

## MIGRATION ALONE CAN PRODUCE PERSISTENCE OF HOST-PARASITOID MODELS

It has long been recognized that the unstable equilibrium of a single-patch predator-prey model cannot be stabilized by diffusive coupling with identical patches, since the coupled system acts exactly like the single-patch system if the patches are synchronized (Maynard Smith 1974; Allen 1975; Reeve 1988). Persistence of coupled locally unstable systems depends on the maintenance of asynchrony among the populations sufficient to buffer crashes (den Boer 1968; Allen 1975; Crowley 1981; Reeve 1988, 1990; Taylor 1988). Three mechanisms have been proposed to maintain this asynchrony (Taylor 1988): heterogeneity among patches, low but nonzero migration rates, and large numbers of patches.

Heterogeneity among patches can take many forms. Several sorts of permanent fixed heterogeneity, such as variability in host apparency (Bailey et al. 1962), existence of refugia (Hassell 1978), biased dispersal (Comins and Blatt 1974), and fixed differences in growth rates and other parameters (Chewning 1975), have been shown to enhance the local stability of host-parasitoid or predator-prey models. Such heterogeneity acts implicitly in the attack rates experienced by individual hosts (Hassell and May 1988; Hassell and Pacala 1990) and thus underlies the stable dynamics possible with the negative-binomial model of host-parasitoid dynamics (May 1978). Heterogeneity produced by adding uncorrelated stochasticity to the parameters governing otherwise identical coupled system has been recently discussed and reviewed in depth by Reeve (1988).

Another sort of heterogeneity has received little explicit consideration to my knowledge: different initial conditions of otherwise identical coupled systems. Crowley (1981) showed that predator-prey oscillations can be reduced in amplitude by this mechanism. I here show that this mechanism can maintain bounded oscillations of even a small number of deterministic Nicholson-Bailey models of host-parasitoid interactions (Hassell 1978) coupled by migration. Single-patch models of this sort are notoriously unstable, exhibiting trajectories with population explosions and crashes of increasing amplitude. Hassell et al. (1991) simulate a similar system of locally coupled equations and demonstrate that persistence and complicated dynamics are possible when the number of patches is large enough. I here examine the parameter values for which stable oscillations exist in a globally coupled system, indicating that low migration rates are indeed necessary for persistence by this mechanism but that increasing the number of patches may not increase probabilities of persistence. I also show that this mechanism of persistence operates even in the presence of some stochasticity in the model parameters.

The equations used in this note are

$$\begin{aligned} H_1(t+1) &= (1 - \mu_h)\lambda H_1(t)e^{-aP_1(t)} + \mu_h\lambda H_2(t)e^{-aP_2(t)}, \\ H_2(t+1) &= (1 - \mu_h)\lambda H_2(t)e^{-aP_2(t)} + \mu_h\lambda H_1(t)e^{-aP_1(t)}, \\ P_1(t+1) &= (1 - \mu_p)H_1(t)(1 - e^{-aP_1(t)}) + \mu_p H_2(t)(1 - e^{-aP_2(t)}), \end{aligned} \quad (1)$$

and

$$P_2(t+1) = (1 - \mu_p)H_2(t)(1 - e^{-aP_2(t)}) + \mu_p H_1(t)(1 - e^{-aP_1(t)}),$$

where  $H_1(t)$  and  $H_2(t)$  are the host populations at time  $t$  in patches 1 and 2, respectively,  $P_1(t)$  and  $P_2(t)$  are parasitoid populations,  $\lambda$  is host reproduction per generation in the absence of parasitism,  $a$  is the area of discovery, and  $\mu_h$  and  $\mu_p$  are the fractions of hosts and parasitoids that migrate in each generation. The sequence of events described by these equations differs slightly from that in Reeve (1988). Note that the parameters in the two patches are identical.

