

# When can dispersal synchronize populations?

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## Abstract

While spatial synchrony of oscillating populations has been observed in many ecological systems, the causes of this phenomenon are still not well understood. The most common explanations have been the Moran effect (synchronous external stochastic influences) and the effect of dispersal among populations. Since ecological systems are typically subject to large spatially varying perturbations which destroy synchrony, a plausible mechanism explaining synchrony must produce rapid convergence to synchrony. We analyze the dynamics through time of the synchronizing effects of dispersal and, consequently, determine whether dispersal can be the mechanism which produces synchrony. Specifically, using methods new to ecology, we analyze a two patch predator–prey model, with identical weak dispersal between the patches. We find that a difference in time scales (i.e. one population has dynamics occurring much faster than the other) between the predator and prey species is the most important requirement for fast convergence to synchrony.

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## 1. Introduction

Synchrony over large spatial scales of oscillating populations is one of the most dramatic qualitative behaviors in population ecology and attempts to understand its mechanisms go back at least as far as Moran's research on the Canadian lynx (Moran, 1953). Synchrony has been observed in predator–prey interactions (Liebhold et al., 2004), disease dynamics (Grenfell et al., 2001), and many other exploiter–victim systems. Explanations of its causes have included both exogenous influences, such as climate, and endogenous factors, such as dispersal or other coupling mechanisms. There have been many studies, both theoretical and experimental, as reviewed in Liebhold et al. (2004), which attempt to elucidate the mechanisms leading to synchrony. In this paper, we attempt to show when migration is or is not likely to be the primary mechanism causing synchrony in a predator–prey model.

The theoretical exploration of the role of dispersal leading to synchrony has included studies of predator–prey systems at many spatial scales, with much of the focus examining

the dynamics of coupled predator–prey oscillators, often using just two patches (Jansen, 2001; Hastings, 2001; Blasius et al., 1999). Basic questions are aimed at understanding when the ultimate (in time) dynamics of the system lead to synchrony and what that means. The phenomenon of spatial synchrony leads us to re-examine what is meant by the term stability. Is the solution in two patches with both predator and prey oscillating in synchrony across space stable while spatially asynchronous oscillations are unstable?

Evaluating the importance of dispersal as the mechanism leading to observed patterns of synchrony naturally leads to the study of coupled oscillators. This topic has a long history, from the seminal work of Christiaan Huygens with pendulum clocks aboard large sailing vessels (Huygens, 1673), to applications ranging from chemical waves (Kuramoto, 1984), neurophysiology (Ermentrout and Kopell, 1991; Somers and Kopell, 1993), epidemic spread (Lloyd and Jansen, 2004), pacemaker cells in the heart (Peskin, 1975), and ecological populations (Blasius et al., 1999).

Although understanding whether synchronous solutions exist and are stable is the first step to understanding the role of dispersal in leading to observed patterns of synchrony, this is only part of the story. Spatially varying perturbations

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affecting natural populations tend to disrupt the patterns of synchrony and may be large enough to force synchronized individual populations far away from synchrony. Thus, rates of convergence to synchrony should play a crucial role in determining the behavior of the system over varying temporal and spatial scales.

While reflection and previous mathematical studies show that it should take a long time for weakly coupled oscillators to synchronize through dispersal, this is not well enough appreciated within the ecological literature. The time necessary for convergence to synchrony of weakly coupled oscillators is roughly the inverse of the coupling rate (Izhikevich, 2000), where time would be naturally measured in terms of the number of oscillations. This suggests that observations of synchrony in ecological systems, as reviewed in Liebhold et al. (2004), are a consequence of either systems being undisturbed for a very long time (highly unlikely); populations having high rates of dispersal over space; or other exogenous forces, such as the Moran effect (Moran, 1953).

There is, however, another possibility that results from the kinds of oscillations that actually occur in many predator–prey (or herbivore–plant) systems. As in the seminal paper by Ludwig et al. (1978), the dynamics of different organisms often occur on different time scales. In this study the characteristic time scale of the budworm is on the order of months, the time needed for trees to replace their foliage is 7–10 years, and the life span of the trees is between 100 and 150 years. This idea of different time scales has been beautifully explored in a series of theoretical papers as summarized by Rinaldi and Scheffer (2000). The presence of this kind of oscillation due to the existence of different time scales, as in the occurrence of a relaxation oscillator, can be used to understand how and when synchrony could take place on a fast enough time scale to be ecologically relevant. Recent mathematical studies have shown that if a system is a relaxation oscillator, i.e. one population experiences outbreaks of short time intervals separated by long periods of low population levels, as is the case in Ludwig et al. (1978), then the approach to synchrony can occur much faster than if a system consists of smooth oscillators, where both populations have similar time scales and the population by time graphs look closer to sine and cosine functions (Somers and Kopell, 1993).

