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19. Wild-type Gα11 cDNA was isolated by the polymerase chain reaction (PCR) after reverse transcription of RNA from mouse S49 lymphoma cells, and its sequence was confirmed by sequencing. Mutations in the Gα11 cDNA were introduced by PCR mutagenesis with wild-type cDNA as a template. The PCR primer pairs used were 5′-TAGCAAGCTTCATATGACTCTGGAGTCCATGATGGC-3′ and 5′CAATGGATCCACTTCCTGCGCTCTGACCTCAGGGCCTCCC-3′ for the Q209L mutation [N.-X. Qian, S. Winitz, G. L. Johnson, *Proc. Natl. Acad. Sci. U.S.A.* **90**, 4077 (1993)] and 5′-ACCTTCTAGAAGACAAGATC-3′ and 5′-CATGCCCGGGTCACACCAGGTTGAACTCCTTCAG-3′ for the Y356F mutation. The PCR fragments were inserted into the corresponding region of the wild-type Gα11 cDNA. Wild-type and mutated Gα11 cDNAs were subcloned into the Hind III site of pCMV5 [S. Andersson, D. N. Davis, H. Dählbach, H. Jörnvall, D. M. Russell, *J. Biol. Chem.* **264**, 8222 (1989)]. Mutations were confirmed by sequencing.
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TECHNICAL COMMENTS

Estimating Chaos in an Insect Population

R. F. Costantino *et al.* (*1*) state that their laboratory data of the population dynamics of the flour beetle *Tribolium castaneum* show convincing evidence of transitions to chaos. Their methodology was similar to earlier studies (*2*) that assessed the population dynamics of a time series by fitting some mechanistic or empirical model and then inspecting realizations from the deterministic skeleton of the fitted model. However, Ellner and Turchin (*3*) argued powerfully that such an approach was flawed because it did not allow for a random component in the dynamics and might lead to the misidentification of series dynamics.

Ellner and Turchin identify three sources of variation that might influence the sensitivity of the system to initial conditions—endogenous dynamics, exogenous dynamics, and measurement error—and ask how fluctuations can be categorized as stochastic or dynamic if the methodology assumes the absence of noise. They presented methods for calculation of the Lyapunov exponent that allow for dynamic noise; these methods have now been supplemented by associated randomization tests that indicate the variability of Lyapunov exponents under two population dynamic hypotheses (*4*). While this new methodology cannot disentangle the relative contributions of measurement error (which is usually assumed to be small) from exogenous dynamics, it does identify the effects of the exogenous dynamics, which is usually the aim of the exercise.

The estimates of the Lyapunov exponents given by Costantino *et al.* must be shown to be robust to the presence of noise [that the authors themselves estimate in their variance-covariance matrix sum (Σ)] if a valid characterization of the *Tribolium* dynamics is to be obtained. We urge Costantino *et al.* to provide such estimates for the stochastic version of their model and then to compare their data with such output, rather than to use estimates from the deterministic skeleton.

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Response: We agree with Perry *et al.* that more study is needed of nonlinear dynamics in the presence of noise. We have computed the Lyapunov exponents (LE) for both the deterministic and stochastic versions of our model (Table 1) by using our published estimates for the model parameters and variance-covariance matrix. If one accepts a positive stochastic LE as a hallmark of chaos, then these results demonstrate that our statements about chaos are "robust to the presence of noise."

We remain unconvinced, however, that the stochastic LE (*2*) advocated by Perry *et al.* should be viewed as an objective hallmark of chaos. Consider, for instance, a population model in which population size, N_t, obeys a stochastic Ricker (discrete time logistic) model

$$N_t = N_{t-1} \exp(r - aN_{t-1} + \sigma Z_t)$$

where r, a, and σ are positive parameters, and Z_t is normal (0, 1) noise. For the value $r = 1.9$, the deterministic skeleton ($\sigma = 0$) predicts a stable equilibrium. For values of σ greater than about 1.5, however, the stochastic LE is positive. Chaos is indicated by the stochastic LE for what many would consider a stable, but noisy, equilibrium. It is not clear to us that ecologists at large would want to classify such a system as chaotic.

Perry *et al.* also urge us to compare our data to the output of the stochastic version of our model. Realizations from the stochastic model mimic well the experimental data (an example is given in Fig. 1 for the chaotic treatment $c_{pa} = 0.35$). As shown in our previous work (*3*, *4*), however, a more rigorous approach is to conduct diagnostic analyses of the differences between the model predictions and the experimental time series (*5*).

