

1 Introduction

2 Heterogeneity in habitat plays a crucial role in population dynamics and is too frequently
3 ignored by ecologists and population biologists studying populations in space. Frequently,
4 both laboratory experiments and theoretical work are conducted in spatially homogeneous
5 settings, even though these conditions are unlikely to occur in natural systems. Qualitative
6 results and conclusions from these studies are then often generalized to hold for systems with
7 slight spatial heterogeneity. The assumption that these two types of systems produce similar
8 dynamics is not necessarily an accurate one. Here, we test this assumption by studying a
9 two patch heterogeneous predator-prey system and analyze the effect of small heterogeneity
10 on the phase dynamics of this system.

Incorporating the effect of spatial dynamics on ecological populations is essential in order
12 to understand the dynamics of many natural populations. An interesting and well observed
13 phenomenon is that of spatial synchrony in oscillating populations, as reviewed for ecological
14 populations in Liebhold *et al.* (2004), and for disease dynamics in Earn *et al.* (1998). Spatial
15 population structure influences the dynamics of a population both because individuals may
16 be more likely to interact with nearby neighbors and because spatial heterogeneity of habitat
17 may exist. Liebhold *et al.* (2006) and Hugueny (2006) simulated linear and log-linear discrete
18 time models, with the result that spatial heterogeneity decreases the level of synchrony,
19 regardless of whether the mechanism inducing this synchrony is spatially correlated noise or
20 dispersal. Kendall & Fox (1998) found that in a two patch, one population, discrete time
21 logistic map, small heterogeneity affects the ratio of the population levels in each patch as well
22 as the qualitative dynamical behavior. Earlier work on heterogeneity in ecological systems
23 has emphasized the role that heterogeneity might play in stabilizing unstable interactions
24 among hosts and parasitoids by looking at stability of steady states (Hassell & May, 1974).
25 A focus on dynamics of oscillatory behavior is a way to complement and extend these studies.

26 Empiricists and theoreticians have shown much interest in understanding what factor
or factors are most important in causing the observed instances of spatial synchrony. The

28 two most common explanations of synchronous behavior are stochastic exogenous influences,
such as climate, known as the Moran effect (Moran, 1953), and endogenous factors, such as
30 dispersal. Ranta *et al.* (1995) analyzed three different discrete time, one species population
models and found that dispersal alone can lead to synchrony. While Peltonen *et al.* (2002)
32 analyzed data for six forest insect species and found that dispersal was not likely to be
the primary process behind synchrony at larger spatial scales for any of the six species.
34 The interest in explaining synchronous behavior comes primarily from the observed and
theoretical phenomenon that persistence and synchrony are inversely related to each other
36 in metapopulations, as can be seen for predator and prey protists in Holyoak (2000).

In this paper, we study a two patch predator-prey model and analyze how spatial het-
38 erogeneity affects the phase dynamics of a system coupled by small amounts of migration.
Specifically, we look at both heterogeneities in the intrinsic dynamics and the coupling of
40 the two oscillators. While the mathematical derivation of phase models only holds for small
amounts of intrinsic heterogeneity, simulations show that these results can often be extended
42 to systems with moderate heterogeneity. This case of small migration is biologically rele-
vant since for populations characterized by large migration rates, this migration would be
44 directly observable or measurable and rapid convergence to synchrony would be the expected
outcome.

46 Much of the theoretical work involving phase dynamics of ecological oscillators has been
focused on coupled predator-prey oscillators (Blasius & Stone, 2000; Hastings, 2001; Jansen,
48 2001), which is the system we will study. We focus on the case where both predator and
prey are limited in their dispersal. This allows us to use the theory of weakly coupled os-
50 cillators (Malkin, 1949, 1956; Ermentrout, 1981; Kuramoto, 1984) to derive a phase model
from our original population model, and then to determine the type of phase locking occur-
52 ring and the rates of convergence to these phase locked states. We follow the method for
this model as introduced in Goldwyn & Hastings (2008) for the homogeneous system, now
54 allowing for and focusing on the important effects of spatial heterogeneity. The key result

from this previous study and from Izhikevich (2000) is that a difference in characteristic
56 time scale between the predator and the prey is necessary for convergence to phase locking
to occur on a biologically relevant time scale. Here, we investigate this difference in time
58 scale in the context of spatial heterogeneity and its effects on the phase locking behavior.

We analyze a spatially heterogeneous model to determine whether small levels of hetero-
60 geneity can alter the dynamics of a population in a way that has ecological consequences.
The consequences we are examining are a change in phase behavior of the system and a
62 decrease in synchrony, presumably leading to an increase in persistence. We incorporate
heterogeneity into both the local dynamics of the system (intrinsic heterogeneity) and into
64 the dispersal rates (asymmetrical coupling). Our analysis is quite general, aside from the
assumptions of weak coupling and weak intrinsic heterogeneity (clearly strong heterogeneity
66 would have a larger effect). In particular, the results should apply to any predator prey
model that is cyclic, with varying effect depending on the existence of a separation in time
68 scales that we analyze.