In the predator–prey model that we examine, we allow for two different time scales: a fast time scale for the prey and a somewhat slower one for the predator, as in the class of models studied in Rinaldi and Scheffer (2000). In addition to this explicit difference in time scales, the dynamics of both species are slow when both population are very small (Rinaldi and Muratori, 1992). The combination of these two temporal factors enables this ecological model to behave similarly to a relaxation oscillator and allow for the possibility of fast convergence to synchronous behavior, even in the case of weak coupling. While the rate of convergence to synchrony also depends on the rate of dispersal, this difference in time scale is a necessary ingredient for rapid convergence to synchrony, as is demonstrated by our results and by Izhikevich (2000).

A recent experimental study (Fontain and Gonzalez, 2005) involving a rotifer and its prey, the green alga, highlights some of the time scale issues. Their goal was to determine whether the Moran effect or dispersal was the primary cause of synchrony. The striking result they found is that synchrony, presumably resulting from dispersal, occurred over just a few predator–prey cycles from initial conditions of populations out of synchrony.

In this paper we analyze a one-predator–one-prey system in two identical patches with symmetric migration. We use the theory of weakly coupled oscillators to derive a phase model from this original population model, and then use this phase model to directly discover what type of phase locking occurs and the rate of convergence to these phase locked states (Winfrey, 1967; Ermentrout, 1981; Kuramoto, 1984). Mathematically derived phase models have been extensively used as a way of analyzing networks of neurons (Izhikevich, 2000; Somers and Kopell, 1993; Ermentrout and Kopell, 1991; Lewis and Rinzel, 2003). Although the phase of ecological oscillators has been studied in order to determine the synchronization of these populations (Blasius et al., 1999; Blasius and Stone, 2000), analysis of phase models based on the approaches used in the neurophysiological studies have not yet been applied to these oscillators. This theory yields important new insights into the mechanisms of synchrony in ecological populations.

## 2. Model

We start with a simple model of a coupled predator–prey system in two patches. This yields a system of four coupled ordinary differential equations. The variables  $H_i$  and  $P_i$  represent the number of prey (or herbivores) and predators respectively in patch  $i$ . We assume logistic growth of the prey species, predation that follows a Holling Type II functional response, and a linear predator death rate. The parameter  $r$  is the intrinsic rate of increase of the prey population and  $K$  is its carrying capacity. The predation term includes parameters  $a$  and  $b$  which determine the functional response, with the parameter  $m$  representing the death rate of the predator. The loss of prey due to predation also depends linearly on  $c$  ( $c > 1$ ), a measurement of the ratio of the loss of prey to the gain in predators, implying that the loss in prey population due to predation is faster than the gain in predators.

We assume that the dynamics within each patch are identical and that migration, as represented by per capita rates  $D_H$  and  $D_P$ , is symmetric between the patches. Each patch represents a hunting region for the predator and a foraging region for the prey such that migration is independent from these activities. This model is the Rosenzweig–MacArthur model (Rosenzweig and MacArthur, 1963) in two patches

$$\begin{aligned} \frac{dH_i}{dt} &= rH_i(1 - H_i/K) - \frac{caP_iH_i}{b + H_i} + D_H(H_j - H_i) \\ \frac{dP_i}{dt} &= \frac{aP_iH_i}{b + H_i} - mP_i + D_P(P_j - P_i) \quad i, j = 1, 2; i \neq j. \end{aligned} \quad (1)$$

In order to simplify the model and gain a better understanding of which parameters are important in determining both the asymptotic and the transient behavior, we nondimensionalize (Nisbet and Gurney, 1982) our system. This process reduces the number of parameters from six to three (plus the two migration parameters) and (1) becomes

$$\begin{aligned} \frac{dh_i}{d\tau} &= \frac{1}{\epsilon} \left( h_i(1 - \alpha h_i) - \frac{p_i h_i}{1 + h_i} \right) + d_h(h_j - h_i) \\ \frac{dp_i}{d\tau} &= \frac{p_i h_i}{1 + h_i} - \eta p_i + d_p(p_j - p_i) \quad i, j = 1, 2; i \neq j \end{aligned} \quad (2)$$

where the following substitutions are made:

$$h_i = (1/b)H_i, p_i = [(ac)/(rb)]P_i, \tau = at, \alpha = b/K, \eta = m/a, \epsilon = a/r, d_H = D_H/a, d_P = D_P/a.$$

Notice that the time scale, with time denoted by  $\tau$ , is now determined by the predation rate. The  $\epsilon$  term is assumed to be small (i.e.  $r$  is larger than  $a$ ),  $0 < \epsilon \leq 1$ , with smaller  $\epsilon$  indicating a larger difference in the two time scales. The system becomes a relaxation oscillator in the limit as  $\epsilon$  approaches zero. We are interested only in the well known cases (Hastings, 1997) where the single patch dynamics produce a stable limit cycle, i.e.  $\alpha < 1$  and  $\eta < \frac{1-\alpha}{1+\alpha}$ .

