

Power spectra reveal the influence of stochasticity on nonlinear population dynamics

Daniel C. Reuman^{*†}, Robert A. Desharnais[‡], Robert F. Costantino[§], Omar S. Ahmad[¶], and Joel E. Cohen^{*†||}

^{*}Laboratory of Populations, The Rockefeller University, Box 20, 1230 York Avenue, New York, NY 10021; [‡]Department of Biological Sciences, California State University, Los Angeles, CA 90032; [§]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721; [¶]Laboratory of Sensory Neuroscience, The Rockefeller University, 1230 York Avenue, New York, NY 10021; and ^{||}Laboratory of Populations, Columbia University, New York, NY 10021

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Stochasticity alters the nonlinear dynamics of inherently cycling populations. The power spectrum can describe and explain the impacts of stochasticity. We fitted models to short observed time series of flour beetle populations in the frequency domain, then used a well fitting stochastic mechanistic model to generate detailed predictions of population spectra. Some predicted spectral peaks represent periodic phenomena induced or modified by stochasticity and were experimentally confirmed. For one experimental treatment, linearization theory explained that these peaks represent overcompensatory decay of deviations from deterministic oscillation. In another treatment, stochasticity caused frequent directional phase shifting around a cyclic attractor. This directional phase shifting was not explained by linearization theory and modified the periodicity of the system. If field systems exhibit directional phase shifting, then changing the intensity of demographic or environmental noise while holding constant the structure of the noise can change the main frequency of population fluctuations.

flour beetle | Fourier transform | strong noise | *Tribolium* | weak noise

The interactions of stochasticity with nonlinear population dynamics are of major interest in ecology (1–3). Environmental and demographic stochasticity can strongly influence dynamics and can play a key role in the fluctuations of populations (4–12). The influence of stochasticity on deterministic population models with a single stable equilibrium has been analyzed using linear approximations about the equilibrium (13–17). Bjørnstad *et al.* (18) applied this theory to populations of Atlantic cod and bluefin tuna. Linearization theory has also been applied to nonequilibrium physical systems (19–21). Both bodies of theory use the power spectrum, or simply *spectrum* (22, 23). However, the spectrum is sometimes not used with population data because estimates of the spectrum based on short time series lack resolution (9).

Our first goal is to propose and test a statistical approach to facilitate the application of the spectrum to the inherent population cycles and nonlinear models of *Tribolium* flour beetles, which have been used for decades in laboratory studies of population dynamics (11, 24, 25). For *Tribolium castaneum*, cannibalism plays a major role in dynamics and is represented by nonlinearities in several models (11). The approach proposed combines qualitative biological knowledge with quantitative information in short time series to improve the resolution of estimates of population spectra. We produce detailed, empirically supported, model-based predictions of the spectra of beetle populations. We map the influence of demographic stochasticity on *Tribolium* dynamics by plotting changes in spectra with gradually increasing stochasticity. This approach may have general utility, not limited to flour beetles.

Our second goal is to show that linear approximation theory sometimes can, and sometimes cannot, explain how stochasticity affects inherently cycling populations. Realistic stochasticity produced frequent unidirectional phase-shifts in population cycling around the deterministic attractor. These phase shifts

caused the dominant frequency of the system to shift, invalidating the predictions of linearization theory. We label this effect “directional phase shifting.”

Nisbet *et al.* (13, 14, 18) concluded that linearization theory is likely to be an effective approximation to the effects of stochasticity on deterministic population models with a single stable equilibrium for all but very small equilibrium populations. For inherently cycling populations, we show that linearization theory will also fail when stochasticity causes substantial directional phase shifting. We give guidelines for determining when shifting may occur and what its effects will be.

Although linearization theory should be tried first in any analysis of interactions between stochasticity and nonlinear dynamics, diverse effects can occur when strong noise renders linearization invalid. We demonstrate such effects and argue that many inherently cycling population systems may be unsusceptible to linearization theory because of strong noise. In-depth exploration is needed of interactions between dynamics and strong stochasticity; we present techniques to describe and understand these interactions.