Figure 1 illustrates a population trajectory generated by these equations. This oscillation persists indefinitely on the computer; to enhance visibility only the first few cycles are illustrated. The mathematical structure of these oscillations is apparently very complex. The oscillation shown is asymmetrical in that the two patches undergo different, though similar, population cycles. The oscillation remains bounded because the two systems remain out of phase. Locally stable, out-of-phase oscillations have been demonstrated to exist in continuous time when two identical systems, each with a stable oscillation when uncoupled, are coupled in various ways (Aronson et al. 1987, 1990), but to my knowledge out-of-phase oscillations have not been demonstrated when the coupled systems display unbounded dynamics in isolation. With other parameter values, several different oscillations can coexist, including symmetrical, asymmetrical, and very long period cycles and apparently chaotic trajectories. This note ignores these complexities and focuses on the existence and general properties of the oscillations. Studies of the properties of identical coupled continuous-time oscillators (Aronson et al. 1987, 1990) have found a complex structure of coexisting locally stable oscillations.

The initial conditions for the simulation shown were chosen at random from a neighborhood of the unstable equilibrium point of the system with the oscillation amplifying and maintaining an initial random asynchrony in the two patches. Since the parameters in the two patches are identical, identical initial conditions would make the two patches act as a single unstable patch. In simulations with overly similar initial conditions, the two patches become synchronized and population sizes explode. Figure 2 illustrates one cross section of the four-dimensional set of initial conditions that converge to a bounded oscillation, chosen in the plane where the parasitoid density in each patch is set initially to its equilibrium value. Note that the region does not come too close to the line of initial synchronization but that initial asynchrony alone is not sufficient to produce persistence. The cross section in the plane where host density is set initially to its equilibrium value is very similar.

If all such oscillations had values of population size varying by many orders of

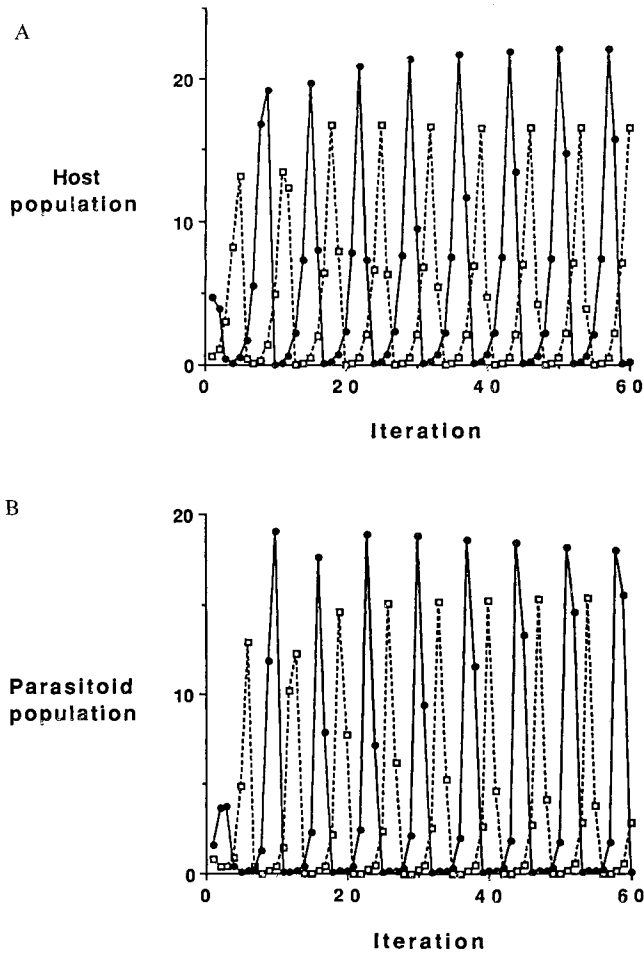


FIG. 1.—Trajectories of system 1. *A*, The dynamics of the host populations in patch 1 (solid line with solid squares) and patch 2 (dotted line with open squares); *B*, the parasitoid population dynamics. Parameter values are  $\lambda = 4$ ,  $\mu_h = \mu_p = \mu_p = .01$ , and  $a = 1$ .

magnitude, they would be of little interest biologically (Morrison and Barbosa 1987). Reeve (1988) used the coefficient of variation of population size over time as a measure of variability, but this approach fails to capture the key problem of unrealistically small populations (i.e., a population oscillating between 100 and 1 has very nearly the same coefficient of variation as one oscillating between 100 and 0.001). Instead, I use the standard deviation of the log host population size through the course of the oscillation as a measure of variability, which strongly correlates with the amplitude of the oscillation of log host population size. Figure 3 illustrates the behavior of this statistic over a range of parameter values. *Small dots* indicate low population variability, *large dots* indicate high variability, and the absence of a dot indicates the absence of a stable oscillation. Figure 3A fixes

