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Period Estimation and Noise in a Neutrally Stable Stochastic Oscillator

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Abstract

The periods of the orbits for the well-mixed cyclic three-species Lotka-Volterra model far away from the fixed point are studied. For finite system sizes, a discrete stochastic approach is employed and periods are found via wavelet analysis. As the system size is increased, a hierarchy of approximations ranging from Poisson noise to Gaussian noise to deterministic models are utilized. Based on the deterministic equations, a mathematical relationship between a conserved quantity of the model and the period of the population oscillations is found. Exploiting this property we then study the deterministic conserved quantity and period noise in finite size systems.

Keywords: stochastic simulation, stochastic oscillators, Gillespie algorithm

1 Introduction

Oscillating populations is a complex behavior that appears in nature. For biological species it is notably seen in the populations of side-blotched lizards [23] and hare-lynx populations [15]. Some of these oscillations occur from the cyclic competition of the species, which is also seen in nature in the form of the aforementioned lizards [23] and competing bacterial strains [18]. These oscillations occur in the mean-field limit model where coexistence states exist due to the presence of a conserved quantity [26, 1], which can be related to the frequency of the oscillations. However, for finite size systems these coexistence states may not last, as stochastic fluctuations will eventually drive one or more species to extinction and, therefore, must be studied using other methods.

Considerable work has been done studying the mean-field limit model [1, 26, 12, 14, 7] and stochastic extensions [5, 19]. In the mean-field limit model it has been shown that a *constant of motion* exists and is a conserved quantity similar to energy or momentum in classical mechanics (though that analogy is not an exact interpretation) [1]. The conserved quantity is invariant over periodic orbits and its value is unique for each orbit. In the stochastic extension work, white [19] or Brown [5] noise was added to a symmetric form of the mean-field model with three and/or four species. Fluctuations of the mean-field conserved quantity were then studied to explore extinction, and concurrently stability, of the system. These stochastic fluctuations, which are related to system size,

also affect the values of the deterministic conserved quantity and oscillation frequency.

We expand upon this previous work by studying the non-symmetric form of the model where all the rates may be different from one another as well as studying the dynamics of the system far away from the fixed point. The relations between the mean-field conserved quantity and the periods/frequencies of oscillations and the dynamic behavior of those quantities are also studied. Depending on the system size there are several different modeling and simulation methods to use, from directly solving a master equation for small populations when the relative noise is large, to the deterministic mean-field ordinary differential equations (ODEs) when the fluctuations are small enough to be considered negligible. This study uses a variety of such schemes to analyze the noise of the deterministic orbit conserved quantity and the period for different system sizes.

In the next section the three species cyclic Lotka-Volterra model is described in detail, and the different simulation schemes are introduced and pedagogically reviewed. These schemes are then compared to illustrate the difficulty in measuring the period for stochastic systems. The section afterwards introduces a drift-diffusion approximation for the deterministic conserved quantity that is applicable for sufficiently large system sizes. It closely follows the methodology of [5], albeit from a different perspective and for the general model. In Section 4 the period of oscillations in both the stochastic and deterministic model are numerically calculated and compared to the mean-field conserved quantity. In the final section we combine the results of the previous two sections

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to solve a drift-diffusion process for the evolution of the noise in the conserved quantity and the period.

2 Model and Background

The following is the cyclic three-species Lotka-Volterra reaction scheme:

where the k_j values can be probabilities or kinetic constants, depending on the modeling context (see Sections 2.1, 2.2 and 2.3 below) [1, 10]. We assume that the species populations are spatially homogeneous and that reaction events occur instantaneously. Let N_A , N_B and N_C denote the populations of species A , B and C , respectively. Since for all the reactions there are two *reactants* consumed and two *products* produced, the total population is constant

$$N_A + N_B + N_C = N. \quad (2)$$

With particle conservation the size of the system is an adjustable parameter and the noise can be more rigorously studied.

2.1 Deterministic Model

As the system size N increases to the large population (thermodynamic) limit, stochastic fluctuations become negligible and the reactions in (1) can be written as a system of ordinary differential equations (ODEs) known as the *reaction rate equations* or *mean-field equations*. For the model in Equation (1) the mean field equations can be written as

$$\begin{aligned} \frac{da}{dt} &= k_1 ab - k_3 ac, \\ \frac{db}{dt} &= k_2 bc - k_1 ab, \\ \frac{dc}{dt} &= k_3 ca - k_2 bc, \end{aligned} \quad (3)$$

where $a(t) = N_A(t)/N$ is the concentration form of the population N_A , with $b(t)$ and $c(t)$ defined similarly [26, 1]. We can utilize the conservation relation Equation (2) to eliminate one equation:

$$\begin{aligned} \frac{da}{dt} &= k_1 ab - k_3 a(1 - a - b), \\ \frac{db}{dt} &= k_2 b(1 - a - b) - k_1 ab. \end{aligned} \quad (4)$$

Throughout this work we will choose the two-species or three-species state representation based on whichever form is more convenient for notational purposes.

Manipulating Equations (3) it can be shown that the quantity $Q = a^{k_2} b^{k_3} c^{k_1}$ is constant in time. When all

populations are nonzero, the existence of the conserved quantity Q shows that the system will exhibit oscillations if it does not start at the fixed point [26, 1]. Through linearization around the fixed point ($a = k_2/k$, $b = k_3/k$, $c = k_1/k$), where $k = k_1 + k_2 + k_3$ and where the value of Q is maximum, it can be shown that the angular frequency and the period of oscillations near the fixed point are approximately [11, 19]

$$\omega \approx \sqrt{\frac{k_1 k_2 k_3}{k}}, \quad T \approx 2\pi \sqrt{\frac{k}{k_1 k_2 k_3}}, \quad (5)$$

respectively.