2 Model

70 2.1 Population Model

We study a model containing one predator and one prey species in two spatial patches.
72 This yields a system of four coupled ordinary differential equations. The prey (victims) and
predator populations are described by the variables V_i and P_i respectively, with the subscript
74 i referring to the patch. We assume logistic growth of the prey species in the absence of
predation with r_i as the intrinsic rate of increase and K_i as the carrying capacity. Predation
76 follows a Holling Type II functional response, with predation rate a_i and half saturation
coefficient b_i . The loss of prey due to predation also depends linearly on c_i ($c_i > 1$), a
78 measurement of the ratio of the loss of prey to the gain in predators. The predator has a
linear death rate m_i . Migration is a linear per capita rate and since we assume no immigration

80 or emigration out of the system, we have two small coupling parameters per species, D_{ij}^V and
 D_{ji}^V (not necessarily equal), which represent the prey migration from patch i to j and j to i
82 respectively (analogous for predator migration). These terms need to be sufficiently small in
order for the system to be weakly coupled and allow for the derivation to the phase model
84 that we do in the next section. 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
86 is the Rosenzweig-MacArthur model (Rosenzweig & MacArthur, 1963) in two patches

$$\begin{aligned}\frac{dV_i}{dt} &= r_i V_i (1 - V_i / K_i) - \frac{c_i a_i P_i V_i}{b_i + V_i} + D_{ji}^V V_j - D_{ij}^V V_i \\ \frac{dP_i}{dt} &= \frac{a_i P_i V_i}{b_i + V_i} - m_i P_i + D_{ji}^P P_j - D_{ij}^P P_i\end{aligned}\quad (1)$$

$i, j = 1, 2; i \neq j$

There are two different types of heterogeneity in (1). Intrinsic heterogeneities arise from
88 the parameters, a_i , b_i , c_i , K_i , m_i , and r_i , not being equal in both patches, asymmetrical
coupling occurs when parameters $D_{ij}^V \neq D_{ji}^V$ and/or $D_{ij}^P \neq D_{ji}^P$. It is the dynamics created
90 by these differences in intrinsic and coupling parameter values that we analyze and compare
to those for the homogeneous case.

92 Equation (1) can be rescaled, reducing the number of parameters and leaving only di-
mensionless quantities. This simplifies the analysis of the system by reducing the number
94 of parameters and allows us to see more specifically how heterogeneity affects each term in
the population model. We first express the heterogeneity by letting the intrinsic parameters
96 $q_1 = q$ and $q_2 = q + \sigma_q q$ ($q = a, b, c, K, m, r$), and the coupling parameters $D_{12}^V = D^V$ and
 $D_{21}^V = D^V + \sigma_{DV} D^V$ (same for coupling in P). The parameter σ_q is the percentage difference
98 between the value of the parameters in the two patches. We then use the following substi-
tutions as in Goldwyn & Hastings (2008)

$$v_i = V_i/b, p_i = [(ac)/(rb)]P_i, \tau = at, \alpha = b/K, \eta = m/a, \epsilon = a/r, d_{ij}^v = D_{ij}^V/a, d_{ij}^p = D_{ij}^P/a.$$

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With the above substitutions, (1) can now be written

$$\begin{aligned} \frac{dv_1}{d\tau} &= \frac{1}{\epsilon} \left(v_1(1 - \alpha v_1) - \frac{p_1 v_1}{1 + v_1} \right) + d^v((1 + \sigma_{dv})v_2 - v_1) \\ \frac{dv_2}{d\tau} &= \frac{1}{\epsilon} \left((1 + \sigma_r)v_2(1 - (1 - \sigma_k)\alpha v_2) - (1 + \sigma_a + \sigma_c) \left(1 - \frac{\sigma_b}{1 + v_2} \right) \frac{p_2 v_2}{1 + v_2} \right) + d^v(v_1 - (1 + \sigma_{dv})v_2) \\ \frac{dp_1}{d\tau} &= \frac{p_1 v_1}{1 + v_1} - \eta p_1 + d^p((1 + \sigma_{dp})p_2 - p_1) \\ \frac{dp_2}{d\tau} &= (1 + \sigma_a) \left(1 - \frac{\sigma_b}{1 + v_2} \right) \frac{p_2 v_2}{1 + v_2} - (1 + \sigma_m)\eta p_2 + d^p(p_1 - (1 + \sigma_{dp})p_2) \end{aligned} \tag{2}$$

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Our analysis focuses only on the case where the intrinsic dynamics lead to oscillatory behavior. This occurs when $\alpha < 1$ and $\eta < \frac{1-\alpha}{1+\alpha}$ (Hastings, 1997). The smaller each of α , η , and $\epsilon < 1$ are, the greater the separation in characteristic time scales between the prey and predator species, with the prey operating on a faster time scale.

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2.2 Phase Model

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Before formulating the phase model, we note the following definitions: the phase of the oscillator, θ , is measured in the interval $[0, 2\pi)$ and represents the location in the cycle of the predator-prey populations; phase locking indicates that the difference in the phase between the two oscillators is constant over time; synchrony occurs when the phases are equal; asynchrony is any non-synchronous phase locked behavior; and antisynchrony is a particular case of asynchrony occurring when the phases are exactly opposite from one another. If phase locking does not occur, then the system experiences phase drift. Figure 1 shows the behavior of the prey populations in patches one and two relative to each other for each of

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synchronous, asynchronous, and phase drift behavior.

118 A system of ordinary differential equations modeling individual populations, such as (1) or
 (2), can be transformed to a system of phase equations describing the phase of the oscillators
 120 so long as the original model produces a strongly attracting limit cycle in the absence of
 coupling, the coupling is sufficiently weak, the oscillators are only weakly heterogeneous,
 122 and these heterogeneities are the same order of magnitude as the coupling (Ermentrout,
 1981; Kuramoto, 1984; Winfree, 2001). Weak coupling implies that the intrinsic dynamics
 124 of the system are at least one order of magnitude larger than the coupling dynamics. For
 the parameter ranges used in our study, we find that this small migration leads to about
 126 one percent of the population migrating per cycle. A derivation of the phase model for the
 spatially homogeneous system of the Rosenzweig-MacArthur model can be found in Goldwyn
 128 & Hastings (2008). With the appropriate function F_i and W_i , the model of two weakly
 asymmetrically coupled non-identical oscillators, as formulated in (1) and (2), can be written
 130 as the general model

$$\begin{aligned}\frac{dX_1}{dt} &= F_1(X_1) + \delta W_1(X_2, X_1) \\ \frac{dX_2}{dt} &= F_2(X_2) + \delta W_2(X_1, X_2)\end{aligned}\tag{3}$$

The variable $X_i = (v_i, p_i)^T$ is the vector of the population sizes in patch i . The functions
 132 F_i and W_i represent the intrinsic dynamics of the populations and the migration in the i^{th}
 patch respectively. The dimensionless quantity δ measures the strength of dispersal.