If directional phase shifting occurs in a cycling field population, then changes in the intensity of the environmental or demographic stochasticity affecting that population may alter the main frequency of its oscillations. Such changes in intensity may occur through climate change, geographic variation, or reduced population sizes. Modification of the periodicity of a fluctuating exploited population may affect the exploiting industry; modification of the periodicity of a fluctuating population of disease vectors may affect public health.

Results

Supporting Information. For further details, see Tables 1–3, Figs. 5–11, and *Supporting Text* sections 1 and 2, which are published as supporting information on the PNAS web site.

Fit and Predictive Ability of the Lattice Stochastic Demographic Larvae-Pupae-Adult (LSD-LPA) Model. The LSD-LPA model (*Methods*) succeeded in fitting well, with the same parameters in both time and frequency domains, all 24 experimental replicates of length 41 (imposed initial conditions plus observations every 2 weeks for 80 weeks). Using model parameters obtained by maximum-likelihood time-domain fitting (*Supporting Text 1.1*), the frequency-domain fit of the LSD-LPA model with all 24 data replicates was tested (Fig. 1, box 2). The six replicates of length 213

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Abbreviations: SD-LPA, stochastic demographic larvae-pupae-adult; LSD-LPA, lattice SD-LPA; nf, normalized frequency.

[†]To whom correspondence may be addressed. E-mail: reumand@rockefeller.edu or cohen@rockefeller.edu.

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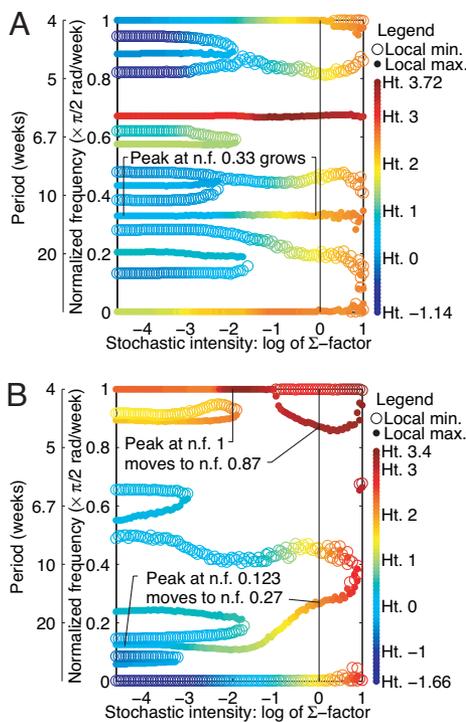


Fig. 4. Spectral peaks and valleys with increasing intensity of stochasticity in the SD-LPA model for the adult life-stage with $c_{pa} = 0.5$ (A) and $c_{pa} = 0$ (B). Vertical axes show frequencies of local maxima (filled circles) and minima (open circles) of log spectra. Color shows the heights (Ht.) of local maxima and minima. Horizontal axis shows intensity of stochasticity (scalar multiple of noise covariance matrix; see Methods). Under very low stochasticity (left), spectra were those of the deterministic model. Vertical black lines show experimental stochasticity (Σ factor 1). For these parameter values and Σ factor 1, LSD-LPA, and SD-LPA model spectral predictions were very similar: lattice effects were small. Stochasticity explains the locations of peaks for the LSD-LPA model (Fig. 3 A and B) by explaining the locations of peaks for the SD-LPA model. The smaller peak in Fig. 3A was induced by stochasticity. The smaller peak of Fig. 3B (nf = 0.27) was the nf = 0.123 peak of the LPA model, shifted by stochasticity (and not further shifted by lattice effects). The main peak of Fig. 3B (nf = 0.87) did not come from the deterministic model peak at nf = 0.877, as was expected before this analysis, but was the nf = 1 deterministic model peak, shifted by stochasticity (and not further changed by lattice effects). The deterministic model peak at nf = 0.877 was eliminated by stochasticity. *Supporting Text 2.3* shows other life stages. No statistical confidence intervals are given for the locations or heights of peaks and valleys because the variability in these quantities is expected to be small (*Supporting Text 1.6* has details of how plots were produced) and no probabilistic conclusions were drawn.

distributions from leading unerringly to bimodal distributions, and vice versa. Peak motion from nf 1 to nf 0.87 corresponds to a change in the average number of time steps between pupae-dominated distributions from $2/1 = 2$ for low Σ factors to $2/0.87 = 2.30$ for experimental levels of stochasticity.

