Environmental Noise Could Promote Stochastic Local Stability of Behavioral Diversity Evolution

Xiu-Deng Zheng,[1] Cong Li,[2] Sabin Lessard,[2,*] and Yi Tao[1,3,†]

[1]*Key Laboratory of Animal Ecology and Conservation Biology, Centre for Computational and Evolutionary Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China*
[2]*Department of Mathematics and Statistics, University of Montreal, Montreal QC H3C 3J7, Canada*
[3]*University of Chinese Academy of Sciences, Beijing 100101, China*

In this Letter, we investigate stochastic stability in a two-phenotype evolutionary game model for an infinite, well-mixed population undergoing discrete, nonoverlapping generations. We assume that the fitness of a phenotype is an exponential function of its expected payoff following random pairwise interactions whose outcomes randomly fluctuate with time. We show that the stochastic local stability of a constant interior equilibrium can be promoted by the random environmental noise even if the system may display a complicated nonlinear dynamics. This result provides a new perspective for a better understanding of how environmental fluctuations may contribute to the evolution of behavioral diversity.

Since the concept of evolutionarily stable strategy (ESS) has been introduced in evolutionary game theory [1], it has been successfully applied to explain the evolution of animal behaviors, in particular, altruistic behaviors (or cooperative behaviors) [2–7]. Studies of evolutionary game dynamics start with the replicator equation [8] and focus to a great extent on the time evolution and long-term maintenance of population states pertaining to behavioral diversity [4–7]. In the archetypal framework of matrix games in discrete time, there are two important assumptions that are usually made or implicit: the first one is that the fitness of an individual is a simple linear function of the expected payoff of its phenotype, and the second one is that the payoff matrix in pairwise interactions is a constant matrix [2,4–7]. However, both these two assumptions cannot be considered to be always true, or completely real. In this Letter, we address the consequences of relaxing these assumptions by considering (i) a random payoff matrix in pairwise interactions, and (ii) a nonlinear, actually exponential, fitness function with respect to the expected payoff.

It may be useful to recall the origins of the replicator equation in evolutionary game theory [2,5,8,9]. The equation in continuous time was obtained by assuming that the payoff is the current growth rate. If n_i is the current number of i strategists in a population of large size $N = \sum_i n_i$, then its time derivative is $\dot{n}_i = n_i \pi_i$ where π_i is the payoff to i assumed to be frequency dependent. This leads directly to the replicator equation $\dot{x}_i = x_i(\pi_i - \bar{\pi})$ where $x_i = n_i/N$ is the relative frequency of i and $\bar{\pi}$ the average payoff. In discrete time, we have the approximation $n_i(t+1) = n_i(t)e^{\pi_i(t)}$, from which $x_i(t+1) = [x_i(t)e^{\pi_i(t)}/\sum_j x_j(t)e^{\pi_j(t)}]$. This is a good approximation if the payoffs change little in the time interval $[t, t+1]$ or if this interval is small. This supports fitness in discrete time defined as an exponential function of the payoff, that is, $f_i = e^{\pi_i}$, which is approached by the linear function $1 + \pi_i$ in the case of weak selection [2,10]. As already known, an exponential fitness may lead to very complicated dynamics even in the case of matrix games with only two phenotypes [11–17].

Our objective in this Letter is not only to study the effects of a nonlinear fitness function on matrix game dynamics but also the effects of introducing stochastic perturbations of the payoffs. Randomness (or uncertainty) in the environment is one of the main characteristics of nature, and this random noise will generally affect the results of interactions between species and between individuals [18–21]. Therefore, variability in payoffs as measured by their variances and covariances have to be taken into account in order to better understand evolutionary outcomes in natural populations. Below are two examples to show that a random payoff matrix is a reasonable assumption in evolutionary game theory and mathematical ecology.

The Lotka-Volterra (LV) equation is one of the most important theoretical models in ecology [18]. This equation for the densities of species near equilibrium assumes that the growth rate in continuous time depends on environmental carrying capacities. This equation can be transformed into the replicator equation by introducing one more species and by changing time [5]. More importantly, the payoffs in this equation are random variables if the carrying capacities are random variables. This is the case with stochastic fluctuations in the environment, which is the rule in nature rather than the exception.