134 In order to apply the theory of weakly coupled oscillators, we must first rewrite (3),

$$\begin{aligned}\frac{dX_1}{dt} &= F(X_1) + \delta W_1(X_2, X_1) \\ \frac{dX_2}{dt} &= F(X_2) + \delta f_2(X_2) + \delta W_2(X_1, X_2)\end{aligned}\tag{4}$$

Equation (4) is obtained directly from equation (3) if, $F_1(X_1) = F(X_1)$ and $F_2(X) =$
136 $F(X_2) + \delta f(X_2)$. We let $f_1(X_1) = 0$, so that the intrinsic heterogeneity is expressed only in
the equation of patch 2. The assumption of weak intrinsic heterogeneity implies that $\delta f_2(X_2)$
138 needs to be an order of magnitude smaller than $F(X_2)$ and the same order of magnitude as
 $\delta W_2(X_1, X_2)$. This implies that $\sigma_q < .01$, which yields a difference in intrinsic parameters
140 on the order of 1%. We now asymptotically expand the non-dimensional population model
(2) around $q_2 = q + \sigma_q q$ for each parameter. After ignoring higher order terms in σ_q , we find
142 $f_2(X)$. Writing our specific system (2) in the general form of (4) requires

$$\begin{aligned}
X_i &= [v_i, p_i]^T \\
F(X_i) &= \left[\frac{1}{\epsilon} \left(v_i(1 - \alpha v_i) - \frac{p_i v_i}{1 + v_i} \right), \frac{p_i v_i}{1 + v_i} - \eta p_i \right]^T \\
W_1(X_2, X_1) &= \left[\frac{d^v}{\delta} (v_2 - v_1 + \sigma_{dv} v_2), \frac{d^p}{\delta} (p_2 - p_1 + \sigma_{dp} p_2) \right]^T \\
W_2(X_1, X_2) &= \left[\frac{d^v}{\delta} (v_1 - v_2 - \sigma_{dv} v_2), \frac{d^p}{\delta} (p_1 - p_2 - \sigma_{dp} p_2) \right]^T \\
f_2(X_2) &= \left[\frac{1}{\epsilon} \left(v_2(\sigma_r - (\sigma_r - \sigma_K)\alpha v_2) - \left(\sigma_a + \sigma_c - \frac{\sigma_b}{1 + v_2} \right) \frac{p_2 v_2}{1 + v_2} \right), \left(\sigma_a - \frac{\sigma_b}{1 + v_2} \right) \frac{p_2 v_2}{1 + v_2} - \sigma_m \eta p_2 \right]^T \\
\delta &= \max(d^v, d^p)
\end{aligned} \tag{5}$$

144 Now, we can derive a phase model describing the change in the phase, θ_i , of each oscillator
over time. The phase model consists of two equations describing the phase of each oscillator
146 as opposed to our original four equation population model.

$$\begin{aligned}
\frac{d\theta_1}{dt} &= \omega_1 + \delta H_1(\theta_2 - \theta_1) \\
\frac{d\theta_2}{dt} &= \omega_2 + \delta H_2(\theta_1 - \theta_2)
\end{aligned} \tag{6}$$

The term ω_i is the frequency of the i^{th} oscillator without coupling and is found by adding

148 the scaled intrinsic frequency of the unperturbed homogeneous oscillator to the effect of
heterogeneity on the frequency of the oscillator. This effect can be found by exploiting a dif-
150 ference in time scales between the unperturbed period and the difference of the homogeneous
and heterogeneous periods through the method of averaging (Kuramoto, 1984),

$$\omega_i = 1 + \frac{\delta}{T} \int_0^T z(t) \cdot f_i(X_i^0(t)) dt \quad (7)$$

152 This average is the integral of the dot product of the functions $z(t)$ (the sensitivity of
the phase of the oscillator to perturbations, described below) and $f_i(X_i^0(t))$ taken over one
154 period. The dot product is used because this is a sum of the effects of heterogeneity on
the prey and predator populations. The functions $X_i^0(t)$ are the limit cycle solutions to
156 the unperturbed oscillator in patch i and are different if the intrinsic parameter values are
different.

The functions, $H_i(\phi)$, measure the effect of coupling on the phase of the oscillator. These
functions are found by averaging the coupling and the sensitivity of the phase to coupling
for each population over one cycle,

$$H_i(\phi) = \frac{1}{T} \int_0^T z(t) \cdot W_i(X_i^0(t), X_i^0(t - \phi)) dt \quad (8)$$

The key function in determining both ω_i and $H_i(\phi)$ is $z(t)$, also known as the infinitesimal
phase response curve or the PRC (Winfree, 1967; Kuramoto, 1984). The PRC measures the
effect of an infinitesimally small and arbitrarily short perturbation on the phase dynamics.
Positive values for the PRC indicate that a perturbation will advance the phase of the
oscillator, while negative values indicate a delay in the phase. The magnitude of this function
measures the degree to which the phase is altered. The PRC can be found by evaluating the

following differential equation and normalization (Kuramoto, 1984).

$$\begin{aligned}\frac{dz(t)}{dt} &= -[D_x F(X^0(t))]^T z(t) \\ 1 &= z(t) \cdot (X^0)'(t)\end{aligned}\tag{9}$$

158 The term $D_x F$ refers to the derivative of F , the function $X^0(t)$ is the periodic solution to the unperturbed oscillator, and the superscript T indicates the transpose of the matrix.