It should be noted that the periodic solutions of the deterministic Equations (3) are stable, as each value of the conserved quantity Q corresponds to a unique periodic orbit. However, none of these orbits are considered to be asymptotically stable or limit cycles because slight perturbations cause the system to go to, and stay on, a different orbit.

2.2 Discrete Time, Discrete State Stochastic Model

When N is small, the population $X(t) = [N_A, N_B, N_C]^T$ (or $X(t) = [N_A, N_B]^T$ with Equation (2)) exhibits relatively large stochastic fluctuations and a discrete state model is appropriate. One approach is to consider discrete time steps. Following [6] we define a *pick random pair* (PRP) time step $\tau_{PRP} = \frac{1}{N}$. At each PRP step, we update $t = t + \tau_{PRP}$ and two particles are chosen at random from the population of N particles. If the particles are of different species then the corresponding reaction R_j in Equations (1) is carried out with a predefined probability p_j . For later notational convenience, we will let $k_j = 2p_j$. When reaction j “fires”, we update the populations as $X = X + \nu_j$ with

$$\nu_1 = \begin{bmatrix} 1 \\ -1 \\ 0 \end{bmatrix}, \quad \nu_2 = \begin{bmatrix} 0 \\ 1 \\ -1 \end{bmatrix}, \quad \nu_3 = \begin{bmatrix} -1 \\ 0 \\ 1 \end{bmatrix}. \quad (6)$$

(The third element in each vector can be excluded if defining $X(t) = [N_A, N_B]^T$ by utilizing Equation (2).)

This process of selecting particle pairs is repeated N times and constitutes one *Monte Carlo (MC) time step*. This generates a master equation qualitatively similar to that seen in reference [6], which uses the probabilities of choosing any pair of different species as well as the probability of choosing the same species to evolve the system to the next time step, which may or may not be the same state as the previous time step.

As the system size gets larger, solving the master equation directly becomes intractable. The solution to the

master equation can be approximated by running an ensemble of statistically exact simulations. A naive simulation algorithm would perform a PRP time step by choosing two particles randomly and then checking if the particles are different species to see which, if any, reaction event occurs. This method has the undesirable feature of selecting many *null events* where two species of the same type are chosen. Each null event advances the (discrete) MC time by $1/N$ without changing the populations. In the best case where the populations of N_A , N_B and N_C are near the fixed point, a null event will occur with probability approaching $1/3$ (when the rates k_j are all equal). However, in the extreme case where one species' population is much larger than the others, the probability of a null event approaches one. A more computationally efficient algorithm first selects the number of τ_{PRP} time steps until the first reaction (non-null) event by generating a random sample from a geometric distribution with event probability $Pr = (k_1 N_A N_B + k_2 N_B N_C + k_3 N_C N_A) / (N(N-1))$. Once the (discrete) time to the next reaction event is selected, the particular event R_j is chosen with probability

$$\begin{aligned} Pr(R_1) &= \frac{k_1 N_A N_B}{k_1 N_A N_B + k_2 N_B N_C + k_3 N_C N_A}, \\ Pr(R_2) &= \frac{k_2 N_B N_C}{k_1 N_A N_B + k_2 N_B N_C + k_3 N_C N_A}, \\ Pr(R_3) &= \frac{k_3 N_C N_A}{k_1 N_A N_B + k_2 N_B N_C + k_3 N_C N_A}. \end{aligned} \quad (7)$$

As shown in the appendix of reference [6], these simulation methods generate statistically exact samples from the distribution described by the PRP master equation.

The discrete time, discrete state model converges to Equations (3) as $N \rightarrow \infty$. To see this, consider a small $\Delta t = \frac{d}{N}$ for integer d and large N . Note we can make Δt arbitrarily small, even for arbitrarily large d with a suitably large choice of N . When d is large, we can approximate the process as a Bernoulli process with “number of trials” parameter $n = d$ and a “probability of success” parameter $p = \bar{p}$. For the parameter $\bar{p}$, we can consider the probability that event R_1 occurs in a single PRP time step τ_{PRP} . Then $\bar{p} = \frac{k_1 N_A N_B}{N(N-1)}$. The outcome of a Bernoulli process with d trials of probability $\bar{p}$ follows a Binomial distribution with mean $\mu = d\bar{p}$ and standard deviation $\sigma = \sqrt{d\bar{p}(1-\bar{p})}$. The approximation would be exact if the populations, and hence the probabilities, did not change at all after each event. For large N , the relative change in the probabilities is small and the approximation is reasonable. If d is increased, the mean μ increases linearly with d while the standard deviation scales as $\sqrt{d}$. That is, the coefficient of variation approaches zero and, hence, the number of events approaches a sure number. If we consider the change in $a = \frac{N_A}{N}$, we get

$\Delta a = d\bar{p} \frac{\nu_{1,1}}{N} = d \frac{k_1 N_A N_B}{N(N-1)}$, where $\nu_{1,1}$ is the first component of ν_1 . If we consider $\frac{\Delta a}{\Delta t}$ in the limit as $N \rightarrow \infty$ we get $\frac{da}{dt} = k_1 ab$, which is the contribution from R_1 in Equation (3). R_1 also contributes the negative term for $\frac{db}{dt}$ in Equation (3). Applying the same procedure to R_2 and R_3 gives the full system of Equations (3).

In the next section we describe a continuous time model for the reaction set in Equation (1). The discrete time and continuous time methods are identical in their sampling of state changes, but they differ in the sampling of time between reaction events. This difference in time sampling is elaborated on in Appendix A. For the remainder of this work we will use the continuous time model for consistency and to avoid errors in time difference. However, most of the analysis can also be applied to the discrete time model and would yield qualitatively similar results to that of the continuous time model.