### 3. Analysis

#### 3.1. A coupled predator–prey model

We start the analysis by considering the general form of a system of two coupled oscillators described by ordinary differential equations, which includes (2) as a special case

$$\begin{aligned} \frac{dX_1}{dt} &= F(X_1) + \delta W(X_2, X_1) \\ \frac{dX_2}{dt} &= F(X_2) + \delta W(X_1, X_2). \end{aligned} \quad (3)$$

In this form,  $X_1$  and  $X_2$  are vectors with components being the prey and the predator populations in patches 1 and 2 respectively. The function  $F$  describes the intrinsic dynamics of the system and depends only on the population levels in that patch, while  $W$  is a function of the populations in both patches representing the coupling. The parameter  $\delta$  is a small number to ensure that the system is weakly coupled. Writing our specific system (2) in the general form of (3) requires

$$\begin{aligned} X_i &= (h_i, p_i)^T \\ F(X_i) &= \left( \frac{1}{\epsilon} \left( h_i(1 - \alpha h_i) - \frac{p_i h_i}{1 + h_i} \right), \frac{p_i h_i}{1 + h_i} - \eta p_i \right)^T \\ W(X_i, X_j) &= \left( \frac{d_h}{\delta} (h_j - h_i), \frac{d_p}{\delta} (p_j - p_i) \right)^T \\ \delta &= \max(d_h, d_p). \end{aligned} \quad (4)$$

We define  $\delta$  as the maximum of the two coupling rates to ensure that both  $\frac{d_h}{\delta}$  and  $\frac{d_p}{\delta}$  are of order 1 or smaller. The superscript  $T$  refers to the transpose of the vector.

The purpose of the following mathematical analysis is to reduce the number of variables in this system and therefore

to gain a clearer picture of how the various parameters affect the dynamics. Since each patch follows a limit cycle solution, we can focus on the phase (the position or location in this limit cycle) of each patch, as opposed to the more classical technique of analyzing the dynamics of the four individual populations. Since we are concerned only with the difference in phase between the two patches, we can further simplify our model by focusing only on this one variable. In a more general setting, this technique can be applied to an  $n$  patch model with  $m$  populations in each patch. This reduces the system of  $n \times m$  equations describing the individual populations, to  $n - 1$  equations describing the difference in phases between each patch and an arbitrary patch.

We define the following: the phase of the oscillator refers to its position in the limit cycle and is parameterized in radians from 0 to  $2\pi$ ; phase locking occurs when the difference in phases between the two oscillators is constant over time; synchrony occurs when both patches have exactly the same phase; asynchrony is any behavior that is not synchronous; antisynchrony is a special type of asynchrony in which the phases are exactly opposite from one another; and near synchrony is a somewhat loose term that refers to asynchronous behavior that is close to synchrony (Pikovsky et al., 2001).

The effect of migration between the two patches on their change in phase difference over the length of one cycle is not constant over time. This effect is quantified by a function called the infinitesimal phase response curve or the PRC (Winfree, 1967; Kuramoto, 1984). The PRC measures the sensitivity of the phase to an outside perturbation based on the timing within the phase that this perturbation occurs and its effect in terms of advancing or delaying the phase. In our model, prey migration occurring at very low population levels of both predator and prey can have a very large impact on the dynamics of the system, much larger than predator or prey migration occurring at other times during the phase, as can be seen in Fig. 1.

#### 3.2. Weakly coupled oscillators

Oscillators are considered to be weakly coupled when the coupling (dispersal as controlled by  $d_h$  and  $d_p$ ) is small relative to the intrinsic dynamics (birth, death, predation) of the system. Specifically, it is necessary for the magnitude of  $F(X_i)$  to be at least an order of magnitude larger than that of  $\delta W(X_i, X_j)$ , for every  $X_i$  and  $X_j$ , as written in (3). This difference in magnitude is necessary in order that the intrinsic properties dominate the dynamics, therefore enabling the use of the method of averaging used in the following section. The parameters  $d_h$  and  $d_p$  need to be sufficiently small for this difference in magnitude to exist; their specific values will depend on the other parameters in (2). For our range of parameter values we choose  $d_h = d_p = .001$ . One way to understand what this means biologically is to determine what fraction of the population migrates during one predator prey cycle. For these values of  $d_h$  and  $d_p$ , this is approximately one per cent of the population of each species per cycle.

A system of weakly coupled oscillators modeling individual populations, as in (1)–(3), can be reduced in a mathematically