160 2.3 Steady States

We are ultimately interested in the difference in phase between the two oscillators, defined 162 as $\phi = \theta_1 - \theta_2$. This difference is the time lag between the phase of the two oscillators and not the spatial lag. Our goal is to analyze how this quantity changes over time by studying 164 its time derivative, $\frac{d\phi}{dt}$. To determine $\frac{d\phi}{dt}$, we simply take the difference of the two equations in (6),

$$G(\phi) = \frac{d\phi}{dt} = \omega + \delta(H_1(-\phi) - H_2(\phi)) = \omega + H(\phi)\tag{10}$$

166 The steady states of the phase model, ϕ^* , called the phase locked states, occur when the difference in the two phases remains constant over time, $\frac{d\phi}{dt} = G(\phi) = 0$. The function 168 $G(\phi)$, called the G-function, is a one dimensional function and therefore the phase locked states are stable when its slope is negative at a fixed point and unstable when the slope is 170 positive. The rate of convergence to a phase locked state at any given difference in phase is the magnitude of the G-function. Convergence to these phase locked states can then be 172 found by integrating this G-function.

The effects of intrinsic heterogeneity and asymmetrical coupling are separated into the 174 term $\omega = \omega_1 - \omega_2$, see (7), and $H(\phi)$, called the H-function (8), respectively. The PRC is used to find both ω and the H-function, and therefore controls both the effects of migration 176 and heterogeneity on the phase dynamics of each oscillator.

If the two oscillators have identical intrinsic dynamics then $\omega = 0$, if coupling is symmetric
178 then $H_1 = H_2$. If both of these events occur, the change in time of the phases difference is
equal to negative two times the odd part of $H_i(\phi)$, as is the case in Goldwyn & Hastings
180 (2008).

3 Results

182 We use the theory of weakly coupled oscillators (Ermentrout, 1981; Kuramoto, 1984) to derive
a phase model from the two patch predator-prey system in equation (1) in order to analyze
184 the effect of heterogeneities on the phase behavior of this system. The crucial function in
studying the phase dynamics of an oscillatory system is the phase response curve (PRC or
186 $z(t)$, equation (9)). This function measures the degree to which an outside perturbation
advances or delays the phase. Because this system is non-linear, the PRC cannot be found
188 analytically. We use the numerical program XPP to find a numerical approximation for the
PRC (for details on XPP see Ermentrout (2002)). Using this approximation, we analyze
190 how intrinsic heterogeneities and small (possibly asymmetrical) coupling affect the change
in phase difference over time between the two oscillators (see Fig. 1 in Goldwyn & Hastings
192 (2008) for graphs of the PRC for this system with the same parameter values used in Figs.
2, 3, 4).

194 Heterogeneity in intrinsic dynamics creates a frequency difference, ω from equation (7),
between the two oscillators. The effect of coupling on the phase difference is quantified by
196 the H-function (8). Using the term ω and the H-function, we find the differential equation
(10), known as the G-function which governs the change in the phase difference between the
198 two oscillators over time. We see from this equation the very important result that the effect
of intrinsic heterogeneities and asymmetrical coupling are independent from one another
200 and therefore can be examined separately. Because the G-function is a one dimensional,
continuous, 2π periodic function, finding the phase locked states (when $G(\phi) = 0$) and

202 their convergence rates is easily done. Several different arrangements of phase locked states
 can occur, depending on the parameter values of the system (Figs. 2, 3, 4). The phase
 204 locking behavior for the special case of two spatially homogeneous predator-prey oscillators
 is examined in Goldwyn & Hastings (2008). The important result from that paper is that in
 206 order for convergence to a phase locked state to occur on a biologically relevant time scale,
 a separation between the characteristic time scales of the prey and predator must exist.
 208 Decreasing any of the three parameters α , η , or ϵ from equation (2) increases this separation
 in time scales. Furthermore, prey migration is much more important than predator migration
 210 in driving the system to phase locked behavior when this difference in time scales exist.
 Specifically, positive perturbations to the prey population when it is at very low density
 212 greatly increase the phase of the oscillator. Here we restrict our focus to the differences in the
 G-function, and therefore on the dynamics of the system, created by intrinsic heterogeneity
 214 and asymmetrical coupling.

3.1 Heterogeneity in Intrinsic Dynamics

216 In order to examine the effect of heterogeneity in intrinsic dynamics on the two oscillators we
 first look at the phase behavior in the special case of homogeneous oscillators with symmetric
 218 coupling. Homogeneous oscillators arising from (1) always have a synchronous stable steady
 state and a (stable or unstable) antisynchronous steady state. Other asynchronous states
 220 may or may not exist depending on the parameter values. The term arising from intrinsic
 heterogeneity is $\omega = \omega_1 - \omega_2$, and it vertically shifts the G-function by that difference (Figs.
 222 2, 3, and 4).

In the case where synchrony and antisynchrony are the only phase locked states, a saddle
 224 node bifurcation occurs at the critical value of $\omega_c = |\max(H(\phi))|$, where the maximum is
 taken over the values of ϕ , the difference in phase between the two oscillators. The two phase
 226 locked solutions disappear when $|\omega| > \omega_c$. This occurs if either the effect of coupling on the
 change in phase difference is small for all phase differences or the effect of heterogeneity is

228 large. The shift resulting in no phase locked states is known as phase drift and can be seen
in figure 2(c). If $|\omega| < \omega_c$, then the shift will move the steady states away from their original
230 locations of synchrony and antisynchrony as in figure 2(b). This bifurcation in steady states
of phase locking due to heterogeneity in frequency of oscillation is discussed in Chapter 4 of
232 Strogatz (1994) for the flashing of male fireflies.