2.3 Continuous Time, Discrete State Stochastic Model

We now consider a *continuous time*, discrete state stochastic model for this system. In the continuous time regime, each reaction channel R_j has an associated *propensity function*, denoted α_j , that specifies the rate at which the reaction is firing, defined as [10, 8]

$$\alpha_j(X(t))dt \equiv \text{probability that reaction } R_j \text{ will occur in } [t, t + dt). \quad (8)$$

For the three-species cyclic Lotka-Volterra model considered here, the propensity functions are

$$\begin{aligned} \alpha_1(X) &= \tilde{k}_1 N_A N_B, \\ \alpha_2(X) &= \tilde{k}_2 N_B N_C, \\ \alpha_3(X) &= \tilde{k}_3 N_C N_A, \end{aligned} \quad (9)$$

where $\tilde{k}_j$ is the stochastic rate constant defined as

$$\tilde{k}_j = \frac{k_j}{N}. \quad (10)$$

The (chemical) master equation (CME) is a set of coupled ordinary differential equations that describes the evolution of the probability of the system being in any state at time t . Defining $P(X, t | X_0, t_0)$ as the probability of being in state $X(t)$ at time t , given $X(0) = X_0$, the CME is

$$\begin{aligned} \frac{\partial P(X, t)}{\partial t} &= \sum_{j=1}^3 \left[\alpha_j(X - \nu_j) P(X - \nu_j, t | X_0, t_0) \right. \\ &\quad \left. - \alpha_j(X) P(X, t | X_0, t_0) \right]. \end{aligned} \quad (11)$$

The CME contains one equation for each possible state of the system. This state space scales as $(N+1)(N+2)/2$. Therefore, the CME quickly becomes computationally expensive or intractable as N grows.

An alternative to solving the CME directly is to use Monte Carlo simulation to approximate the solution. The definition of the propensity function equations (8), combined with the spatially homogeneous assumption, means that the process is Markovian with each reaction channel firing according to an exponential distribution. By the properties of exponential random variables, the time τ and index j of the next reaction, given X and t , can be described by the probability density function

$$p(\tau, j | X, t) = \alpha_j(X) e^{-\sum_{i=1}^3 \alpha_i(X)\tau}. \quad (12)$$

Equation (12) leads naturally to Gillespie's *Stochastic Simulation Algorithm* (SSA) [10, 8]. Any implementation that repeatedly selects τ and j from Equations (12) will generate statistically exact samples of the CME. Many such algorithms and implementations exist, with different performance and scaling attributes (see reference [22] for an overview). Figures 1, 2 and 3 show the results of several stochastic trajectories and the chemical master equation compared to the deterministic model. In Figures 1 and 2, the system size $N = N_A + N_B + N_C = 100$, while $N = 1000$ in Figure 3. As the system size increases, the relative noise decreases, resulting in solutions that tend to be closer to the deterministic model, as seen in the differences in the spread of the probability between Figures 2 and 3.

2.4 Tau-leaping and Chemical Langevin Model

As a statistically exact approach, the SSA simulates every reaction event. Unlike many numerical algorithms, the step size is not an algorithm parameter in the SSA. Instead, the SSA step size is determined by the model, following an exponential distribution with the rate equal to the sum of the propensities. The tau-leaping algorithm sacrifices exactness in exchange for increased efficiency by taking larger step sizes and firing multiple reaction events per step [9, 3].

The tau-leaping algorithm selects a step size τ and approximates the number of firings of each reaction channel as a Poisson process with mean $\alpha_j(X)\tau$:

$$X(t + \tau) = X(t) + \sum_{j=1}^3 \text{Poisson}(\alpha_j(X)\tau) \nu_j, \quad (13)$$

where each *Poisson* is an independent Poisson random variate. Tau-leaping treats the propensities as constant over the interval $[t, t + \tau)$ and is analogous to the Forward

Figure 1: Master equation solution (background fill), deterministic solution (white), and five stochastic trajectories (gray) of one half of a deterministic period $t \approx 5.64875$ for initial condition $N_A(0) = 50$, $N_B(0) = 25$, $N_C(0) = 25$ (white dot) and rate constants $k_1 = k_2 = k_3 = 1$. The deterministic fixed point is shown in green. If the system size $N = N_A + N_B + N_C$ was much larger, the master equation probability and the stochastic trajectories would be closer to the deterministic solution (see Figure 3).

Figure 2: Master equation solution (background fill), deterministic solution (white), and five stochastic trajectories (gray) of one deterministic period $t \approx 11.2975$ for initial condition $N_A(0) = 50$, $N_B(0) = 25$, $N_C(0) = 25$ (white dot) and rate constants $k_1 = k_2 = k_3 = 1$. The deterministic fixed point is shown in green. Note the bright spot near $N_A = 0$, $N_B = 100$ that indicates extinction of species A and C .

Figure 3: Master equation solution (background fill), deterministic solution (white), and five stochastic trajectories (gray) of one deterministic period $t \approx 11.2975$ for initial condition $N_A(0) = 500$, $N_B(0) = 250$, $N_C(0) = 250$ (white dot) and rate constants $k_1 = k_2 = k_3 = 1$. The deterministic fixed point is shown in green.

Euler method for numerical solution of ordinary differential equations. As N increases, tau-leaping becomes more accurate (for the same step size τ) and the computational efficiency gains versus the SSA improve.