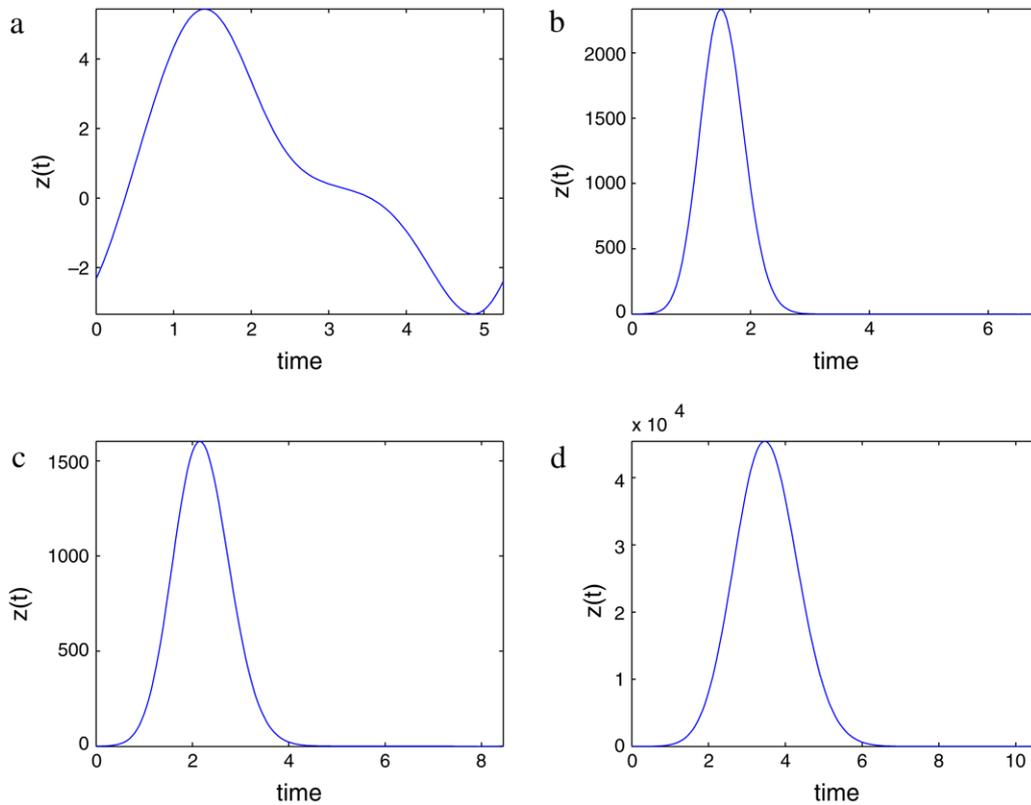


Fig. 1. The Phase Response Curve (PRC) of the prey population found by numerically approximating Eq. (7) for different parameter values, based on the original population model (2). The PRC measures the sensitivity of the prey species to an outside perturbation, such as migration. The y-axis represents the magnitude of the PRC or  $z(t)$ . The x-axis is time, with  $t$  ranging from 0 to  $T$ , the period of one unperturbed cycle. We vary the three non-dimensional parameters,  $\epsilon$ ,  $\alpha$ , and  $\eta$  across the four graphs. In (a)  $\epsilon = .1$ ,  $\alpha = .4$ , and  $\eta = .4$ , (b)  $\epsilon = .05$ ,  $\alpha = .28$ , and  $\eta = .38$ , (c)  $\epsilon = .1$ ,  $\alpha = .3$  and  $\eta = .3$ , and (d)  $\epsilon = .1$ ,  $\alpha = .4$ , and  $\eta = .15$ . Smaller values of any of these three parameters corresponds to larger differences in time scales and therefore a more sensitive system to prey perturbations when the prey population is small. This increased sensitivity can be seen in the very large maxima for (b), (c), and (d), with these maxima corresponding to the timing of small prey populations.

rigorous way (Ermentrout, 1981; Kuramoto, 1984), to a system of equations describing the phase of oscillation. This phase of oscillation is described by the variable  $\theta \in [0, 2\pi)$  which represents the position in the oscillation of the two populations. We briefly sketch the reduction to a phase model below.

### 3.3. Phase equations

The system of phase equations, when derived from Eq. (3), for two identical oscillators with symmetric coupling describes the change in the phase,  $\theta_i$ , of the oscillation in each patch with respect to time. The general two patch phase model is commonly written

$$\begin{aligned} \frac{d\theta_1}{dt} &= 1 + \delta H(\theta_2 - \theta_1) \\ \frac{d\theta_2}{dt} &= 1 + \delta H(\theta_1 - \theta_2). \end{aligned} \tag{5}$$

Eq. (5) incorporates the change in phase of the  $i$ th oscillator due to both its internal dynamics and coupling. The first quantity in the equations, the number 1, is a scaled version of the frequency of the unperturbed oscillator. The  $H$ -function can be found by evaluating an integral obtained by averaging the effect of coupling on the phase over one cycle. In the case of

two populations per patch this integral is

$$\begin{aligned} H(\phi) &= \frac{1}{T} \int_0^T z_h(t) W_h(h_0(t), h_0(t - \phi)) \\ &\quad + z_p(t) W_p(p_0(t), p_0(t - \phi)) dt. \end{aligned} \tag{6}$$

The integrand in (6) is comprised of the sum of the products of the functions  $z$  (defined below) and  $W$  (the coupling) for both the prey and predator components (the integrand is the dot product of  $z$  and  $W$ ). The parameter  $T$  is the period of the unperturbed oscillation and  $\phi = \theta_1 - \theta_2$  is the difference in phase between oscillator one and oscillator two. The function  $h_0(t)$  is the periodic solution, with  $h_0(t) = h_0(t + T)$  (analogous for  $p_0$ ), to the one patch version of (3). As can be seen in (6), the  $H$ -function is a scalar valued function depending on  $\phi$  and is very important in finding the nature and rate of convergence, as we show in the next section.