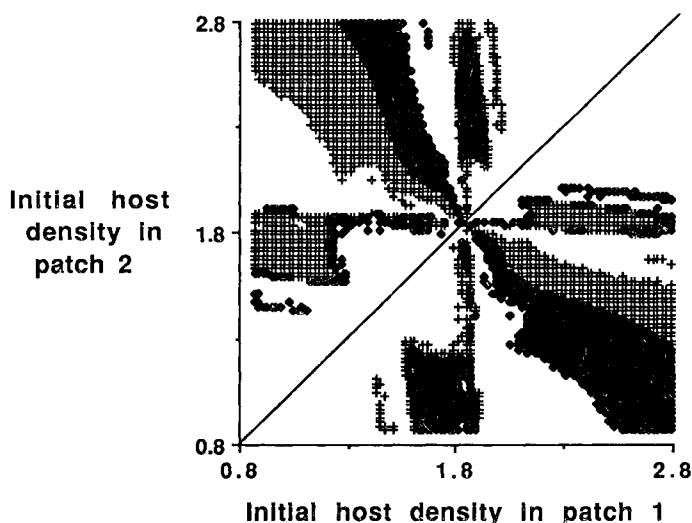


FIG. 2.—Cross section of the basin of attraction for the oscillation shown in fig. 1 where the initial value of each parasitoid population has been set equal to its equilibrium value. The *diagonal line* indicates the set of points where the two host initial conditions take the same value. Initial conditions that converge to an oscillation with larger amplitude in patch 1 than patch 2, as shown in fig. 1, are represented by the *hatched area*; the *solid area* represents the reverse.

host reproduction  $\lambda$  at the intermediate value of 4 and examines the effects of the two migration rates. “Low” variability (standard deviation of log host population size of less than two) is associated with migration rates of approximately 0.05, which lie near the maximum migration rates that produce persistence. Existence of oscillations seems to be enhanced when host migration is higher than parasitoid migration, although the “island” of persistent migration rates above the diagonal defies ready explanation. Figure 3B fixes the two migration rates to be equal and plots persistence and variability as a function of migration and of host reproduction. Lower growth rates are associated with greater persistence and generally with lower variability. Note, however, that persistence is much less likely for  $\lambda = 2$  than for  $\lambda = 3$ , with other simulations indicating that there is a threshold growth rate near two below which persistence is impossible.

To check whether the oscillations would persist in the presence of stochasticity in the parameters, I added noise to the model parameters by choosing their values, independently in each patch, uniformly from a range centered on the mean with length set by a given “noise level.” For example, with a noise level of 0.1, parameter values would be chosen uniformly from the set spanning 0.9–1.1 times the deterministic value. The coefficient of variation of such a distribution is about 0.82 times the noise level. The lognormal and gamma parameter distributions used by Reeve (1988) differ in that randomly generated parameters can take on very large or very small values even when coefficients of variation are small.