The population state occupied by the LPA model on alternate time steps orbits gradually around c_1 . For time steps not spent on c_1 , the state orbits around c_2 . The result is modulation of the magnitude of the nf 1 population oscillations: the model oscillates between heavily pupae-dominated and heavily bimodal distributions; it then oscillates between moderately pupae-dominated and moderately bimodal distributions, and repeats (*Supporting Text 2.4*). The frequency of modulation of population variability is nf 0.123. The peak in Fig. 4B at this frequency for low Σ factors depicts the modulation. Motion of this peak from nf 0.123 to nf 0.27 with increasing stochasticity (Σ factor) corresponds to a change in the period of the modulation from $2/0.123 = 16.26$ time steps to $2/0.27 = 7.41$ time steps.

Patterns of change in spectral peaks other than those observed for $c_{pa} = 0$ and 0.5 occurred with increasing stochasticity for other c_{pa} values (*Supporting Text 2.3*). The numerical methods of this study allow the model-hypothesized role of stochasticity in establishing the dominant population fluctuations of the beetle system to be explicitly mapped. Developing analytical methods to undergird these numerical methods remains a challenge for the future.

Explanation of Spectral Changes with Stochasticity. Linearization theory explains interactions between sufficiently weak stochasticity and nonlinear deterministic dynamics with a finite attractor (*Supporting Text 1.7*). The growth of the peak at nf 0.33 for $c_{pa} = 0.5$ can be explained by using linearization theory, as can other aspects of Fig. 4A. In contrast, linearization theory cannot explain the peak motion in Fig. 4B.

High adult-on-pupae cannibalism. The LPA model, now denoted $(L_{t+1}, P_{t+1}, A_{t+1}) = g(L_t, P_t, A_t)$, was put on the square-root scale: $\mathbf{x}_{t+1} = (l_{t+1}, p_{t+1}, a_{t+1}) = (L_{t+1}, P_{t+1}, A_{t+1})^{1/2} = f(l_t, p_t, a_t) = g(l_t^2, p_t^2, a_t^2)^{1/2}$. Perturbations due to stochasticity were approximately normally distributed on this scale (*Supporting Text 1.1*). The model $\mathbf{x}_{t+1} = f(\mathbf{x}_t)$ has stable attractor $A = (\mathbf{a}_1, \mathbf{a}_2, \mathbf{a}_3)$ for $c_{pa} = 0.5$. The susceptibility matrices, $S_1 = J_{a_3} J_{a_2} J_{a_1}$, $S_2 = J_{a_1} J_{a_3} J_{a_2}$, and $S_3 = J_{a_2} J_{a_1} J_{a_3}$ (where J_x is the Jacobian of f at \mathbf{x}) for this model all have eigenvalues $-0.77, 0.65$, and 0. The dominant eigenvalue is negative, so theory predicts a component of overcompensatory decay of perturbations from the stable attractor of the square-root-scale model, and a corresponding spectral peak in the adult life stage at nf $1/3 = 0.33$ (half the frequency of the deterministic system). The eigenvalue 0.65 is also large, so a component of undercompensatory decay of perturbations from the attractor will also occur, producing a spectral peak at nf 0 for the square-root-scale model. Theory predicts that these peaks will increase in size and prominence with stochasticity increasing from zero. Taking the square root of populations does not affect locations and relative heights of spectral peaks, so theory explains the peaks at nf 0.33 and 0 for the SD-LPA model (Figs. 3A and 4A).