In Blasius *et al.* (1999), a tritrophic predator-prey resource model that was able to gen-
234 erate dynamics having uniform phase chaotic amplitude (UPCA) was used to study the well
known Canadian hare-lynx cycle. With a two patch coupled model, they found that in-
236 creasing the coupling rate from no coupling past two numerically determined thresholds led
from phase drift, to asynchrony, to synchrony (see Fig. 2 in that paper). This is the same
238 phenomenon that we see in Fig. 3 in this paper when the effect of intrinsic heterogeneity on
the frequency of the oscillator is decreased.

240 If the homogeneous system has stable asynchronous phase locked states in addition to
the stable synchronous state, then shifting the H-function by ω can eliminate, by means of
242 a saddle node bifurcation, some, but not all of the phase locked states. This occurs when ω
is larger than one or more of the local extrema of the H-function. The synchronous stable
244 states are usually the first to be eliminated by this saddle node bifurcation, leaving only
asynchronous stable steady states as in Fig. 3. This shift will also move the other steady
246 states away from their original locations. We find that differences as small as 0.1% in a
given parameter value can be sufficient to allow for either type of saddle-node bifurcation
248 discussed above, and therefore lead to qualitative changes in the behavior of the system.

As discussed in Goldwyn & Hastings (2008), the H-function has a larger maximum mag-
250 nitude when there is a difference in time scales between the prey and predator populations
and this maximum magnitude can vary by many orders of magnitude, as is the case in Fig. 3
252 and 4 as opposed to Fig. 2. The reason behind these differences in the maximum magnitude
of the H-function in the case of a large difference in time scales is because the unperturbed
254 dynamics have a saddle steady state point at the origin (where both the prey and predator

populations are zero). The dynamics of the system are very slow when the populations are
256 near this point. Larger differences in time scales between the predator and the prey lead the
system getting closer to this saddle point, where the effect of an external perturbations to
258 the prey is very large. This yields a large maximum magnitude of the H-function.

Our analysis shows that while the magnitude of ω varies due to the type of intrinsic
260 heterogeneity and the specific dynamics of the system, it is not necessarily larger when
there is a difference in time scale between the two populations. For our range of parameter
262 values, the maximum value of $|\omega|$ is on the order of 10^{-2} . This indicates that for intrinsic
heterogeneity to cause phase drift in our model with symmetric coupling, it is necessary both
264 that there is not a separation of time scales between the two predator and prey species, and
the heterogeneities produce large sufficiently ω .

266 **3.2 Asymmetric Coupling**

We analyzed two different types of asymmetric coupling. One occurs when a larger percent-
268 age of the population of predator or prey migrates from patch i to patch j , than patch j
to patch i . The most extreme case of this is one directional migration. The other type of
270 asymmetric coupling occurs when the two patches are of different sizes (these patches can
still have homogeneous intrinsic dynamics as the populations can be thought of as densities).
272 While the rates of migration may be the same in either direction, clearly migration from the
larger patch to the smaller patch has more of an impact than migration occurring in the op-
274 posite direction. A greater migration rate from patch i to j behaves qualitatively similarly
to a system with patch i being larger than j . These two types of asymmetrical coupling
276 are similar in their effects on the phase behavior of the system, so we will only explain the
details of asymmetries in direction of coupling here.

278 In this model, small levels of asymmetrical coupling do not have large effects on the G-
function, and therefore the phase dynamics. This is in contrast with intrinsic heterogeneity
280 where even very small levels of heterogeneity can have large effects on the G-function and

qualitatively change the phase dynamics of the system.

282 Whereas heterogeneity in intrinsic dynamics shifts the G-function vertically by the term
284 ω , the effect of asymmetric coupling depends on the phase difference and therefore it alters
286 the shape of the G-function as in Fig. 4(b). We also notice that for the case of a difference
288 in time scale between the prey and predator species, asymmetries in prey migration have
290 a larger effect on the G-function than those in predator migration. As the asymmetry
292 in coupling is increased, the steady states of phase locking will go through saddle node
294 bifurcations similarly to what occurs when intrinsic heterogeneity is increased. In this case
296 the most asynchronous steady states are the first to be eliminated. For systems that are
298 very strongly asymmetrically coupled (as is the case in one directional migration), $H(\phi) = 0$
300 occurs only when ϕ is near synchrony. This indicates that an intrinsically homogeneous,
302 strongly asymmetrically coupled system will only have one stable steady state which is very
304 near to synchrony. This steady state will correspond to patch 1 being slightly ahead in phase
of patch 2 if all the migration is moving from patch 1 to patch 2. In that sense patch 1 is
pulling or synchronizing patch 2 to itself. We can see from Fig. 4(b), that the G-function
is very small when positive. Therefore if this asymmetrically coupled system has intrinsic
heterogeneity that increases the frequency of oscillator 2 (shifting the G-function down),
such as a smaller predation rate in patch 2 than in patch 1, there will be no phase locked
states and the system will exhibit phase drift, Fig. 4(c). This is a consequence of the PRC
being almost entirely positive for this range of parameter values. Oscillator 2 will be only
positively perturbed by oscillator 1, increasing its frequency. If oscillator 2 has a higher
frequency than oscillator 1, then the coupling will never allow for oscillator 1 to slow it down
sufficiently to allow for phase locking. Notice that phase drift was not a possible outcome
with the parameters used in Fig. 4 with intrinsic heterogeneity alone.

4 Discussion

306 The fundamental question that we address in this paper is: what are the effects of intrinsic
heterogeneity and asymmetrical coupling on the dynamics of spatially extended populations?
308 Specifically, we analyze the difference in behavior between spatially heterogeneous and ho-
mogeneous populations to see if even small heterogeneity can produce qualitatively different
310 behavior. Since it is much easier to formulate and analyze spatially homogeneous popula-
tions in a theoretical setting, it is these models that have been more extensively studied.
312 The results from these studies are then often generalized and assumed to hold for systems
having slight heterogeneities. For the phase model analyzed here, just a 0.1% difference in
314 parameter values can produce qualitatively different phase behavior. This shows the power
and importance of small heterogeneity to produce dynamics that are observably different. It
316 also indicates the risk of assuming that results for a homogeneous model or experiment will
also hold for heterogeneous environments.