For sufficiently large N , one can approximate the three Poisson random numbers in the tau-leaping update formula (13) with three Normal random variables:

$$X(t + \tau) = X(t) + \sum_{j=1}^3 \text{Normal}(\mu = \alpha_j(X)\tau, \sigma = \sqrt{\alpha_j(X)\tau})\nu_j, \quad (14)$$

where we have now transitioned from a discrete-valued population to a continuous-valued population $X(t)$. Combining the stoichiometry vectors to form a stoichiometric matrix

$$\mathcal{V} = [\nu_1 \quad \nu_2 \quad \nu_3] = \begin{bmatrix} 1 & 0 & -1 \\ -1 & 1 & 0 \\ 0 & -1 & 1 \end{bmatrix}, \quad (15)$$

Equation (14) can be rewritten as

$$X(t + \tau) = X(t) + \mathcal{V} \cdot \begin{bmatrix} \alpha_1(X(t)) \\ \alpha_2(X(t)) \\ \alpha_3(X(t)) \end{bmatrix} \tau + \text{Normal}_3 \left(\mu = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, \sigma = \begin{bmatrix} \sqrt{\alpha_1(X(t))\tau} \\ \sqrt{\alpha_2(X(t))\tau} \\ \sqrt{\alpha_3(X(t))\tau} \end{bmatrix} \right), \quad (16)$$

where we use Normal_3 to denote three independent, uncorrelated Normal random variables with the means and standard deviations given in the vectors μ and σ . If we replace τ in Equation (16) with infinitesimal dt and we replace $\text{Normal}(\mu, \sigma)$ with $\mu + \sqrt{\sigma} \text{Normal}(0, 1)$, we arrive at a stochastic differential equation (SDE), which is the population form of what is known as the (Chemical) Langevin Equation (CLE) [25]:

$$X(t + dt) - X(t) = \sum_{j=1}^3 \nu_j \alpha_j(X) dt + \sum_{j=1}^3 \nu_j \sqrt{\alpha_j(X)} \text{Normal}(\mu = 0, \sigma = 1) \sqrt{dt}, \quad (17)$$

or equivalently

$$dX = \mathcal{V} \alpha(X) dt + \mathcal{V} \sqrt{\alpha(X)} \text{Normal}_3(\mu = 0, \sigma = 1) \sqrt{dt} \quad (18)$$

for vector valued μ and σ . Note that the first term on the right-hand side of Equations (17) and (18) is the population form equivalent of the right-hand side of Equation (3). Since the populations and propensities scale as $O(N)$ but the noise term scales as $O(\sqrt{N})$, in the large population limit the noise term becomes insignificant.

3 A Diffusion Process for the Deterministic Conserved Quantity

In Section 2.1, the deterministic conserved quantity Q was introduced. While Q stays constant along any particular deterministic orbit, in the finite system size regime, Q varies as the stochasticity perturbs the state onto different deterministic orbits. The noise term in Equation (18) can be interpreted as the rate at which the noise around the particular deterministic solution is growing. Each of the three reactions R_j contributes a zero-mean normal random variable in the direction of the stoichiometry vector ν_j .

The instantaneous rate of noise growth in the N_A - N_B plane can be written as a linear combination of these three normal distributions, resulting in a bivariate normal with mean $\mu = [0, 0]^T$ and covariance matrix Σ that is growing as

$$\begin{aligned} d\Sigma(X) &= \mathcal{V} \cdot \text{diag}(\alpha(X)) \cdot \mathcal{V}^T dt \\ &= \begin{bmatrix} \alpha_1(X) + \alpha_3(X) & -\alpha_1(X) \\ -\alpha_1(X) & \alpha_1(X) + \alpha_2(X) \end{bmatrix} dt \\ &= \begin{bmatrix} \sigma_A^2 & \rho\sigma_A\sigma_B \\ \rho\sigma_A\sigma_B & \sigma_B^2 \end{bmatrix} dt, \end{aligned} \quad (19)$$

where ρ is the correlation coefficient between the noise in the N_A and N_B directions.

Let W_t and Z_t be standard correlated Brownian motions with $dW_t dZ_t = \rho dt$. Then we can define A_t and B_t as the noise in the N_A and N_B directions, respectively, as

$$\begin{aligned} dA_t &= \sigma_A dW_t \\ dB_t &= \sigma_B dZ_t \end{aligned} \quad (20)$$

Next, we define f as the normalized form of the deterministic model's conserved quantity $Q/Q_{\max}$:

$$\begin{aligned} f(N_A(t), N_B(t), t; N, k_1, k_2, k_3) &= \frac{Q(t)}{Q_{\max}} \\ &= \frac{\left(\frac{N_A}{N}\right)^{k_2} \left(\frac{N_B}{N}\right)^{k_3} \left(\frac{N - N_A - N_B}{N}\right)^{k_1}}{k_1^{k_1} k_2^{k_2} k_3^{k_3} \left(\frac{1}{k}\right)^k} \\ &= \frac{a^{k_2} b^{k_3} (1 - a - b)^{k_1}}{k_1^{k_1} k_2^{k_2} k_3^{k_3} \left(\frac{1}{k}\right)^k}. \end{aligned} \quad (21)$$

Using Equation (20) and Ito's lemma [16], we have

$$\begin{aligned} df &= \left[\frac{1}{2} \sigma_A^2 f_{AA} + \frac{1}{2} \sigma_B^2 f_{BB} + \rho \sigma_A \sigma_B f_{AB} \right] dt \\ &\quad + \sigma_A f_A dW_t + \sigma_B f_B dZ_t, \end{aligned} \quad (22)$$

where the subscripts on f denote partial derivatives with respect to A_t and B_t . We note that the right-hand side of Equation (22) depends on the particular state of the system defined by N_A, N_B , and N .

When N is large, the noise is relatively small and there is a separation of scales between the fast deterministic periodic process and the slow noise process. One can then average the noise over a period [13, 5] to construct a drift-diffusion process for $Q(t)/Q_{\max}$.

