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Demographic noise slows down cycles of dominance

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ABSTRACT

We study the phenomenon of cyclic dominance in the paradigmatic Rock–Paper–Scissors model, as occurring in both stochastic individual-based models of finite populations and in the deterministic replicator equations. The mean-field replicator equations are valid in the limit of large populations and, in the presence of mutation and unbalanced payoffs, they exhibit an attracting limit cycle. The period of this cycle depends on the rate of mutation; specifically, the period grows logarithmically as the mutation rate tends to zero. We find that this behaviour is not reproduced in stochastic simulations with a fixed finite population size. Instead, demographic noise present in the individual-based model dramatically slows down the progress of the limit cycle, with the typical period growing as the reciprocal of the mutation rate. Here we develop a theory that explains these scaling regimes and delineates them in terms of population size and mutation rate. We identify a further intermediate regime in which we construct a stochastic differential equation model describing the transition between stochastically-dominated and mean-field behaviour.

1. Introduction

Many mathematical models in ecology are well-known to be capable of generating oscillatory dynamics in time; important examples stretch right back to the initial work of Lotka and Volterra on predator-prey interactions (Britton, 2005; Guckenheimer and Holmes, 1988; Krupa, 1997; May and Leonard, 1975; Nowak, 2006; Toupo and Strogatz, 2015). Such models, although dramatic simplifications when compared to real biological systems, have a significant impact in shaping our understanding of the modes of response of ecological systems and are helpful in understanding implications of different strategies for, for example, biodiversity management, and the structure of food webs (Reichenbach et al., 2006).

Competition between species is a key driver of complex dynamics in ecological models. Even very simple competitive interactions can yield complex dynamical behaviour, such as the well documented example of the different strategies adopted by three distinct kinds of side-blotched lizard (Sinervo and Lively, 1996). Similar cyclical interactions occur in bacterial colonies of competing strains of *E. coli* (Kerr et al., 2002; Kirkup and Riley, 2004; Weber et al., 2014). In mathematical neuroscience dynamical switches of this type have been referred to as 'winnerless competition' since there is no best-performing state overall (Rabinovich et al., 2001; Tsai and Dawes, 2013).

Evolutionary Game Theory (EGT) provides a useful framework for modelling competitive interaction, in particular the replicator equations (see Taylor and Jonker, 1978; Schuster and Sigmund, 1983) give a dynamical systems interpretation for models posed in game-theoretic language. Work by many authors, including in particular Hofbauer and Sigmund (1988) and Hofbauer (1994) has resulted in a very good understanding of replicator equation models for competing species. Recent work has extended these deterministic approaches to consider stochastic effects that emerge from consideration of finite, rather than infinite, populations. The classic Rock–Paper–Scissors (RPS) provides an important example of stochastic phenomena in ecological dynamics. When mutation (allowing individuals to spontaneously swap strategies) is added to the replicator equations for the RPS game, the deterministic system can exhibit damped oscillations that converge to a fixed point. In Mobilia (2010), it was shown that stochastic effects present in finite populations cause an amplification of these transient oscillations, leading to so-called quasi-cycles (McKane and Newman, 2005). For smaller values of mutation rate, the deterministic system passes through a Hopf bifurcation, and a limit cycles appears. Some past studies exist on the role of noise around limit cycles, such as Boland et al. (2008; 2009), in which small-scale fluctuations around the mean-field equations are explored using Floquet theory. More recently, it has been discovered that noise can induce much stronger effects including counterrotation and bistability (Newby and Schwemmer, 2014).

In this paper we combine deterministic and stochastic approaches in order to present a comprehensive description of the ef-

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fect of demographic fluctuations around cycles of dominance in the RPS model. We determine three regimes, depending on the scaling of population size N and mutation rate μ. The basic link between stochastic individual-based dynamics and population-level ODEs is a theorem of Kurtz (1978), allowing us to construct a consistent set of individual-level behaviours corresponding to the mean-field replicator dynamics for the RPS model that we take as our starting point. Between these two views of the dynamics lies a third: the construction of a stochastic differential equation (SDE) that captures the transition between them. Changing variables to the asymptotic phase of the ODE limit cycle reveals that the contribution of the stochasticity is to speed up some parts of the phase space dynamics and to slow down others but that the overall effect is to markedly increase the oscillation period. Our central conclusion is that as the stochastic effects become more important, the period of the oscillations increases rapidly, and this slowing down is a significant departure from the prediction of oscillation periods made on the basis of the mean-field ODE model.

The structure of the remainder of the paper is as follows. In Section 2 we introduce the replicator dynamical model for the rock-paper-scissors game with mutation. The mean-field ODE version of the model is well-known and we derive a self-consistent individual-based description; this is not as straightforward as one might initially imagine. We show numerically that the two models give the same mean period for the cyclic dynamics when the mutation rate μ is large but disagree when it is small.

In Section 3 we summarise the computation to estimate the period of the limit cycle when μ is small. This follows the usual approach, dividing up trajectories into local behaviour near equilibrium points, and global maps valid near the unstable manifolds of these saddle points. Section 4 turns to the stochastic population model and analyses the dynamics in terms of a Markov chain. This leads to a detailed understanding of the individual-level behaviour in the limit of small mutation rate μ. Section 5 then fills the gap between the analyses of Sections 3 and 4 by deriving an SDE that allows us to understand the relative contributions of the stochastic behaviour and the deterministic parts in an intermediate regime. Finally, Section 6 discusses our results and concludes.