The function  $z(t)$ , in general, is a vector with  $m$  components (in our case  $z(t)$  has two components, with  $z(t) = (z_h(t), z_p(t))$ ) and is commonly referred to as the infinitesimal phase response curve or the PRC (Winfree, 1967; Kuramoto, 1984). The PRC measures the degree to which an arbitrarily short and infinitesimally small perturbation advances (positive valued) or slows (negative valued) the phase. The PRC is a function of one variable,  $t \in [0, T)$ , the timing of the

perturbation (see Fig. 1) and is found by solving the following linear differential equation and normalization (Kuramoto, 1984):

$$\frac{dz(t)}{dt} = -D_x F(X_0(t))^T \times z(t) \quad (7)$$

$$1 = z(t) \times X'_0(t).$$

$D_x F$  is the derivative matrix of  $F$  with respect to  $X$  and the superscript  $T$  refers to the transpose of the matrix.

### 3.4. Numerical analysis

Because of the non-linearities in (2), neither the  $H$ -function nor the PRC can be determined analytically. Therefore, we will numerically approximate these functions. We use the program XPP (see Ermentrout (2002) for a full explanation of this program) to find the periodic solution of the unperturbed oscillator. After that step, XPP can numerically solve the adjoint equation (7) backwards in time to obtain an approximation of the PRC. From there we numerically approximate the  $H$ -function by computing the integral in (6). Now we can transform the system of four coupled ordinary differential equations into two phase equations (5) as described above.

As we see in the following section, the  $H$ -function can be used to find the effect of migration on the difference of the two phases,  $\phi = \theta_1 - \theta_2$ . Note that this difference is measured as the difference in time between the two oscillators, not the difference in space. The differential equation  $\frac{d\phi}{dt}$  describes the change in this quantity over time and governs the type and number of phase locked states, their stability, and their rates of convergence.

### 3.5. Steady states

The steady states of this phase model, or phase locked states,  $\phi^*$ , occur when the difference in phases of the two oscillators is constant over time, i.e.  $\frac{d\phi}{dt} = 0$ . We are interested in the effect that the parameters have on the rates of convergence to the phase locked states as well as the regions in parameter space where different types of phase locking exist, i.e. synchrony or asynchrony. As we see below,  $\frac{d\phi}{dt}$  is a function of only one variable (phase difference,  $\phi$ ), easily enabling us to find both the nature of the stability and the convergence rates for each  $\phi^*$ . The type of phase locking and rate of convergence to that state will help in both explaining observed cases of synchrony in populations and determining whether it is likely that a species will persist both in shorter and in longer time scales.

The equation for  $\frac{d\phi}{dt}$  can be found by taking  $\frac{d\theta_1}{dt} - \frac{d\theta_2}{dt}$  from equation (5).

$$G(\phi) = \frac{d\phi}{dt} = \delta(H(-\phi) - H(\phi)) = -2\delta H_{\text{odd}}(\phi). \quad (8)$$

The function  $G(\phi) = \frac{d\phi}{dt}$  is a one-dimensional, continuous,  $2\pi$ -periodic function. As described above, the steady states of the phase equation occur when  $G(\phi^*) = 0$  and are stable when the slope of  $G(\phi^*) < 0$  and unstable when the slope of  $G(\phi^*) > 0$ . The rate of convergence at any given difference in

phase, measured in radians per time, is the magnitude of  $G(\phi)$  at that difference. Because the two oscillators are identical, they have a symmetrical effect on each other and therefore the  $G$ -function is odd.

The  $G$ -function being odd and  $2\pi$  periodic, guarantees steady states at synchrony as  $G(0) = G(2\pi) = 0$ , and antisynchrony as odd  $G$ -function implies  $G(\pi) = -G(-\pi)$  and periodic implies  $G(\pi) = G(-\pi)$ , and therefore  $G(\pi) = 0$  (Fig. 2). This does not imply anything about the stability of these steady states. Other asynchronous steady states may or may not exist depending on the values of the parameters.

By integrating  $G(\phi)$ , we can observe the convergence of any initial condition to a steady state. Because  $G(\phi)$  is continuous, the magnitude of  $G(\phi)$  approaches zero as  $\phi$  approaches  $\phi^*$ , thus the convergence of  $\phi(t)$  to a steady state is asymptotic (Fig. 3).

## 4. Results and discussion

### 4.1. Effects of synchrony

The importance of synchronization in ecological oscillators arises because populations exhibiting extreme oscillations often lead to very low levels of one or more species, increasing the chance of extinction (Hastings, 2001). As a result of migration, metapopulations or spatially explicit populations can mitigate the effects of these extreme oscillations through either recolonization or the ‘Rescue Effect’ (Brown and Kodric-Brown, 1977). Asynchronous populations can therefore increase the chance of persistence over longer time scales as is thought to be the case in the experimental studies of Huffaker (1958) and Holyoak (2000). However, if the population levels are similar over the spatial habitat, as is the case when synchronous behavior occurs, the oscillations will not decrease in severity, and extinction is again a likely outcome.