Another example is provided by the payoff matrix in the case of repeated rounds of the same matrix game between the same two players chosen at random. This is the case, for

instance, with the strategies TFT and AllD in a repeated Prisoner's Dilemma for modeling the evolution of co-operation. If the number of repetitions of the game is a random variable (e.g., a geometric random variable in the case where each round is followed by a next round with some fixed probability [6,21]), then the payoff matrix is a random matrix. More generally, a random payoff matrix is a reasonable assumption in evolutionary game theory in order to deal with more realistic or more complex situations.

In order to take into account stochastic fluctuations in the surrounding environment, deterministic evolutionary concepts such as evolutionary stability and convergence stability have to be extended. Random payoffs received by randomly pairwise interacting individuals in an infinite population undergoing discrete, nonoverlapping generations were considered till recently in a two-phenotype setting, and the concepts of stochastic evolutionary stability (SES) and stochastic convergence stability (SCS) were developed [21]. Although this study shows that a random environmental noise may have an important impact on the stability nature of an equilibrium and, therefore, on the evolution of animal behavior, it still assumes that the fitness of an individual is a linear function of the expected payoff of the exhibited phenotype, which corresponds to an assumption of weak selection. Here we will consider the more general case of an exponential function.

A two-phenotype model.—For simplicity, consider a two-phenotype evolutionary game in an infinite population with discrete, nonoverlapping generations. The two phenotypes (or strategies) are denoted by R_1 and R_2, respectively, and the payoffs in pairwise interactions at time step t (with $t \geq 0$) are given by the matrix

$$\mathbf{A}(t) = \begin{pmatrix} a_{11}(t) & a_{12}(t) \\ a_{21}(t) & a_{22}(t) \end{pmatrix} = \begin{pmatrix} a_t & b_t \\ c_t & d_t \end{pmatrix}, \quad (1)$$

where $a_{ij}(t)$ is the payoff to strategy R_i against strategy R_j for $i, j = 1, 2$. In general, these payoffs are assumed to be random variables with $\langle a_{ij}(t) \rangle = \bar{a}_{ij}$, $\langle (a_{ij}(t) - \bar{a}_{ij})^2 \rangle = \sigma_{ij}^2$, and $\langle (a_{ij}(t) - \bar{a}_{ij})(a_{kl}(t) - \bar{a}_{kl}) \rangle = \sigma_{ij,kl}$ for $i, j, k, l = 1, 2$ with $(i, j) \neq (k, l)$. As for $s \neq t$, the payoffs $a_{ij}(s)$ and $a_{kl}(t)$ are assumed to be independent of each other so that $\langle (a_{ij}(s) - \bar{a}_{ij})(a_{kl}(t) - \bar{a}_{kl}) \rangle = 0$ for $i, j, k, l = 1, 2$ [21]. Besides, a further technical assumption is that there exist real numbers $A, B > 0$ such that $\mathbb{P}(A \leq a_{ij}(t) \leq B) = 1$ for all $i, j = 1, 2$.

Let x_t denote the frequency of strategy R_1 at time step t and, similarly, $1 - x_t$ the frequency of strategy R_2. Assuming random pairwise interactions, the expected payoffs of R_1 and R_2 at time step t are given by $\pi_{1,t} = x_t a_t + (1 - x_t) b_t$ and $\pi_{2,t} = x_t c_t + (1 - x_t) d_t$, respectively. The fitnesses of R_1 strategists and R_2 strategists at time step t are defined as $f_{1,t} = e^{\pi_{1,t}}$ and $f_{2,t} = e^{\pi_{2,t}}$, respectively [11–14,16,17]. Then, the average fitness of the population at time step t is $\bar{f}_t = x_t f_{1,t} + (1 - x_t) f_{2,t}$, and the frequency of R_1 at time step $t + 1$ can be expressed as

$$x_{t+1} = \frac{x_t e^{\pi_{1,t}}}{x_t e^{\pi_{1,t}} + (1 - x_t) e^{\pi_{2,t}}} \quad (2)$$

for $t \geq 0$ [14,15].