The theoretical mechanism producing the nf 0.33 peak was supported by experimental data on the perturbations of real population vectors from points in the LPA model attractor. Let \mathbf{v}_i denote the eigenvector of S_i with eigenvalue -0.77 . If the mechanism of overcompensatory decay is correct, then when a square-root-scale population vector \mathbf{x}_t deviates slightly from \mathbf{a}_i with a component in the direction of \mathbf{v}_i , the vector \mathbf{x}_{t+3} should deviate from \mathbf{a}_i with a component in the direction of $-\mathbf{v}_i$. The latter deviation should, on average, be smaller than the former. These patterns held for data (*Supporting Text 2.5*).

Zero adult-on-pupae-cannibalism. Linearization theory does not immediately apply for $c_{pa} = 0$ because the square-root-scale LPA model with $c_{pa} = 0$ has a nonfinite attractor. However, the components of the attractor, $c_1^{1/2}$ and $c_2^{1/2}$, can substitute for a stable two-point attractor. Making this approximation, we applied linearization theory to the $c_{pa} = 0$ treatment (*Supporting Text 2.5*). Linearization theory predicts, correctly for weak noise, that locations of spectral peaks will not change with increasing stochasticity. The (deterministic) LPA model peaks at 0.123, 0.887 and 1 were not greatly affected by weak demographic stochasticity (log Σ factors less than about -2.5). The prediction is incorrect for stronger noise: peaks shifted unexpectedly for larger Σ factors (Fig. 4B). How can peak motion for higher Σ factors be explained?

The LPA model with $c_{pa} = 0$ had an unstable equilibrium, e , about midway between c_1 and c_2 . Spectral peaks began to move when stochasticity was strong enough to move population vectors occasionally at least as far from c_1 and c_2 as e (*Supporting Text 2.5*). Linearization theory failed when this occurred because linearization at points in the attractor does not capture the

dynamical behavior of the LPA model at points farther from the attractor than e . For weak stochasticity, the SD-LPA model initialized with a population vector near c_i will produce in one time step a vector nearer c_j ($j \neq i$) than c_i . Stronger stochasticity will cause the model to occasionally produce a vector closer to c_i , shifting the phase of the n th oscillation of the system (26). The relative frequency of phase shifting, as a function of the Σ factor, becomes appreciably greater than 0 for the same range of Σ factors at which stochasticity becomes strong enough to move populations further from the attractor than e , and peak motion begins (Supporting Text 2.5).

For experimental levels of stochasticity (i.e., Σ factor 1), a phase shift occurs on $\approx 12.5\%$ of time steps (Supporting Text 2.5). Whereas the deterministic system switches from c_1 to c_2 or vice versa 100 times in 100 time steps, the stochastic system switches from a neighborhood of c_1 to a neighborhood of c_2 about $100 - 12.5 \approx 87$ times in 100 time steps. This finding corresponds to a $\approx 12.5\%$ reduction in the primary frequency of the deterministic system, explaining the main peak at $\text{nf } 0.87 \approx 1 - 0.125$ for the stochastic models and for experimental time series. The percentages of times that each experimental time series phase shifted were 22.5%, 10.0%, and 15.0%; these percentages agreed approximately with those of the simulation (Supporting Text 2.5), but had more scatter because experimental time series had only 40 transitions from one census to the next. Stochastically induced failures to switch at each time step between a pupae-dominated age distribution and a bimodal age distribution caused peak motion in Fig. 4B.

Comparison of High and Zero Adult-on-Pupae Cannibalism. In contrast to the $c_{pa} = 0$ case, phase shifting did not affect the locations of spectral peaks for $c_{pa} = 0.5$ (Fig. 4A). In typical length-1024 output of the SD-LPA model, phase shifting occurred about as frequently (on 11.1% of time steps) for $c_{pa} = 0.5$ as for $c_{pa} = 0$. However, for $c_{pa} = 0.5$, two opposite types of phase shifting along the 3-cycle attractor occurred, canceling each other: backward and forward shifting with respect to time evolution of the deterministic system. If the deterministic system moves in one time step from \mathbf{a}_1 to \mathbf{a}_2 , then a forward (backward) phase shift of the stochastic system is movement of the population vector in one time step from a neighborhood of \mathbf{a}_1 to a neighborhood of \mathbf{a}_3 (\mathbf{a}_1). A backward phase shift is a failure to advance to a neighborhood of \mathbf{a}_2 (backward compared with the deterministic model). Forward (backward) shifts occurred on $\approx 8.7\%$ (2.4%) of time steps for $c_{pa} = 0.5$. Forward shifts that can be paired with backward shifts at another time do not affect the frequency of oscillation of the system. Forward shifts not cancelled by backward shifts at another time contribute to increasing the frequency of the system; these occurred rarely (on only $6.3\% = 8.7 - 2.4\%$ of time steps) for $c_{pa} = 0.5$, not enough to have a noticeable effect. In contrast, for $c_{pa} = 0$, phase shifting on the approximate 2-cycle comprised of c_1 and c_2 occurred in only one direction; forward and backward shifts on a 2-cycle are the same. Phase shifts could not cancel each other, explaining why peak locations changed for $c_{pa} = 0$ but not for $c_{pa} = 0.5$, and why linearization theory applied for $c_{pa} = 0.5$ but not $c_{pa} = 0$.