### 4.2. Time scale effects

We examine the effect a separation in time scales has on the behavior of (2). Decreasing any of  $\epsilon$ ,  $\alpha$ , or  $\eta$  increases the difference in time scales between the two species. A small  $\epsilon$ , ( $0 < \epsilon < 1$ ), increases the speed of every aspect of the intrinsic prey rates relative to those of the predator and in the limit as  $\epsilon$  goes to zero, the system becomes a relaxation oscillator. Decreasing  $\alpha$  increases the carrying capacity, thereby increasing both the magnitude of the prey outbreak and the time between outbreaks. A slower predator death rate  $\eta$  increases the amount of time necessary for the predator population to become sufficiently small so as to allow for a prey outbreak, increasing the amount of time in the cycle with low prey population.

A system that is more sensitive to a perturbation (migration) at a specific time in the phase, will have a PRC with a larger maximum magnitude at that point. In our model, a greater difference in time scales, specifically the more time spent near the saddle point at the origin, leads to a larger maximum magnitude of the prey component of the PRC. This can be seen by the large maximum magnitude in Fig. 1(b), (c), (d) as opposed to Fig. 1(a). Larger maximum magnitudes

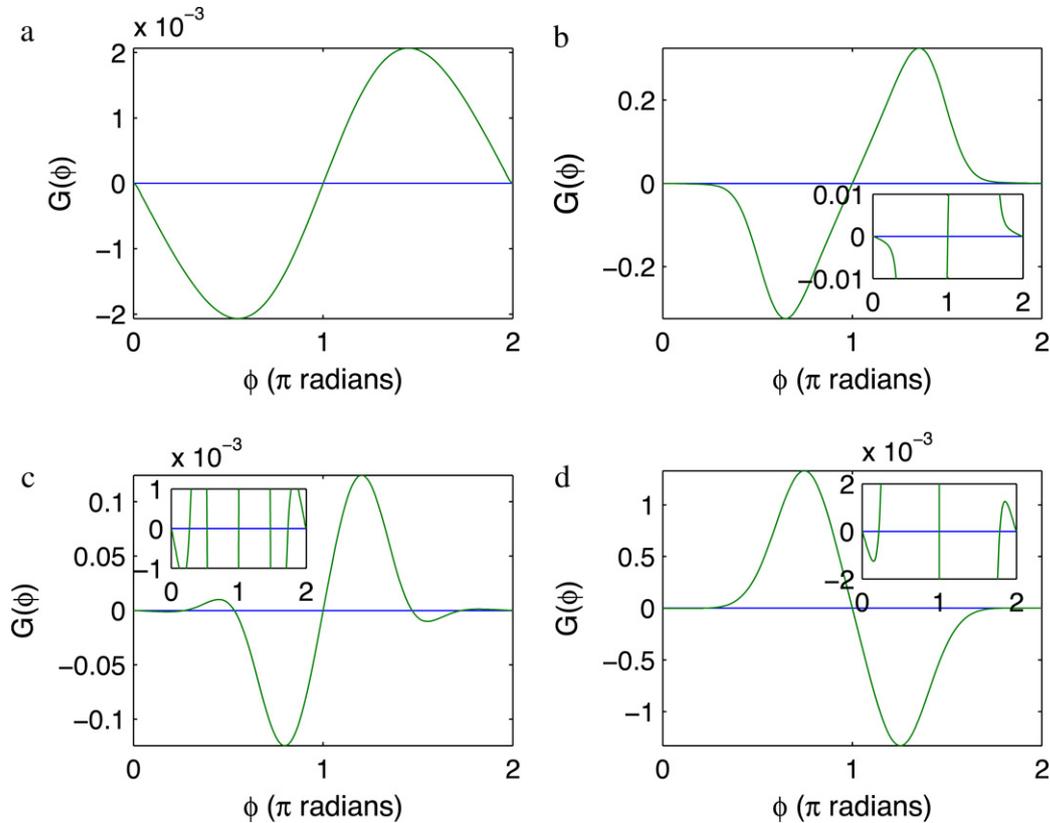


Fig. 2. Plots of the  $G$ -function, found using Eq. (8) for the same set of parameter values as in Fig. 1, with dispersal parameters  $d_h = d_p = .001$ . Insets show behavior near  $G(\phi) = 0$  not apparent because of the large magnitude of  $G(\phi)$  in the full figures. The  $G$ -function describes the rate of change of phase between two patches. The steady states or phase locked states occur when  $G(\phi) = 0$ , and are stable when the slope of  $G(\phi)$  is negative at the fixed point and unstable when the slope is positive. The larger maximum magnitude of the PRC corresponds to a larger maximum magnitude of these  $G$ -functions and faster convergence to the stable phase locked states and is the result of a greater separation in time scales. Case (a) will have the slowest convergence of the four while cases (b), (c), and (d) will all have very fast convergence at certain times in the phase accompanied by slower rates elsewhere, as we will see in Fig. 3.

of the PRC indicate that migration will have a greater impact on the convergence to a stable steady state, and the faster this convergence will be. This corresponds with the larger maximum magnitude of the  $G$ -functions in Fig. 2(b), (c), (d) and the fast convergence in Fig. 3(b), (c), (d), as opposed to Fig. 2(a) and Fig. 3(a).