The results shown in figure 4 were generated by simulating system 1, starting

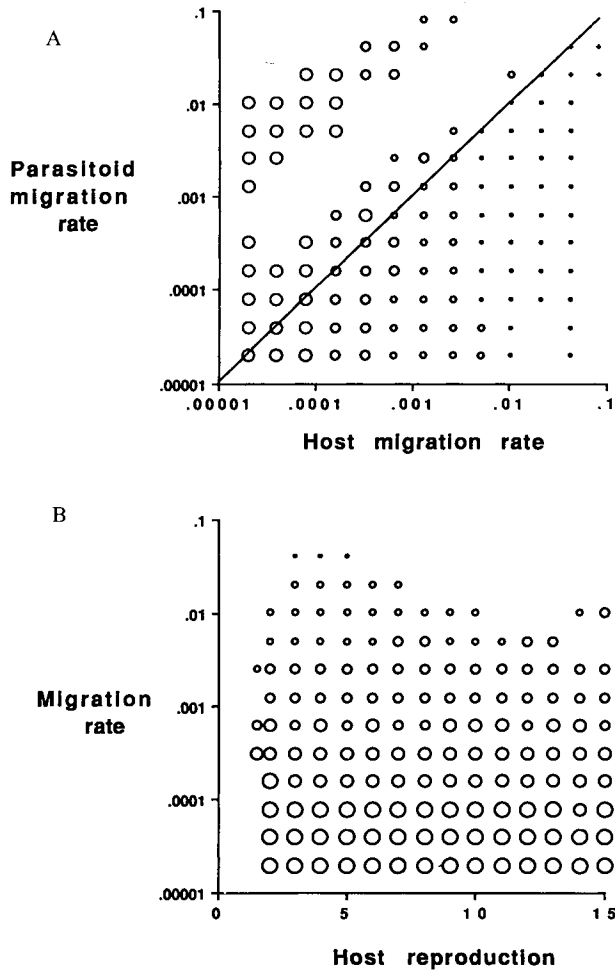


FIG. 3.—Persistence and variability of trajectories of system 1 as a function of parameter values. Dot size indicates the SD of log host population sizes over the course of 500 iterations. The smallest dot represents an SD of between one and two, the next smallest an SD of between two and three, and so on. A blank space indicates that no oscillation was found. Fig. 3A fixes  $\lambda = 4$ , while fig. 3B fixes  $\mu_h = \mu_p$ . Both fix  $a = 1$ .

from initial conditions chosen at random from a four-dimensional neighborhood of the equilibrium point of extent roughly equal to that shown in figure 2. The system is said to persist if trajectories remain bounded between  $10^4$  and  $10^{-4}$  for 500 iterations. Persistence probabilities drop off nearly linearly when noise is added to the area of discovery  $a$  or to the growth rate  $\lambda$ , not reaching zero until the noise level reaches one. Noise in the migration rates has a much smaller effect. Adding noise to all parameters simultaneously acts essentially multiplicatively. Other simulations indicate that these results are somewhat sensitive to the

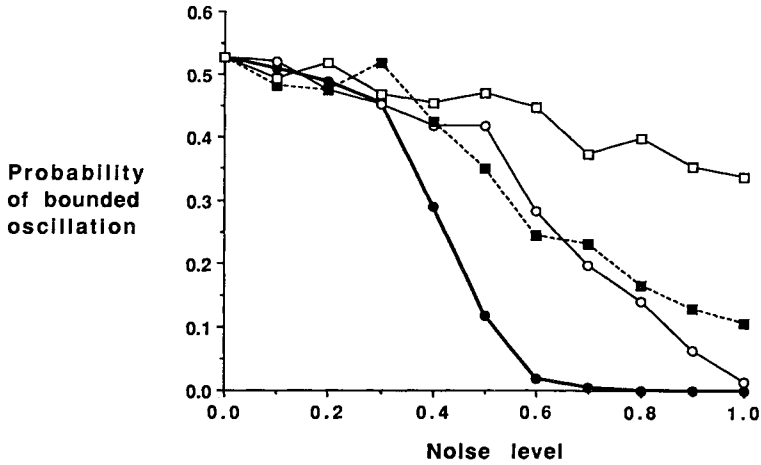


FIG. 4.—Probability that a two-patch system with noise remains bounded for 500 time steps for a range of noise levels (see text). Probabilities are computed as the fraction of initial conditions chosen randomly from a neighborhood of the equilibrium that lead to bounded dynamics. The curves show results when noise is added to the area of discovery  $a$  (*dashed line with solid squares*), the growth rate  $\lambda$  (*solid line with open circles*), the migration levels  $\mu_h$  and  $\mu_p$  (*solid line with open squares*), and all parameters simultaneously (*thick line with solid circles*). Mean parameter values are  $\lambda = 4$ ,  $\mu_h = \mu_p = .01$ , and  $a = 1$ .

size of the neighborhood from which the initial conditions are chosen, but the general pattern appears robust.