Random environmental noise and stochastic local stability.—In the absence of random environmental noise, that is, in the situation where $\sigma_{ij}^2 = 0$ for all $i, j = 1, 2$ so that the payoff matrix in Eq. (1) is a constant matrix $\mathbf{A}(t) = \begin{pmatrix} \bar{a} & \bar{b} \\ \bar{c} & \bar{d} \end{pmatrix}$, Eq. (3) reduces to a deterministic recurrence equation. For this deterministic recurrence equation, it has been shown that (i) only one equilibrium with x^* with $0 < x^* < 1$ (called interior equilibrium) exists and is given by $x^* = (\bar{b} - \bar{d})/\gamma$ if $\bar{b} - \bar{d}$ and $\bar{c} - \bar{a}$ are both positive or both negative, where $\gamma = \bar{b} - \bar{d} + \bar{c} - \bar{a}$, (ii) x^* is globally asymptotically stable if $0 < \gamma < 2/x^*(1 - x^*)$, and (iii) as γ increases such that $\gamma > 2/x^*(1 - x^*)$, there are period-doubling bifurcation and chaos [15]. In the special case where $x^* = 1/2$, for instance, only one stable periodic two-cycle is possible for $\gamma > 8$.

If at least one σ_{ij}^2 for $i, j = 1$ or 2 is nonzero, which means that the random environmental noise is not degenerate, then Eq. (3) is a stochastic recurrence equation. In order to study the asymptotic (or long-run) behavior of the process $\{x_t\}$, suppose that $\tilde{x}$ is a constant (nonrandom) equilibrium of $\{x_t\}$, that is, an equilibrium of Eq. (3) that does not depend on the randomness of the payoff matrix. Obviously, both $\tilde{x} = 0$ and $\tilde{x} = 1$ are constant equilibria of Eq. (3) (called also the fixation states or the boundary equilibria of the system). Moreover, $\tilde{x}$ is called a constant interior equilibrium if it satisfies $0 < \tilde{x} < 1$ [21–23]. Based on definitions introduced in Karlin and Liberman [22,23], a constant equilibrium $\tilde{x}$ is said to be stochastically locally stable (SLS) if for any $\epsilon > 0$ there exists $\delta_0 > 0$ such that $\mathbb{P}(x_t \to \tilde{x}) \geq 1 - \epsilon$ as soon as $|x_0 - \tilde{x}| < \delta_0$, while a constant equilibrium $\tilde{x}$ is said to be stochastically locally unstable (SLU) if $\mathbb{P}(x_t \to \tilde{x}) = 0$ as soon as $|x_0 - \tilde{x}| > 0$.

Using the above definitions, we give below simplified mathematical arguments for the stochastic local stability of a constant equilibrium (the more rigorous mathematical proofs are similar to those in Ref. [21]).

Let $u_t = x_t/(1 - x_t)$. Then Eq. (3) can be equivalently expressed as

$$u_{t+1} = u_t e^{\pi_{1,t} - \pi_{2,t}}. \quad (3)$$

Consider first the stochastic local stability of the boundary equilibrium $\tilde{x} = 0$, which corresponds to $\tilde{u} = 0$. Notice that $u_t \to 0$ if and only if $x_t \to 0$. Iterating the above recurrence equation leads to

$$\frac{1}{n}(\log u_n - \log u_0)$$

$$= \frac{1}{n} \sum_{t=0}^{n-1} \left((b_t - d_t) + (a_t - b_t - c_t + d_t) \frac{u_t}{1 - u_t} \right). \quad (4)$$

Therefore, if $u_t \to 0$ and $\bar{b} - \bar{d} \neq 0$, then the strong law of large numbers guarantees that

$$0 \geq \lim_{n \to \infty} \frac{1}{n} (\log u_n - \log u_0) \approx \lim_{n \to \infty} \frac{1}{n} \sum_{t=0}^{n-1} (b_t - d_t) = \bar{b} - \bar{d}. \tag{5}$$

We conclude that the boundary equilibrium $\tilde{x} = 0$ is SLU if $\bar{b} - \bar{d} > 0$. On the other hand, using Egorov's theorem, it can be shown that $\tilde{x} = 0$ is SLS if $\bar{b} - \bar{d} < 0$ [21,23].