For the cases with large time scale differences, the prey PRC has a maximum value several orders of magnitude larger than that of the predator. With only predator migration, the behavior of the oscillators is much less rich and for almost all parameter values we find only stable steady states at synchrony and an unstable steady state at antisynchrony, with much slower convergence rates than in the case of prey migration

In addition to playing a large role in the rate of convergence, varying  $\epsilon$ ,  $\alpha$  or  $\eta$  in (2) also affects the type of convergence. If all the other parameters are held constant and any one of these three parameters is increased (decreasing both the difference in time scales and the time spent near the saddle steady state with zero population for both species), either a subcritical pitchfork bifurcation or a saddle node bifurcation will occur, depending on the other parameters. In either case, when prey and predators have similar characteristic time scales, the result is a synchronous stable steady state and an unstable asynchronous steady state. Increasing the separation of these time scales yields both stable synchronous

and asynchronous (often antisynchronous) steady states with an additional unstable asynchronous steady state between the two stable states, see Fig. 2.

#### 4.3. Rate of convergence to synchrony

Since natural systems are continually subject to spatially varied environmental or other exogenous factors slow convergence to stable steady states of phase locking indicates that these steady states are unlikely to be reached. That synchrony has been observed in a variety of experimental and natural systems in ecology, as reviewed in Liebhold et al. (2004), indicates that the rates of convergence to synchrony must be very fast. Our research and others' (Somers and Kopell, 1993; Izhikevich, 2000) show that convergence to fixed points is much faster in the case of relaxation oscillators or oscillators having large time scale differences than those having a more sinusoidal type wave form. This implies that if dispersal is the mechanism causing these observed cases of synchrony, these time scale differences must exist.

The convergence rates are linearly dependent on the migration rates  $d_h$  and  $d_p$ . While larger migration rates allow for faster convergence to synchrony, it is more likely that time scale differences are causing the observed instances of synchrony as they have the ability to decrease convergence