We can consider the "drift" term proportional to dt in the right-hand side of (22) averaged over one period:

$$\mu(f) = \frac{1}{T(f)} \int \left[\frac{1}{2} \sigma_A^2 f_{AA} + \frac{1}{2} \sigma_B^2 f_{BB} + \rho \sigma_A \sigma_B f_{AB} \right] dt, \quad (23)$$

where $T(f)$ is the period. In the case $k_1 = k_2 = k_3$, the integrand is constant. In the case $k_1 = k_2 = k_3 = 1$, the terms can be algebraically simplified we get $\mu(f) = \frac{-3}{N} f$, which agrees with the results of Dobrinevski and Frey who considered $f = Q$ instead of $f = Q/Q_{\max}$ for $k_1 = k_2 = k_3 = 1$ [5].

If we consider the "diffusion" terms involving dW_t and dZ_t in the right-hand side of Equation (22), by the sum of correlated normal random variables, we have

$$\begin{aligned} \sigma_A f_A dW_t + \sigma_B f_B dZ_t &= \\ \sqrt{(\sigma_A f_A)^2 + (\sigma_B f_B)^2 + 2\rho \sigma_A \sigma_B f_A f_B} dB_t, \end{aligned} \quad (24)$$

where B_t is a standard Brownian motion. Taking the average over a period, we define

$$D(f) = \frac{1}{T(f)} \int (\sigma_A f_A)^2 + (\sigma_B f_B)^2 + 2\rho \sigma_A \sigma_B f_A f_B dt. \quad (25)$$

We can now define a stochastic differential equation for the evolution of $f = Q/Q_{\max}$:

$$df = \mu(f)dt + \sqrt{D(f)}dB_t, \quad (26)$$

where now, in contrast to Equation (22), the right-hand side of Equation (26) does not depend on the particular state of N_A, N_B , and N , but rather depends only on the value of $f = Q/Q_{\max}$. However, the calculation of μ and D in Equations (23) and (25) does depend on knowledge of the deterministic period. We discuss methods for determining the period T in the next section.

4 Deterministic and Stochastic Methods of Determining the Period

To determine the period in the deterministic model, a numerical integral method to compute the period as a function of $Q/Q_{\max}$ was developed. Details of this method are outlined in Appendix B. This method can be done with all equal or different rates k_j and the results of this method can be seen in Figure 4, where they are compared to periods found from Runge-Kutta simulations for verification. Since this method uses Equations (3) we are inferring the relation between the period and $Q/Q_{\max}$ only in the case for $N \rightarrow \infty$ and a different method must be employed to find the period of the stochastic system.

In order to determine the period for the stochastic system, wavelet analysis was used [24] to approximate the period at a single point in time. The stochastic runs used the SSA scheme but modified to not allow a species to go extinct. Preventing the species from going extinct allows for longer trajectories and only affects the analysis at low values of $Q/Q_{\max}$ and species' populations. For a single stochastic run a wavelet analysis, with details summarized in Appendix C, is performed on the population of a species as a function of time. This yields a power spectra as seen in Figure 5, where at each point in time a power spectrum for a range of periods is given. An example of such a power spectrum for a single point in time is given in Figure 6, which has a maximum at around period 14 and agrees with the population trajectory seen in Figure 7.

The period at which the power spectrum is maximum can then be plotted as a function of time as seen in Figure 8 and compared to $Q/Q_{\max}$. It is found that they are

Figure 4: Comparison of period calculations from the numerical integral method (points) and periods found from Runge-Kutta simulations of Equations (3) using different reaction rates $\{k_1, k_2, k_3\}$.

Figure 6: A time slice of the wavelet power spectra seen in Figure 5 at time 4250. The maximum is located at the period of 13.4254749. The population of the species at the time is $N_A = 627$, $N_B = 2481$, and $N_C = 392$ and corresponds to a $Q/Q_{\max}$ of roughly 0.384. The numerical integral method yields a period of 13.3098.

Figure 5: A sample wavelet transform of N_A for a stochastic trajectory for a run with $k_1 = k_2 = k_3 = 1$ and initial condition $N_A = 2000$, $N_B = 1000$, and $N_C = 500$.

Figure 7: The number of species A as a function of time around the area of the wavelet power spectra time slice seen in Figure 6.

Figure 8: The maximum period signal and the conserved quantity ratio $Q/Q_{\max}$ as a function of time. Note that they are anti-correlated. The run parameters are the same as Figure 5 with $k_1 = k_2 = k_3 = 1$ and initial condition $N_A = 2000$, $N_B = 1000$, and $N_C = 500$.

anti-correlated, with small $Q/Q_{\max}$ values far from the fixed point corresponding to longer periods and $Q/Q_{\max}$ values near unity corresponding to shorter periods. A scatter plot of the period at which the power spectrum is maximum and the value of $Q/Q_{\max}$ can be made. However, to better compare the stochastic results to the integral method period results more stochastic data is needed. For several different parameter sets, 1000 SSA trajectories with an end time of $t = 8192$ and output recorded at integer intervals were performed. A wavelet analysis, as described before, was done for each of these simulations. Only the data from integer times 2048 to 6144 were kept, because the wavelet analysis needs a window of data around the time of interest for optimal performance, and hence does not perform well near the beginning and end of the time series [24]. This data, consisting of the deterministic conserved quantity ($Q/Q_{\max}$) and period (T) were gathered in $\sqrt{Q/Q_{\max}}$ bins of size 0.01. The statistics of the periods in each $\sqrt{Q/Q_{\max}}$ bin are then computed yielding a mean and standard deviation. The mean period and its standard deviation are plotted in Figure 9. They agree very well with and approach the integral method period results as the system size (N) gets larger.