318 In our two patch model, intrinsic heterogeneity can manifest itself through different prey
birth rates, prey carrying capacities, predation rates, predator half saturation coefficients,
320 or predator death rates. These differences between the two model patches can result from
a variety of biological factors including unequal amounts of resources for prey to consume,
322 varying habitat which impacts the ability of the prey to evade predation, varying population
densities, and others.

324 Results from our analysis indicate that even slight differences in any of these attributes
can yield dramatically different behavior for the heterogeneous case as opposed to the homo-
326 geneous one. The differences become more pronounced when the prey and predator operate
on similar characteristic time scales, at which point even small intrinsic heterogeneity pre-
328 vents synchronous behavior from occurring. While the results based on the phase model
strictly hold only in the case of small heterogeneities, simulations indicate that the qualita-
330 tive results will also hold for larger heterogeneities.

Another possible heterogeneity in the system is the occurrence of asymmetrical coupling,

332 or dispersal. Unlike with intrinsic heterogeneity, in order for asymmetric coupling to have
a qualitative effect on the system, the asymmetry must be somewhat large (on the order
334 of 10%), before qualitative changes in the dynamics occur. One example of asymmetri-
cal coupling is when migration does not flow evenly in both directions, as would occur in
336 the presence of air or water currents. Another possibility is patches having different sizes
but identical population densities. The combination of asymmetrical coupling and intrinsic
338 heterogeneity is also very likely to reduce or prevent synchrony from occurring.

One type of behavior that is possible with two heterogeneous patches is that there will
340 be no phase locked states and the system will have phase drift. Phase drift behavior is
qualitatively different from any type of phase locking, and heterogeneity which creates this
342 behavior is clearly much different from the homogeneous case. The exception is if the drifting
of the phases is slow. Natural populations are often observed on short time scales and if the
344 phase drift is sufficiently slow, which occurs when the G-function is close to zero for some
given phase difference (as occurs for the ϕ value corresponding with the minimum of $G(\phi)$
346 in Fig. 2 and the local maxima of $G(\phi)$ in Fig. 4), it may be difficult to differentiate from
phase locked behavior.

348 Careful studies of spatiotemporal dynamics of coupled predator-prey systems in nature
are, of course, very difficult, so the current results must be used as more of a guide. However,
350 more careful studies have been made of the dynamics of a different exploiter-victim system,
namely human childhood diseases. A particularly well studied case is measles in the United
352 Kingdom. This is essentially an exploiter victim system having heterogeneities caused by
extreme differences in city size from London to the very smallest cities. In this case, the
354 result is a traveling wave of disease outbreaks, as analyzed by Grenfell *et al.* (2001). Although
the systems may seem extremely different, our results on asynchronous phase locking with
356 heterogeneity are consistent with the idea of traveling waves. Our work approaches the
problem from the view of a simple model whose behavior we attempt to understand using
358 analytic tools to characterize classes of dynamic behavior and thus complements the data

based approach of Grenfell *et al.* (2001). One theme we emphasize, namely the importance of
360 perturbations at the ‘trough’ of the cycle, is consistent with the discussion of the importance
of cases that set off epidemics. Also, we focus here on the role of heterogeneity. Future work
362 extending our analytical approach to look at epidemic systems would be very interesting.

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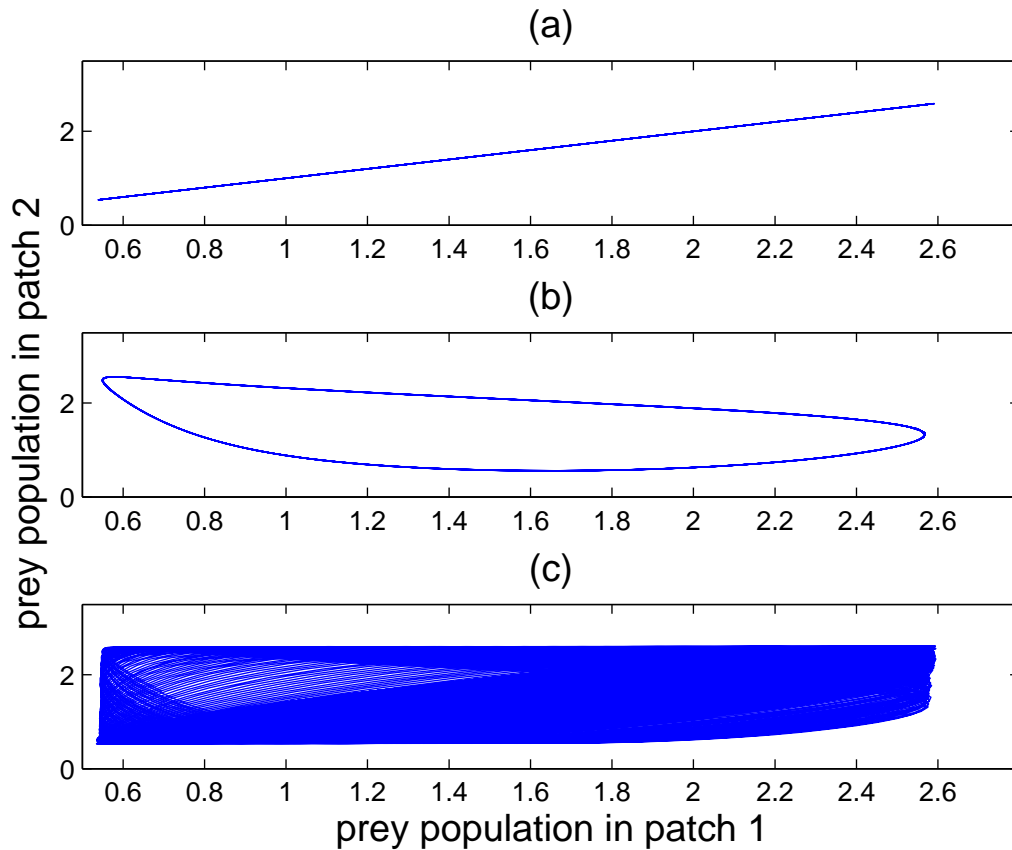