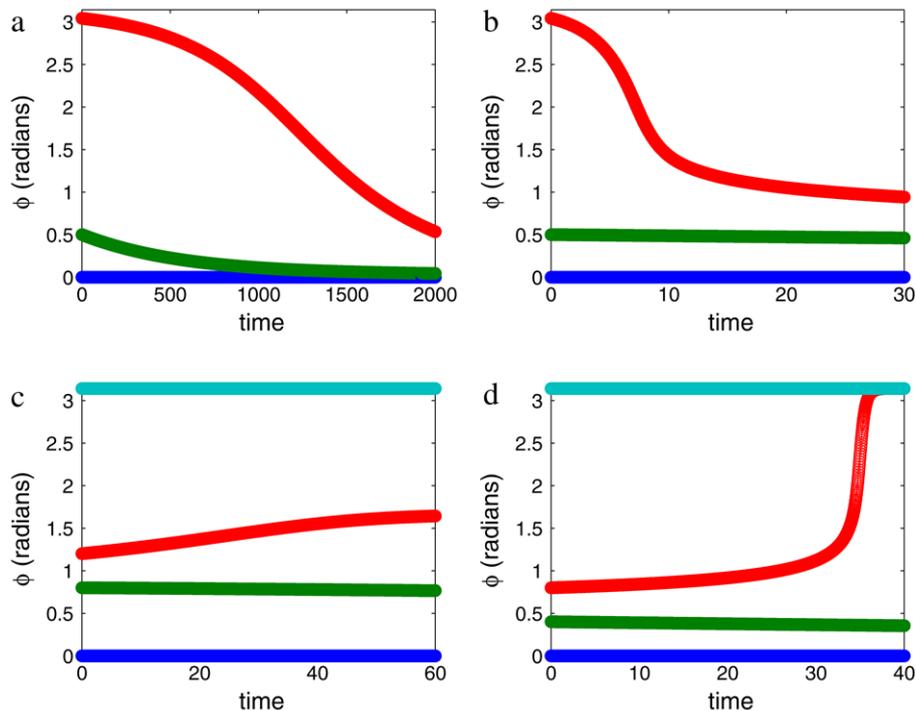


Fig. 3. Plots of the phase difference,  $\phi$ , between the two patches for different parameter values and initial conditions. The parameter values for the predator–prey dynamics and dispersal are the same as in Figs. 1 and 2. Notice that the  $x$ -axis, time, is not the same in each of the graphs and that time is scaled by the nondimensionalized reproductive rate of the prey. All four graphs have initial conditions of synchrony,  $\phi_0 = 0$ , which will always be stable for the range of parameters used in Eq. (2). Each graph also has two other asynchronous initial conditions: In (a) and (b)  $\phi_0 = .5, \pi - .1$ , (c)  $\phi_0 = .8, 1.1$ , and (d)  $\phi_0 = .4, .8$ . Graphs (a) and (b) both have only one stable fixed point, synchrony. The phase difference in (b) very quickly converges to near synchrony and then slowly converges to synchrony as the phase difference becomes smaller. The phase difference in (a) also converges to synchrony, but at a much slower and more uniform rate. The parameters used in (c) lead to a stable asynchronous fixed point which has very fast convergence, in addition to the stable synchronous state having much slower convergence. Case (d) has a stable asynchronous steady state with very fast convergence as well as a synchronous steady state with slow convergence. The time scale of convergence in figures (b), (c), and (d) corresponds to a few oscillations, whereas (a) takes much longer. In the cases of (a) and (b), the system will return to synchrony even after a perturbation, whereas in (c) and (d), only a small perturbation preserves synchrony, while a sufficiently large perturbation can result in the system converging to asynchronous behavior very quickly.

times by several orders of magnitude (provided that migration remains in the category of weak coupling) as in Fig. 3.

For parameters yielding both stable asynchronous and synchronous stable steady states, the convergence to asynchrony is much faster than the convergence to synchrony, as in Fig. 3(c) and (d). In this case, if a population is in synchrony and is perturbed past the unstable asynchronous steady state, convergence to the stable asynchronous steady state occurs very quickly, whereas the convergence to synchrony after a smaller perturbation is much slower.

## 5. Conclusion

There has been a longstanding debate in the ecological community over potential explanations for widespread synchrony in natural populations. Among the leading contenders are the Moran effect (Ranta et al., 1997b) and the synchronizing role played by dispersal. As even recent reviews show (Liebhold et al., 2004), distinguishing between these two explanations is a very difficult task and would, presumably, require more detailed information than is typically available.

Yet, as we first point out here, theoretical consideration of the response over time of systems of coupled predator–prey systems to perturbations of somewhat limited spatial extent

may provide clues to the causes of synchrony. A full study of large systems of coupled oscillators is very difficult, so here we begin with a more detailed analysis of the dynamics of two coupled patches, each having predator–prey interactions. In particular, as has not been sufficiently appreciated in the ecological literature, if dispersal is relatively weak, then the rate at which two such oscillating predator–prey systems would reach synchrony is very slow, often taking many cycles. The exception is the case in which the predator–prey oscillation is of the relaxation type, which enables convergence to synchrony in only a handful of cycles. This occurs only if there is sufficient separation of time scales in the dynamics, as is the case of the spruce budworm (Ludwig et al., 1978). Moreover, such a separation of time scales, should be observable in that either the amplitude of the oscillation of the prey population in the would be relatively large (as measured by the ratio of the maximum to the minimum population size), or the prey population would experience very rapid increases and decreases of its population, or both.

Thus, we suggest that dispersal can be the mechanism for synchrony only if either dispersal is strong, or if there is a separation of time scales between predator and prey. Meeting the second of these necessary conditions, that dispersal be the stabilizing mechanism, requires either a potentially long

time frame without an outside perturbation that would force the system in or out of synchrony, or a system with a large separation of time scales. We would expect, however, that if strong coupling by relatively large dispersal rates is the mechanism, than this dispersal should be directly observable or measurable. In our analysis, we have shown that prey migration is the major force in driving these systems to synchrony and that even when only one percent of the prey population migrates per cycle, synchrony may still occur in only a few cycles. Predator migration, so long as it is sufficiently small to allow for weak coupling, has very little impact on both the types of steady states and convergence rates.

Turning to specific ecological systems, we suggest that cases of recurring insect outbreaks, which typically do satisfy the condition of large amplitude oscillations (Liebhold and Kamata, 2000), are candidates for systems in which dispersal is the synchronizing mechanism. Conversely, systems like the hare-lynx oscillation (Ranta et al., 1997a) do not exhibit very large amplitude oscillations and therefore either strong dispersal or the Moran effect are likely explanations for synchrony.

Recently, there is a new thought that transient dynamics are important in understanding ecological systems (Hastings, 2004). Studies of transient dynamics have been difficult since the kinds of tools typically used to analyze models in ecology, like stability analysis, provide limited insights into transient dynamics. Additionally, simply running large numbers of numerical solutions can be both prohibitively time consuming and lead to analyses that are difficult to carry out automatically. The use of the phase model and the  $G$ -function approach which we have introduced into ecological systems here, from neuroscience, is a major step towards more comprehensive analyses of transient dynamics in ecological systems. Although some numerical work is still required, this analysis applies to a whole class of systems, and the restriction to weak dispersal is to a class precisely where transients may be important.

More work on extending the kind of analysis presented here to systems with heterogeneity, a greater number of species, or larger spatial extent is needed. However, the analysis presented here provides new insights into how detailed measurements of dispersal behavior or dynamics will provide further understanding into biological dynamics.

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