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in Drosophila Metapopulations with Low Migration Rates"

Sutirth Dey, *et al.*

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Response to Comment on "Stability via Asynchrony in *Drosophila* Metapopulations with Low Migration Rates"

Sutirth Dey and Amitabh Joshi*

Ranta and Kaitala find asynchrony in our experiment unexpected and suggest stochasticity as a possible causal mechanism using simulated two-patch metapopulations. However, their mechanism can yield either subpopulation synchrony or asynchrony. We extend their approach to a nine-patch system approximating our experiment and show that asynchrony is not only not unexpected but extremely likely in real metapopulations with low migration.

Ranta and Kaitala (*1*) state that the observed asynchrony among subpopulations at low migration rates (*2*) is "unexpected" and propose a possible reason for this based on stochasticity and differences in initial population sizes (IPS). However, asynchrony at low migration rates among subpopulations with different intrinsic growth rates (*r*) has been predicted by theoretical studies that did not incorporate either noise or variation in IPS (*3*, *4*). This observation does not invalidate the results of (*1*) but indicates that stochasticity or differences in IPS are not necessary conditions for asynchrony among subpopulations. Moreover, we show that asynchrony among subpopulations at low migration rates in real metapopulations is likely to be quite common.

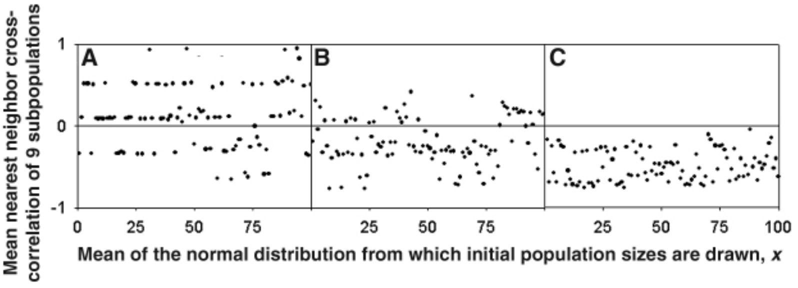

Fig. 1. Average nearest neighbor cross-correlation coefficients in nine-patch Ricker-based metapopulations, with 10% nearest neighbor migration and periodic boundary conditions. The *r* and *K* in each subpopulation were fixed at 2.8 and 40 respectively, and only the first 100 iterations were considered, without discarding any transients. The abscissa represents the mean (*x*) of the normal distribution (SD = 10*x*) from which the starting population sizes were drawn. The starting values were rounded off to the nearest integer, and negative values were replaced by zeroes. (**A**) When the starting population sizes were randomly chosen, both synchrony and asynchrony were observed, even in the absence of any other kind of noise. (**B**) When stochasticity was introduced in the form of noise in the parameter *r*, the fraction of cases leading to asynchrony increased. (**C**) Adding further stochasticity in the form of probabilistic extinctions resulted in asynchrony in almost all cases, indicating that stochasticity interacts with starting population sizes in producing asynchrony. See text for more details of the simulations.

Under low rates of migration, in-phase and out-of phase dynamics form fractal basin boundaries on the IPS space, irrespective of the absence (*5*) or presence (*1*) of noise. If the two types of basins of attraction are evenly distributed, as in some of the panels of (*1*), then contra (*1*), noise is equally likely to lead the subpopulations to either synchrony or asynchrony and, on average, one would expect neighboring subpopulation sizes to be uncorrelated. Strictly speaking, the mechanism proposed by (*1*) does not therefore explain the statistically significant subpopulation asynchrony seen in (*2*). However, this contention is based on the results of two-patch metapopulation simulations (*1*, *5*). Because the actual outcome of the mechanism in (*1*) depends on the fine structure of the basin boundaries, one would need to refer to a corresponding nine-dimensional IPS space for making similar observations on our experimental system (*2*). Because it is not possible to visualize such a space, we instead look directly at the effects of variation in IPS and stochasticity on the synchrony of subpopulations in a nine-patch metapopulation, as used in our experiment in (*2*). As high migration (30%) invariably led to synchrony (positive cross-correlation coefficient of first-differenced ln-transformed population sizes) under all conditions studied, here we restrict ourselves to the effects of low migration (10%).