In order to study the effects of patch number on persistence, system 1 must be expanded to include an arbitrary number ( $k$ ) of patches. The equations used for these simulations are

$$H_i(t + 1) = (1 - \mu_h)\lambda H_i(t)e^{-aP_i(t)} + \frac{\mu_h\lambda}{k} \sum_{j=1}^k H_j(t)e^{-aP_j(t)}$$

(2)

and

$$P_i(t + 1) = (1 - \mu_p)H_i(t)(1 - e^{-aP_i(t)}) + \frac{\mu_p}{k} \sum_{j=1}^k H_j(t)(1 - e^{-aP_j(t)}).$$

Probability of persistence was found as in figure 4 by choosing initial populations for each patch from a region around the equilibrium and counting the fraction of simulations that remain bounded indefinitely. Figure 5A shows the results when the model is run without noise, and figure 5B shows the results when the model is run with a small and with a moderate amount of noise. Most obviously, the results with no noise or low noise show a large effect of parity, with small even numbers of patches persisting with much higher probability than small odd numbers of patches. Apparently, the fact that systems with an odd number of patches cannot be divided into two counterbalancing portions of equal size makes persis-

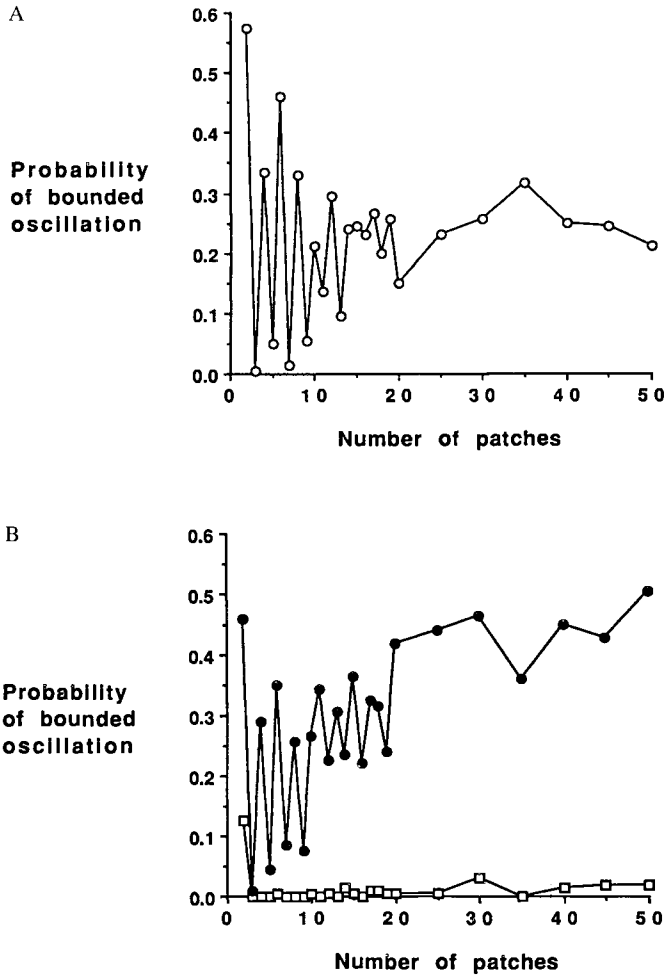


FIG. 5.—Probability that dynamics remain bounded for 500 time steps as a function of the number of patches. Probabilities are computed as in fig. 4. *A*, Results with no stochasticity; *B*, results with a low noise level of 0.1 added to all parameters (*solid circles*) and a moderate noise level of 0.5 added to all parameters (*open squares*). Mean parameter values are  $\lambda = 4$ ,  $\mu_h = \mu_p = .01$ , and  $a = 1$ .

tence highly unlikely. With no noise, the parity ceases to matter after sufficiently many patches have been added, and the probability of persistence approaches an asymptotic value roughly equal to the average of those for small systems of both parities. With low noise, the probability of persistence tends to increase at large patch numbers. With moderate noise, the probability of persistence is appreciably higher than zero only with two patches. Except for the strong effect of parity, results depend on the size of the region from which initial conditions are chosen, and generalization of these results to any more realistic measure of persistence

probability is unwarranted. These results contrast with the simulations of Hassell et al. (1991), in which a system of locally coupled Nicholson-Bailey equations on a square lattice could persist only if the lattice were sufficiently large.