The model presented in our report (*1*) was based on detailed biological knowledge of the well-studied flour beetle system (*6*) and has been validated by extensive diagnostic analyses using time series residuals from independent data sets (*3*, *4*). The time series (*1*) were generated from an experiment that was designed to test qualitative transitions in dynamics that were predicted a priori by this nonlinear model. Our study should not be classified with other claims of chaos that are based on unvalidated descriptive models fitted to historical data sets.

In contrast with our approach, the statistical methods (*2*) advocated by Perry *et al.* for estimating the stochastic LE from data involve estimating the structure of the deterministic skeleton with various nonparametric regression methods without regard to the biological mechanisms producing the data. The efficacy of these methods for reconstructing ecological dynamics has been tested only on simple models (*2*, *7*), with mixed results. Different regression methods frequently yielded different conclusions for the same data (*2*). In short, we are skeptical that the value of an index calculated from one of several curve-fitting algorithms constitutes reliable evidence of chaos.

We concentrated in our report on what seemed to be the more testable aspects of chaos theory in ecology. The heart of the scientific debate about ecological chaos revolves around whether simple deterministic models with chaotic dynamics can be useful representations of ecological systems (*8*). One of the main take-home messages of nonlinear dynamics is the prediction of transitions in system behaviors in response to changing parameter values. In our studies (*1*, *9*), the transitions of the attractor of a deterministic model (our skeleton, the "LPA model") in and out of chaos, invariant loops, and cycles provided strikingly accurate predictions of the responses of our experimental populations to parameter manipulations. With this approach, the hypothesis that simple feedback mechanisms cause complex population dynamics is far more vulnerable to empirical refutation.

Ecological systems are stochastic, so much so that the low-dimensional dynamic models of theoreticians are widely derided by empirical ecologists. Theoretical ecology needs more studies in which mathematical models survive experimental challenges as serious scientific hypotheses.

Table 1. Deterministic and stochastic Lyapunov exponents (*LE*) for the model and parameter estimates of Costantino *et al.* (*1*)

Experimental treatment (C_{pa})	Deterministic LE	Stochastic LE
Control	−0.0448	−0.0441
0.00	−0.2989	−0.0729
0.05	−0.0257	0.0339
0.10	0.0000	0.0561
0.25	0.0245	0.0608
0.35	0.1029	0.0493
0.50	0.0665	0.0396
1.00	−0.1871	0.0312

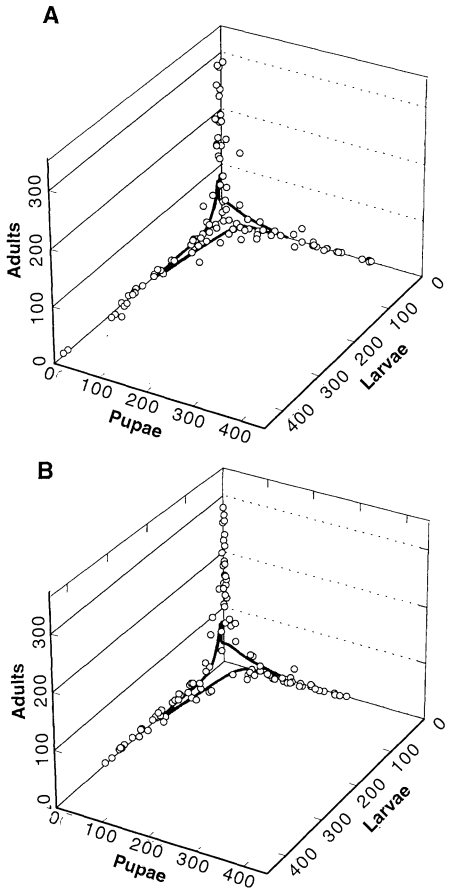

Fig. 1. Three-dimensional phase space plots of the output of the stochastic model (**A**) and the experimental data (**B**) for the chaotic treatment $c_{pa} = 0.35$ of Costantino *et al.* (*1*). Experimental data are for three replicate populations from $t = 10$ to 45 (70 weeks). Simulation data are for three realizations of the stochastic model from $t = 10$ to 45 started with the same values observed in each experimental replicate at $t = 10$. In both plots, the solid dots represent the chaotic attractor of the deterministic skeleton.

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