We call phase shifts that occur predominantly in one direction around an attractor “directional phase shifts.” “Phase dissipation” refers to phase shifts that occur approximately equally in both directions around an attractor. Phase dissipation blunts spectral peaks without changing their location. All phase shifts are directional on a 2-cycle.

Discussion

Linearization theory, which describes the decay of small deviations from a deterministic attractor, predicts that only the magnitudes (not the frequencies) of stochastically induced phenomena change as the magnitude of stochasticity changes. It

explains the influence of stochasticity on dynamics for one experimental treatment of this study but fails for another treatment. Ecologically realistic levels of stochasticity can move populations too far from a deterministic attractor for linear approximations rooted at points in the attractor to be valid (27), and can cause directional phase shifting that changes the dominant periodicity of a system. Theory accounting for directional phase shifts and dynamics far from an attractor is needed.

The *Tribolium* laboratory system is very controlled, but stochasticity (primarily demographic; ref. 24) was still too great for linearization to apply in one case we considered. The intensity of demographic stochasticity relative to population density is proportional to the inverse square root of population size (14, 25, 28). Demographic stochasticity affecting a field system could be stronger or weaker than the stochasticity affecting the *Tribolium* system according to whether the field system has smaller or larger populations. Both demographic and environmental stochasticity affect field systems. If total stochasticity affecting a field system is comparable to or less than the stochasticity affecting the *Tribolium* system, linearization theory may apply.

Whether linearization theory explains the effects of stochasticity on a particular nonlinear model also depends on the details of deterministic dynamics (18). If a deterministic model's attractor is close to, for example, unstable equilibria, other attractors, or zero-population boundaries, then low levels of stochasticity may suffice to invalidate predictions of linearization theory. If points of a finite attractor are close together, low levels of stochasticity may cause frequent phase shifting, which may be directional. Phase shifting can also occur for quasiperiodic and chaotic dynamics. Linearization theory will be relatively less useful for weakly stable deterministic models (such as the $c_{pa} = 0$ treatment here) for which perturbations from the attractor decay slowly.

Our numerical spectral techniques for examining the biological effects of strong stochasticity (Figs. 1 and 4) may apply to ecological and other systems, and may generalize to continuous-time models, models with a spatial component, and wavelet analysis. How often the spectrum enhancement method gives correct spectral predictions when using a realistic model and how often it gives incorrect spectral predictions when using an unrealistic model remain to be determined.

The strategy of Fig. 1 should be used only with a mechanistic model. A mechanistic model that fits well in the spectral and time domains can be used for detailed spectral analysis even when long experimental time series are lacking (Fig. 1). The additional detail in spectral estimates from long model-generated time series reflects biological hypotheses encoded in the functional form of the model. Detailed estimates are testable hypotheses for population spectra based on all available observations and mechanistic theory (deterministic and stochastic).

Methods

Experiments. We set adult mortality rate (μ_a) at 0.96, and manipulated effective adult-on-pupae cannibalism (c_{pa}) to obtain values $c_{pa} = 0, 0.05, 0.10, 0.25, 0.35, 0.50,$ and 1.00 in seven treatments of three replicates each (29). A control treatment was not manipulated. The larval, pupal, and adult stages were counted (eggs were discarded) every two weeks (one time step) for 80 weeks, giving trivariate time series of length 41 (the initial condition plus 40 time steps). The treatment with $c_{pa} = 0.35$ and the controls were continued for 424 weeks, giving six time series of length 213 (24).