Figure 1: Plots of the prey populations in patch one versus patch two after the transient behavior is finished. The parameters in (a) are $a = 1$, $b = 2$, $c = 4$, $K = 5$, $m = .4$, and $r = 10$. This yields a synchronous steady state and equal populations in the two patches. In (b) asynchronous behavior occurs due to heterogeneity in the predator death rate, m , and the populations form a closed loop. In (c), heterogeneity in the carrying capacity, K , causes phase drift which results in no correlation between the populations in patches one and two.

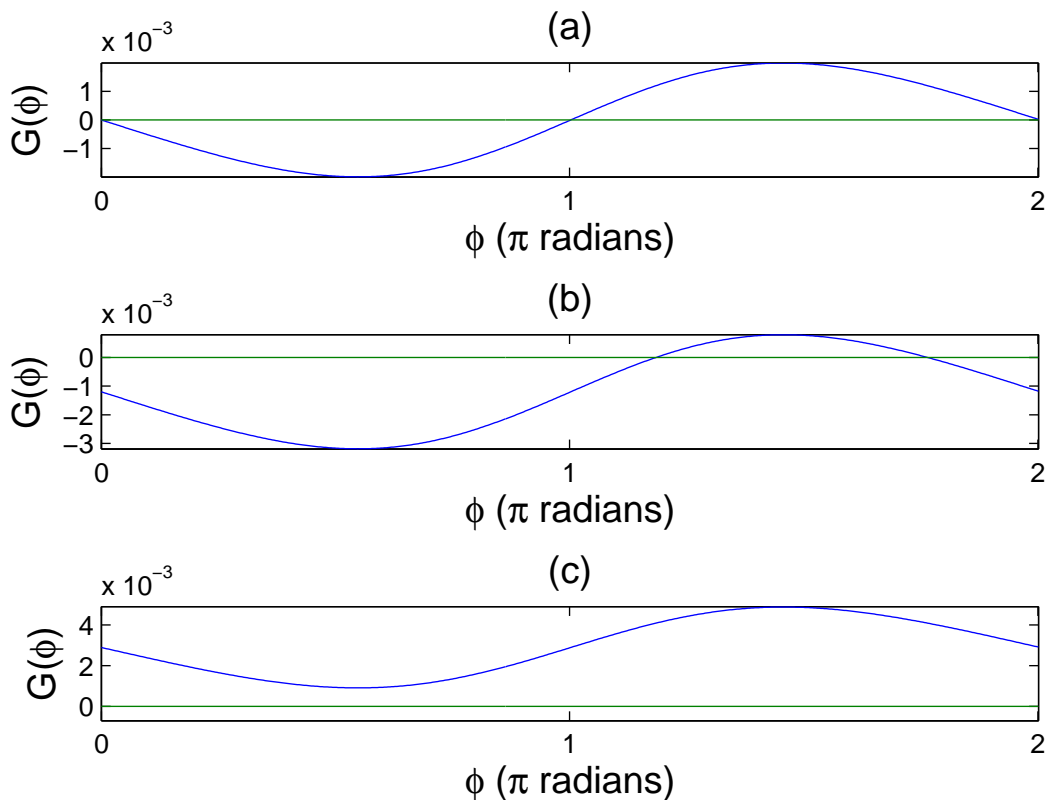


Figure 2: Plots of the G-function which describes the rate of change of the phase differences between two oscillators. The parameters in each of the graphs are the same as in Fig 1. (b) includes a 0.1% increase in the predator death rate, m , in patch 2, increasing the frequency of oscillation in that patch and shifting the G-function down. (c) has the same percentage increase in the carrying capacity, K . The sensitivity of the oscillators to the heterogeneity in carrying capacity, leads to a sufficiently large difference in frequency, to lead to phase drift, whereas the change in the predator death rate in (b) still leaves a stable phase locked state, though it is no longer perfectly synchronous.

