richest in patterns in the “grey” zone (Fig. 7, $\alpha = 0.4$), including some 11-cycles on the border of the “grey” and “noisy” zone ($\alpha = 1$). Patterns, similar to the periodic orbits are practically not detected in the “noisy” zone (Fig. 7, $\alpha = 3$). We have shown recently that this dynamical system is on the border “grey” and “noisy” zone in this experiment (Domokos and Scheuring, 2004). This implies a peculiar situation where the sturdy cycles of the DD systems can still be detected and the 11-cycle of the DC system can already be observed. Since environmental noise is suppressed meaningfully in this (and every other) experimental situation, we suspect that sturdy cycles of the corresponding DD and DC systems could not be detected significantly in chaotic field population data sets, even if they are longer than this experimental data.

The direct consequence of this conclusion is that the NC model provides generally a good approximation of real population dynamics (as we stressed earlier in (Domokos and Scheuring, 2004)), however the sturdy periodic cycles of the DD model will be present in the form of nearly-periodic patterns in populations with low noise levels. The latter is realized either in laboratory experiments or under special circumstances in Nature.

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References