The unrealistic nature of the Nicholson-Bailey model and the migration regime make it unlikely that the detailed output of these simulations has direct implications for the field. However, the results indicate that a hitherto neglected sort of heterogeneity, that of different initial conditions in otherwise identical weakly coupled patches, can suffice to maintain bounded oscillations in even a highly unstable model. The oscillations occur in the nonlinear range of the model, which makes possible a sensitive response to details of the initial conditions. This mode of persistence, meaningful mainly when stochasticity is not too large, appears to be distinct from the stochastically generated asynchrony described by Reeve (1988) in systems of many patches at higher noise levels. In this case, a low level of variation in the parameters acts to break up an existing pattern of spatial heterogeneity, while in the other a high level of variation creates persistence-promoting spatial heterogeneity. Finally, persistence in this model does not have a simple relationship with the number of patches.

#### ACKNOWLEDGMENTS

I thank P. L. Chesson, J. D. Reeve, and an anonymous reviewer for critical and imaginative comments that forced me to correct and improve earlier drafts. This research was partially supported by Department of Energy grant DE-FG02-90ER60933 to S. Levin.

#### LITERATURE CITED

- Allen, J. C. 1975. Mathematical models of species interactions in time and space. *American Naturalist* 109:319-342.
- Aronson, D. G., E. J. Doedel, and H. G. Othmer. 1987. An analytical and numerical study of the bifurcations in a system of linearly coupled oscillators. *Physica D* 25:20-104.
- Aronson, D. G., G. B. Ermentrout, and N. Kopel. 1990. Amplitude response of coupled oscillators. *Physica D* 41:403-445.
- Bailey, V. A., A. J. Nicholson, and E. J. Williams. 1962. Interaction between hosts and parasites when some host individuals are more difficult to find than others. *Journal of Theoretical Biology* 3:1-18.
- Chewning, W. C. 1975. Migratory effects in predator-prey models. *Mathematical Biosciences* 23:253-262.
- Comins, H. N., and D. W. E. Blatt. 1974. Prey-predator models in spatially heterogeneous environments. *Journal of Theoretical Biology* 48:75-83.
- Crowley, P. H. 1981. Dispersal and the stability of predator-prey interactions. *American Naturalist* 118:673-701.
- den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* 18:165-194.
- Hassell, M. P. 1978. *The dynamics of arthropod predator-prey systems*. Princeton University Press, Princeton, N.J.
- Hassell, M. P., and R. M. May. 1988. Spatial heterogeneity and the dynamics of parasitoid-host systems. *Annales Zoologici Fennici* 25:55-61.
- Hassell, M. P., and S. W. Pacala 1990. Heterogeneity and the dynamics of host-parasitoid interactions.



- Philosophical Transactions of the Royal Society of London B, Biological Sciences 330: 203–220.
- Hassell, M. P., H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in insect population dynamics. *Nature (London)* 353:255–258.
- May, R. M. 1978. Host-parasitoid systems in patchy environments: a phenomenological model. *Journal of Animal Ecology* 47:833–843.
- Maynard Smith, J. 1974. *Models in ecology*. Cambridge University Press, Cambridge.
- Morrison, G., and P. Barbosa. 1987. Spatial heterogeneity, population "regulation" and local extinction in simulated host-parasitoid interactions. *Oecologia (Berlin)* 73:609–614.
- Reeve, J. D. 1988. Environmental variability, migration and persistence in host-parasitoid systems. *American Naturalist* 132:810–836.
- . 1990. Stability, variability, and persistence in host-parasitoid systems. *Ecology* 71:422–426.
- Taylor, A. D. 1988. Large-scale spatial structure and population dynamics in arthropod predator-prey systems. *Annales Zoologici Fennici* 25:63–74.

FREDERICK R. ADLER\*

CENTER FOR APPLIED MATHEMATICS AND  
SECTION OF ECOLOGY AND SYSTEMATICS  
CORNELL UNIVERSITY  
ITHACA, NEW YORK 14853

*Submitted August 23, 1991; Revised March 23, 1992; Accepted April 29, 1992*

\* Present address: Departments of Mathematics and Biology, University of Utah, Salt Lake City, Utah 84112.

*Associate Editor: Peter Chesson*