Note that in Figure 10 that the period (T) as a function of $Q/Q_{\max}$ appears linear on a log scale, which implies a relationship of the form

$$T = \gamma \ln(Q/Q_{\max}) + T_0. \quad (27)$$

For each case we fit the integral method data points to Equation (27) comparing the cases where k_1 is changed as

Figure 9: The distribution of the maximum period signal vs the conserved quantity ratio $Q/Q_{\max}$ for SSA simulations as well as period integral solutions (Comp) with $k_1 = k_2 = k_3 = 1$. The initial conditions for the SSA simulations was $N_A = N_B = N_C = N/3$. For the SSA simulations a bin size of 0.01 was used for $\sqrt{Q/Q_{\max}}$ to gather statistics for the period. $\sqrt{Q/Q_{\max}}$ was used for the horizontal axis for visualization purposes.

Figure 10: Fits (lines) of the integral solution period as a function of $Q/Q_{\max}$ (points) for the case of different reaction rates $\{k_1, k_2, k_3\}$ with respect to Equation (27).

Table 1: Values for the fits of $T = \gamma \ln(Q/Q_{\max}) + T_0$ in Figure 10, with different reaction rates, as well as comparisons to the linearization results of Equation (5).

$\{k_1, k_2, k_3\}$	Fitted γ	Fitted T_0	T_0 by Eq. (5)
$\{1.0, 1.0, 1.0\}$	-2.902(5)	10.39(3)	~ 10.88
$\{1.0, 1.0, 1.5\}$	-2.271(4)	9.23(2)	~ 9.59
$\{1.0, 1.5, 1.5\}$	-1.720(3)	8.10(1)	~ 8.37
$\{1.0, 1.5, 2.0\}$	-1.455(2)	7.48(1)	~ 7.69
$\{2.0, 2.0, 2.0\}$	-7.027(1)	5.319(9)	~ 5.441
$\{1.0, 1.0, 5.0\}$	-1.438(1)	7.311(6)	~ 7.434

well as the period value that linearization yields (Equation (5)) and display the results in Table 1. The fit could be improved by using a more complex function than the simple linear-log function considered here.

5 Results and Conclusions

Using the deterministic period from the previous section, we can now calculate Equations (23) and (25). First, we define

$$\begin{aligned}\bar{\mu} &= N\mu, \\ \bar{D} &= ND.\end{aligned}$$

Figures 11 and 12 show the effective drift and diffusion rates of $Q/Q_{\max}$. We can then rewrite Equation (26) as

$$df = \frac{1}{N}\bar{\mu}(f)dt + \frac{1}{\sqrt{N}}\sqrt{\bar{D}(f)}dB_t, \quad (28)$$

or as the equivalent Fokker-Planck equation for the evolution of the probability $P(f, t)$ of the system being at the deterministic scaled conserved quantity $f = Q/Q_{\max}$ over time

$$\frac{\partial P(f, t)}{\partial t} = \frac{1}{N} \left[\frac{\partial}{\partial f} (\bar{\mu}P(f, t)) + \frac{1}{2} \frac{\partial^2}{\partial f^2} (\bar{D}P(f, t)) \right]. \quad (29)$$

We can now solve Equation (29), a one-dimensional PDE, for the evolution of $Q/Q_{\max}$. Additionally, we can use Equation (29) and the relation between $Q/Q_{\max}$ and the period (see Section 4) to describe the evolution of the noise in the period. Figures 13 and 14 show the solution of Equation (29) for different parameter sets and initial conditions. Figure 15 shows the solution of Equation (29), with the horizontal axis rescaled to show the evolution of the period rather than $Q/Q_{\max}$ for two different parameter sets. The approximations are very close to the master equation solution for sufficiently large N . When the values of k_j are more unequal, a larger value of N is required to achieve an accurate approximation. For

Figure 11: Effective drift rate $\bar{\mu}$ for the evolution of deterministic conserved quantity $Q/Q_{\max}$, computed by solving Equation (23) and scaling as in Equation (28). Note that the drift is generally negative, indicating a bias toward extinction over time.

Figure 12: Effective diffusion rate $\bar{D}$ for the evolution of deterministic conserved quantity $Q/Q_{\max}$, computed by solving Equation (25) and scaling as in Equation (28).

Figure 13: Solution to Equation (29) for $N = 1000$ and $k_1 = k_2 = k_3 = 1$ with initial condition $N_A = 500$, $N_B = 250$. The initial value of $Q/Q_{\max}$ is 0.84375. The curves (black) show the solution at $t = 11.2975$ (curve with highest peak), $t = 22.595$ (middle curve), and $t = 33.8925$, where $t \approx 11.2975$ is the deterministic period for the initial condition. Equation (29) was solved using a finite difference scheme with a reflective boundary condition at $Q/Q_{\max} = 1$ and an absorbing boundary condition at $Q/Q_{\max} = 0$. The semi-transparent blue histograms are the master equation solutions at the same time points.

Figure 14: Solution to Equation (29) for $N = 3000$ and $k_1 = 1$, $k_2 = 1$, $k_3 = 5$ with initial condition $N_A = 331$, $N_B = 1653$. The value initial value of $Q/Q_{\max}$ is 0.5001191. The curves (black) show the solution at $t = 8.341676$ (curve with highest peak), $t = 16.68335$ (middle curve), and $t = 25.02503$, where $t \approx 8.341676$ is the deterministic period for the initial condition. The semi-transparent blue histograms are the master equation solutions at the same time points.

example, if a value of $N = 1000$ is used for the rate constants in Figure 14, there is a perceptible error between the solution to Equation (29) and the master equation solution, particularly near the boundary $Q/Q_{\max} = 1$.