Models. The lattice stochastic demographic LSD-LPA model, a discrete-time discrete-state nonlinear stochastic model, can be constructed in three steps: (i) start with the LPA model, a deterministic model; (ii) include stochasticity (SD-LPA); and (iii) constrain populations to integer values (LSD-LPA).

The LPA model is $L_{t+1} = bA_t \exp(-(c_{el}/V)L_t - (c_{ea}/V)A_t)$, $P_{t+1} = (1 - \mu_l)L_t$, $A_{t+1} = (1 - \mu_a)A_t + P_t \exp(-(c_{pa}/V)A_t)$, where L_t , P_t , and A_t are the numbers of larvae, pupae, and adults at week $2t$; b is fecundity per adult per unit time; μ_l , μ_a are mortality rates per unit time per larva and per adult; c_{el} is the probability that a single larvae encounters and eats a single egg during a small time interval, Δt (24); c_{ea} and c_{pa} are similar coefficients for rates of cannibalism per adult on eggs and on pupae, respectively; V is habitat volume in units equal to the volume of 20 g of flour. The initial stage vector $(L_0, P_0, A_0) = (250, 5, 100)$ was used for all experiments and simulations of this study.

The SD-LPA model adds square root scale trivariate normally distributed noise (demographic stochasticity) with covariance matrix Σ after each time step of the LPA model. The LSD-LPA model rounds populations to the nearest integer after each time step of the SD-LPA model. “Lattice” here refers not to a spatial lattice but to the requirement that population counts be integers. For the SD-LPA and LSD-LPA models, stochasticity is modified in intensity by multiplying each entry of Σ by a single positive “ Σ factor.” Experimentally, demographic stochasticity relative to population density can be decreased by increasing beetle habitat size (25). The LSD-LPA model is considered the most realistic model of this study. Model parameter values and equations are given in *Supporting Text 1.1*.

Figures show spectra of adult time series only; spectra of other life-stages are different in detail but had peaks of the same relative heights in the same locations. Frequency-domain fit P values take account of all life stages.

Statistical Tests. We used new simulation-based statistical tests to see whether nonlinear stochastic models with fixed parameters could generate time series with spectral estimates similar to those of data time series. Two tests give approximate P values to describe the quality of the frequency-domain fit between model and data (see *Supporting Text 1.2*; see also refs. 22, 30, and 31). The “spectrum distance fit test” measures the sum, across all

frequencies, of the squared distances between the mean of log spectra of many model-generated time series and the log spectrum of an experimental time series (this is the squared “ L_2 distance”). The test indicates a good fit if the data log spectrum is closer to the mean model log spectrum under the L_2 distance than a large enough percentage of model log spectra. The “spectrum shape fit test” measures the correlation between the mean model log spectrum and the log spectrum of an experimental time series. A good fit occurs if the data log spectrum has shape closer to that of the mean model spectrum than a large enough number of model log spectra. Another technique, similar to techniques applied previously (32–34), provides a visual comparison between spectral estimates from data and distributions of spectral estimates from model-generated time series. These tests reject (or fail to reject) biological hypotheses expressed as stochastic dynamical models.

These spectral fit tests do not use linear approximation. They make no assumptions on the functional form of the spectrum. They have no *a priori* relationship to traditional time-domain fitting methods (5, 29). A good time-domain fit does not necessarily imply a good frequency domain fit, or vice versa (*Supporting Text 1.3*; ref. 30).

The fit of a population model should be verified in both domains where feasible (7, 33, 34). A substantially inappropriate model will fail to fit short population time series, for all parameter values, in the frequency and the time domains. A moderately inappropriate model functional form may fit acceptably in both domains, but with different parameter values (examples in *Supporting Text 1.3*). Such a functional form must be rejected (30). A good model should fit well in both domains with the same parameters.

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