When IPS varied among subpopulations, both synchrony and asynchrony were observed, even without stochasticity (Fig. 1A). On introducing noise by adding ε (0 < ε < 0.2) to *r* in each patch at every generation, as in (*2*), the fraction of IPS combinations leading to asynchrony increased (Fig. 1B). Increments in either *r* or the level of noise in *r* further increased the proportion of IPS combinations leading to asynchrony. Upon adding a 50% probability of extinction when subpopulation size fell below four, in conjunction with noise in *r* [as in (*2*)], we observed asynchrony in almost all the cases (Fig. 1C). Thus, while differences in IPS can give rise to either synchrony or asynchrony (*1*) (Fig. 1A), incorporating stochasticity and probabilistic extinction greatly increases the proportion of IPS conditions leading to asynchrony. Even if all the IPS are the same, stochasticity in *r* alone can induce asynchrony (Fig. 2A), at least for some of the IPS sets, and this proportion increases on increasing *r* or the noise in *r*. If probabilistic extinction is added to noise in *r*, almost all IPS sets lead to asynchrony (Fig. 2B). These observations indicate that in a multipatch system, stochasticity alone can induce asynchrony under low migration rates, and differences in IPS can enhance this effect (compare Figs. 2A and 1B). Thus, our simulations show that intrinsic growth rate and different conditions of stochasticity and IPS can interact in a complex manner to produce out-of-phase behavior in subpopulations.

In natural metapopulations, stochasticity in demographic parameters, probabilistic extinction, and variation in IPS are all likely ubiquitous. Our simulations suggest that under such circumstances, asynchrony among subpopulations is almost inevitable (Fig. 1C). One possible reason for this might be that under such conditions the multidimensional IPS space may lose the fractal structure and consist primarily of basins of attraction for asynchrony. Thus, the combination of low migration and high subpopulation growth rates is very likely to lead to stability via among-patch asynchrony in metapopulations in the laboratory or in nature.

References

1. E. Ranta, V. Kaitala, *Science* **314**, 420 www.sciencemag.org/cgi/content/full/314/5798/420a (2006).
2. S. Dey, A. Joshi, *Science* **312**, 434 (2006).
3. M. Gyllenberg, G. Söderbacka, S. Ericsson, *Math. Biosci.* **118**, 25 (1993).
4. B. E. Kendall, G. A. Fox, *Theor. Popul. Biol.* **54**, 11 (1998).
5. A. Hastings, *Ecology* **74**, 1362 (1993).

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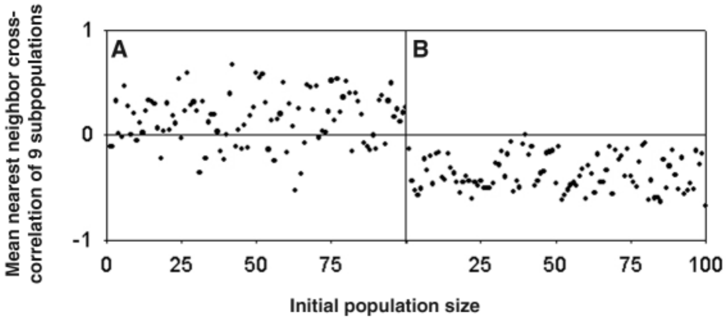

Fig. 2. Simulations as in Fig. 1, except that the initial population size was kept the same for all subpopulations. (**A**) Even when all populations are started from the same initial point, stochasticity in *r* is sufficient to lead to asynchrony in several cases. (**B**) Adding a probability of extinction results in asynchrony in almost all cases. Comparison of Figs. 1 and 2 indicates that stochasticity alone can induce asynchrony at least in some cases, but its effect is enhanced when there are differences in the starting size of the subpopulations.