In this work, the cyclic three-species Lotka-Volterra model is studied using a hierarchy of modeling approaches based on system size. This model is a “neutrally stable” stochastic oscillator. Unlike an asymptotically stable system, where small perturbations tend to revert to a limit cycle, small perturbations in this model, including those due to finite size effects, push the system to a new neutrally stable orbit. Quantifying the period in a neutrally stable stochastic oscillator away from a fixed point is not straightforward, given that a particular trajectory is unlikely to return exactly to the initial condition after one period. For small system sizes, the time at which the mean or mode of the complete probability density passes nearest the initial condition can be computed from the CME solution. At large system sizes, a deterministic approach as utilized in Section 4 works well. We have shown that wavelet analysis works well for determining the “instantaneous” period for a given point in time at intermediate system sizes, and the period estimates converge to the deterministic approach as the system size increases.

The deterministic approximation contains a quantity Q that is conserved along the periodic orbits. However, in a stochastic model, the noise in the system causes this

Figure 15: Period distribution for $k_1 = k_2 = k_3 = 1$ (curves with larger periods) and $k_1 = k_2 = k_3 = 2$ for $N = 1000$ and initial condition $N_A = 500$, $N_B = 250$ after approximately one (highest peaks), two, and three periods. The three curves with larger periods correspond to the $Q/Q_{\max}$ values in Figure 13. The periods for $k_1 = k_2 = k_3 = 2$ are half that of $k_1 = k_2 = k_3 = 1$; doubling the rate constants effectively rescales time by a factor of one half. Curves were calculated by solving the Fokker-Planck Equation (29) and then converting the $Q/Q_{\max}$ value to the corresponding deterministic period based on the results in Section 4.

quantity to vary. Using the Langevin approximation, we derive a drift-diffusion process for $Q/Q_{\max}$ that is valid for any set of parameters, given a suitably large system size. Probability distributions for the value of Q can then be used to determine the “instantaneous” period probability distribution.

The methods and multiscale approach applied in this work can be used on observable and theoretical systems which display oscillations. A prime example of observable systems are the lizard [23] and hare-lynx [15] systems, from which instantaneous periods can be taken from data. Results of studies can be used to determine the current stability of the system, as studies show that longer timescales are indicative of a population collapse [4]. The methods presented in this paper can also be applied to and verify theoretical results that deal with large diversities of species [26, 17]. How these techniques can be applied and extended to systems with spatial degrees of freedom would also be important as they tend to have more complex phenomena such as coarsening domains [21], spirals [20], and spirals within spirals [2].

Future work will explore extending model and analytic techniques to different reaction schemes and modeling on a lattice structure. For a spatial extension we propose population models where competition or reaction events occur at interfaces by using a graph representation where populations exist on the vertices and competitive interactions along the edges. This will also allow for modeling spatially-dependent interactions, including density dependent competition strategies.

A Comparing Monte Carlo discrete time to continuous time steps

One Monte Carlo time step is N pick random pair (PRP) steps. Consider one pick random pair step, which is equivalent to $\tau_{PRP} = \frac{1}{N}$ Monte Carlo time step. We will compare to τ_G , the continuous Gillespie time step.

It is clear that these approaches are not equivalent because with τ_G , there is a non-zero probability that more than 1 reaction will occur in time $\frac{1}{N}$, while with the discrete time step approach, exactly 0 or 1 events will occur in τ_{PRP} . Therefore, the distributions in time produced by these two approaches will differ from each other.

Let's consider a specific example. Suppose $p_1 = p_2 = p_3 = 1$ (PRP probabilities) and $a = .5$, $b = .25$, $c = .25$ with $N = 20$, so that $N_A = 10$, $N_B = 5$, $N_C = 5$. Then the probability of an event occurring in $\tau_{PRP} = \frac{1}{N}$ is

$$\frac{p_A \cdot N_A \cdot N_B + p_B \cdot N_B \cdot N_C + p_C \cdot N_C \cdot N_A}{N \cdot (N - 1)/2} \approx .65789.$$

Comparing to the SSA, where the next event fires according to an exponential distribution with rate $= \alpha = \tilde{k}_1 \cdot N_A \cdot N_B + \tilde{k}_2 \cdot N_B \cdot N_C + \tilde{k}_3 \cdot N_C \cdot N_A$, choosing $\tilde{k}_j = \frac{k_j}{N} = \frac{2 \cdot p_j}{N}$ leads to the same limiting ODE when $N \rightarrow \infty$. Considering our specific example from above with $N = 20$, we get $\alpha = 12.5$. The probability of observing *at least one* event in time $t = \frac{1}{20}$ is ≈ 0.4647386 , which can be determined by the cumulative density function of an exponential distribution with rate 12.5. The mean number of events in time t will be larger than 0.4647386 because more than one event can fire. This mean can be computed numerically from the CME and will typically be *close* to the discrete time probability but not identical.

As N gets larger, the discrete and continuous time approaches converge. For example, with a, b, c as defined above and $N = 1000$, then $N_A = 500$, $N_B = 250$, $N_C = 250$, and the probability of an PRP event in time $\frac{1}{1000}$ is ≈ 0.6253127 . When we consider the continuous time approach with $\tilde{k}_j = \frac{2 \cdot p_j}{N}$, we get $\alpha = 625$. Again, the probability of observing at least one event in $\tau = \frac{1}{N} = \frac{1}{1000}$ is ≈ 0.4647386 . But it is not a coincidence that $\frac{1}{1000} \cdot 625 = .625$. Note that in this example .625 is the limiting probability of an R_1 event in τ_{PRP} as $N \rightarrow \infty$. As N gets larger, the propensity in the continuous time model approaches $\alpha = .625N$. Using the Bernoulli process approximation on the discrete time process as in Section 2.2 and the Poisson approximation on the continuous time process as in Section 2.4, the two approaches converge to Equation (1).