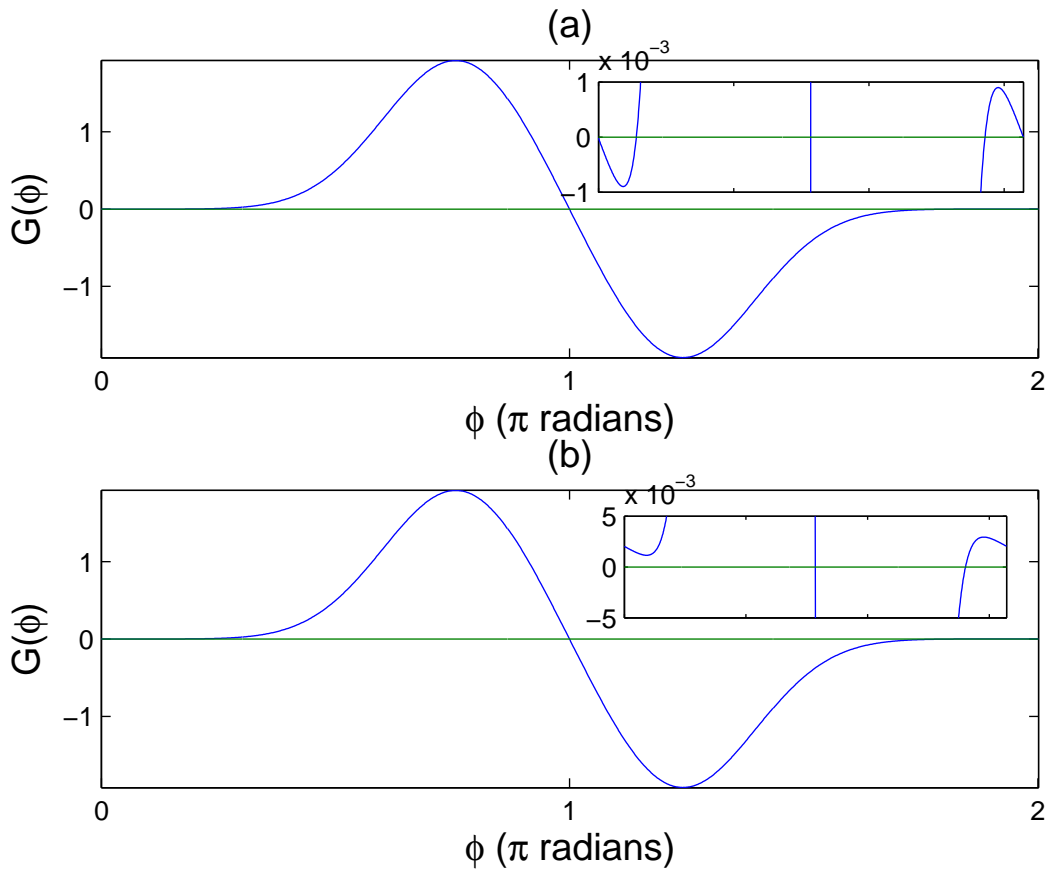


Figure 3: Plots of the G-function with (a) having parameter values $a = 1$, $b = 2$, $c = 5$, $K = 5$, $m = .15$, and $r = 10$. Inset shows behavior near $G(\phi) = 0$. Heterogeneity is introduced in (b) with the carrying capacity, K , increased by 0.1%. In the homogeneous case (a), there are stable phase locked states at synchrony and antisynchrony. The difference in frequency created by the heterogeneity removes the synchronous stable state and leaves the system with only one near antisynchronous stable phase locked state.

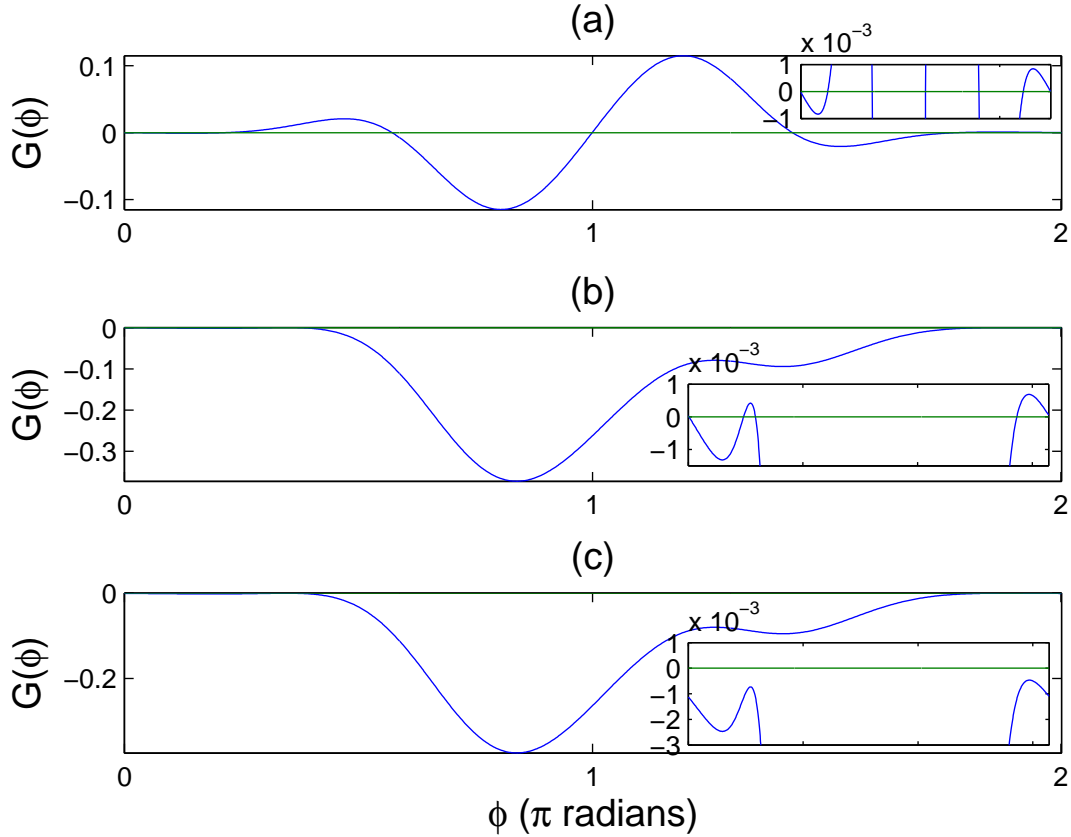


Figure 4: Plots of the G-function with (a) having parameter values $a = 1$, $b = 1.5$, $c = 4$, $K = 5$, $m = .3$, and $r = 10$. Graphs (b) and (c) have asymmetry with 40% less migration going from patch 2 to patch 1 than the opposite direction. In graph (c), intrinsic heterogeneity is introduced with the predation rate, a , decreased by 0.1% in patch 2. Inset shows behavior near $G(\phi) = 0$. In graph (a) there are stable steady states at synchrony and asynchrony, and unstable steady states at antisynchrony and near synchrony. Asymmetry alone leads to stable synchronous and near synchronous states. Adding heterogeneity by decreasing the predation rate in patch two slows the frequency of oscillation of that patch and shifts the G-function downwards. This removes all phase locked states and yields phase drift.