2. Models for Rock–Paper–Scissors with mutation

2.1. Rock–Paper–Scissors with mutation

Rock–Paper–Scissors (RPS) is a simple two-player, three-state game which illustrates the idea of cyclic dominance: a collection of strategies, or unchanging system states, in which each state in turn is unstable to the next in the cycle. In detail: playing the strategy ‘rock’ beats the strategy ‘scissors’ but loses to the strategy ‘paper’; similarly, ‘scissors’ beats ‘paper’ but loses to ‘rock’. When the two players play the same strategy the contest is a draw.

This information is summarised in the payoff matrix

$$P := \begin{pmatrix} 0 & -1-\beta & 1 \\ 1 & 0 & -1-\beta \\ -1-\beta & 1 & 0 \end{pmatrix} \tag{1}$$

where $\beta \geq 0$ is a parameter that indicates that the loss incurred in losing contests is greater than the payoff gained from winning them. When $\beta = 0$, the row and column sums of P are zero: this is the simplest case. When $\beta > 0$, the game becomes more complicated, particularly when we would like to relate the behaviour at the population level to the individual level, as we discuss later in Sections 2.2 and 2.3.

2.2. Deterministic rate equations

Setting the RPS game in the context of Evolutionary Game Theory (EGT), one considers a large well-mixed population of N players playing the game against opponents drawn uniformly at random from the whole population. We are then interested in the proportions of the total population who are playing different strategies at future times. The state of the system is given by the population fractions $(x_a(t), x_b(t), x_c(t)) := (N_A(t), N_B(t), N_C(t))/N$ where $N_{A,\,B,\,C}(t)$ are the numbers of players playing strategies A, B and C respectively.

The proportions of the population playing each strategy are expected to change over time according to the typical payoff received, as compared to the average over the whole population. The simplest mean field model for the resultant dynamics are the replicator equations

$$\dot{x}_i = x_i(t)\left(\sum_j P_{ij}x_j(t) - \sum_{j,k} P_{jk}x_j(t)x_k(t)\right), \tag{2}$$

where the subscripts i, j, k take values in $\{a, b, c\}$ and the proportions x_i sum to unity.

A common variant of the model introduces the additional mechanism of mutation between the three strategies, occurring between any pair with equal frequency. Mutation affects the rate of change of strategy i over time since the strategies other than i will contribute new players of i at rates μ while i will lose players at a rate given by $2\mu x_i$ as these players switch to a different strategy.

In the particular case of Rock–Paper–Scissors, the combined effects of the replicator dynamics together with mutations between strategies gives rise to the ordinary differential equations

$$\begin{aligned}
\dot{x}_a &= x_a[x_c - (1+\beta)x_b + \beta(x_ax_b + x_bx_c + x_ax_c)] + \mu(x_b + x_c - 2x_a),\\
\dot{x}_b &= x_b[x_a - (1+\beta)x_c + \beta(x_ax_b + x_bx_c + x_ax_c)] + \mu(x_a + x_c - 2x_b),\\
\dot{x}_c &= x_c[x_b - (1+\beta)x_a + \beta(x_ax_b + x_bx_c + x_ax_c)] + \mu(x_a + x_b - 2x_c).
\end{aligned} \tag{3}$$

We note that these equations are to be solved in the region of $\mathbb{R}^3$ where all coordinates are non-negative. This region is clearly invariant under the vector field (3). Moreover, the constraint $x_a + x_b + x_c = 1$ is required to hold at all times.

The system (3) possess a single interior equilibrium point $x^* = (1/3, 1/3, 1/3)$, in which the three strategies are balanced. Straightforward linear stability analysis shows that this equilibrium is stable when $\mu > \mu_c = \beta/18$. Previous work by Mobilia (2010) has shown that the system undergoes a Hopf bifurcation as μ is lowered and that for $\mu < \mu_c$ trajectories of (3) spiral away from x^* and are attracted to a unique periodic orbit which is stable, i.e a limit cycle.

2.3. Stochastic chemical reactions

The replicator equations shown above are expected to hold in the limit of infinitely large population size. In finite populations, however, the behaviour of many competing individuals is more appropriately modelled as a Markov process describing the random timing of individual events. It is common practice to specify such a stochastic model as a chemical reaction scheme, which, chosen appropriately should recover the ODEs (3) in the limit of large systems. It is interesting to note that different stochastic individual-based models may give rise to the same mean-field ODEs, so that the question of constructing a stochastic reaction scheme starting from a particular set of ODEs does not have a unique answer. Moreover, the construction of the stochastic model is subject to a number of natural constraints, for example that all reaction rates are at all times non-negative.

With the goal of studying dynamics around the fixed point x^* a reaction scheme was proposed in Mobilia (2010) based on consideration of the frequency-dependent Moran model with rates chosen to match the mean-field equations as required in the infinite system limit. Although that scheme is well motivated and perfectly