B Numerical Computation of the Period

A method to calculate the period from the conserved quantity ratio $Q/Q_{\max}$ of the deterministic system described in Equations (3) is outlined here. It closely follows appendix A of reference [5], but diverges due to no explicit solutions found for some quantities.

First, the minimum and maximum values of a given an $Q/Q_{\max}$ value must be found. Assuming that the time derivative of a is zero at the minimum/maximum and using the conserved quantities, $a + b + c = 1$ and $Q = a^{k_2} b^{k_3} c^{k_1}$, the values of $a_{\min}$ and $a_{\max}$ are the real roots of the equation

$$a^{k_2} (1 - a)^{k_1 + k_3} = Q \left(1 + \frac{k_1}{k_3}\right)^{k_1 + k_3} \left(\frac{k_3}{k_1}\right)^{k_1} = \tilde{Q} \quad (30)$$

where a new constant $\tilde{Q}$ is introduced to simplify further equations. Equation (30) can be numerically solved by finding where the functions of the left-hand side and right-hand side intersect. The left-hand side of (30) has the form of a beta distribution and the right-hand side is a

Figure 16: Example of the intersections for the left and right-hand sides of Equation (30).

constant. An example showing the intersections of the left and right-hand side functions is shown in Figure 16. Note that since all of the reaction rates are greater than zero the shape of the left-hand side of Equation (30) will always be concave down.

Second, the values of b need to be found given a value of a and Q . b can take two values because it can differ between the two trajectories of a going from $a_{\min}$ to $a_{\max}$ and $a_{\max}$ to $a_{\min}$. If a and Q are free parameters and manipulating $a^{k_2}b^{k_3}(1-a-b)^{k_1} = Q$, the values of b can be found from numerically solving

$$\left(\frac{b}{1-a}\right)^{k_3} \left[1 - \left(\frac{b}{1-a}\right)\right]^{k_1} = \frac{Q}{(1-a)^{k_1+k_3}a^{k_2}} \quad (31)$$

which can be solved similarly to the method used to solve for the minimum and maximum of a , or explicitly if $k_1 = k_3$. Once the values of b are solved for the value of c is trivially found through the relation $a + b + c = 1$. The value of $\frac{da}{dt}$ is used to differentiate the two solved values of b between branches, because $\frac{da}{dt} > 0$ when going from $a_{\min}$ to $a_{\max}$ and $\frac{da}{dt} < 0$ when going from $a_{\max}$ to $a_{\min}$. These values of b will be denoted as b_+ and b_- , respectively.

Finally, given a value of $Q/Q_{\max}$ from which the values of $a_{\min}$ and $a_{\max}$, and a method to find b given a and Q the following integral can now be performed to find the period T as a function of conserved quantity Q :

$$\begin{aligned} T(Q) &= \int_0^{T(Q)} 1 \, dt = \oint_Q \frac{da}{\left(\frac{da}{dt}\right)} \\ &= \int_{a_{\min}}^{a_{\max}} \frac{da}{\left(\frac{da}{dt}\right)} + \int_{a_{\max}}^{a_{\min}} \frac{da}{\left(\frac{da}{dt}\right)} \end{aligned} \quad (32)$$

or equivalently

$$\begin{aligned} T(Q) &= \int_{a_{\min}}^{a_{\max}} \frac{da}{a[k_1b_+(a) - k_3(1-a-b_+(a))]} \\ &+ \int_{a_{\max}}^{a_{\min}} \frac{da}{a[k_1b_-(a) - k_3(1-a-b_-(a))]} \end{aligned} \quad (33)$$

using Equation (4). Note that due to the symmetry breaking of having arbitrary rates k_j the integral must be split into two branches and computed separately.

Integrals over a period, such as in Equations (23) and (25), can then be performed.

C Wavelet Analysis

This appendix is a short summary of how the wavelet analysis was performed using reference [24] as a guide. Much like a Fourier transform where data is multiplied by sines and cosines to map the data frequency space, a wavelet transform is when data is multiplied by a wavelet function. The wavelet function used for the analysis in the main text is the Morlet wavelet, which consists of a plane wave modulated by a Gaussian:

$$\psi(\eta) = \pi^{-1/4} e^{i\omega_0\eta} e^{-\eta^2/2}, \quad (34)$$

where ω_0 is set to 6 for reasons that are detailed in reference [24]. A discrete data set $(x_n, \text{ where } n = 0, 1, \dots, N-1)$ is then wavelet transformed by convolution with the wavelet function

$$W_n(s) = \sum_{n'=0}^{N-1} x_{n'} \psi^* \left[\frac{(n' - n)\delta t}{s} \right] \quad (35)$$

where n is a discrete variable called the localized time index which controls where the wavelet is centered, s is a continuous variable called the wavelet scale which is directly related to the period, and δt is the time series time step (which is 1 time step in the simulations).

Since s is continuous it has to be discretized for computational purposes. It is discretized via $s_j = s_0 2^{j\delta j}$, where $j = 0, 1, \dots, J$ where s_0 is the smallest period, δj is your period resolution and $J = \frac{1}{\delta j} \log_2(N\delta t/s_0)$. For the analysis $s_0 = 2$ and $\delta j = 0.01$. An example of an analysis is given in the background heat map plot of Figure 5.

The power spectra of the wavelet transform is simply $|W_n(s)|^2$, for the purposes of finding the period with the strongest signal.

Author Contributions

K. R. Sanft and B. F. M. Intoy both contributed to the analysis, writing code, creating figures, and writing and editing the manuscript.

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