Suppose that there exists $\tilde{u} > 0$ such that $\tilde{u}(a_t - c_t) = d_t - b_t$ for all possible $t \geq 0$. Then the random payoff matrix can be expressed as

$$\begin{pmatrix} a_t & b_t \\ c_t & d_t \end{pmatrix} = \begin{pmatrix} c_t + z_t & b_t \\ c_t & b_t + \tilde{u}z_t \end{pmatrix}$$
$$= \begin{pmatrix} a_t & d_t - \tilde{u}z_t \\ a_t - z_t & d_t \end{pmatrix}, \tag{6}$$

where $z_t = a_t - c_t$. In this situation, Eq. (3) admits a constant interior equilibrium, given by $\tilde{x} = \tilde{u}/(1 + \tilde{u})$ with $0 < \tilde{x} < 1$. Moreover, the previous analysis ascertains that the two fixation states $\tilde{x} = 0$ and $\tilde{x} = 1$ are both SLS if $\bar{z} = \bar{a} - \bar{c} > 0$ and both SLU if $\bar{z} = \bar{a} - \bar{c} < 0$. Now, in order to study the stochastic local stability of $\tilde{x} = \tilde{u}/(1 + \tilde{u})$, let Eq. (4) be rewritten as

$$u_{t+1} = u_t e^{-\tilde{u}z_t + (1+\tilde{u})z_t \frac{u_t}{1+u_t}}. \tag{7}$$

A Taylor expansion around $\tilde{u}$ leads to the approximation

$$u_{t+1} - \tilde{u} \approx \left(1 + \frac{\tilde{u}}{1 + \tilde{u}} z_t\right)(u_t - \tilde{u}), \tag{8}$$

from which

$$\lim_{n \to \infty} \frac{1}{n} (\log(u_n - \tilde{u})^2 - \log(u_0 - \tilde{u})^2)$$
$$\approx \left\langle \log \left(1 + \frac{\tilde{u}}{1 + \tilde{u}} z_t\right)^2 \right\rangle. \tag{9}$$

Then it can be shown that the constant interior equilibrium $\tilde{x} = \tilde{u}/(1 + \tilde{u})$ is SLS if

$$\langle \log (1 + \tilde{x}z_t)^2 \rangle < 0, \tag{10}$$

and SLU if the inequality is reversed. Developing $\log(1 + \tilde{x}z_t)^2$ around $\bar{z} = \bar{a} - \bar{c}$ yields

$$\langle \log (1 + \tilde{x}z_t)^2 \rangle \approx \log(1 + \tilde{x}\bar{z})^2 - \left(\frac{\tilde{x}}{1 + \tilde{x}\bar{z}}\right)^2 \sigma_z^2, \tag{11}$$

where $\sigma_z^2 = \sigma_a^2 + \sigma_c^2 - 2\sigma_{a,c}$. Therefore, as long as the random environmental noise does not vary too much, the constant interior equilibrium $\tilde{x} = \tilde{u}/(1 + \tilde{u})$ is SLS if

$$\sigma_z^2 > \left(\frac{1 + \tilde{x}\bar{z}}{\tilde{x}}\right)^2 \log(1 + \tilde{x}\bar{z})^2, \tag{12}$$

and SLU if the inequality is reversed. This result shows not only that the two boundary equilibria ($\tilde{x} = 0$ and $\tilde{x} = 1$) and the constant interior equilibrium [$\tilde{x} = \tilde{u}/(1 + \tilde{u})$] can be simultaneously SLS, but also that an increase in the variance of the environmental noise (σ_z^2) will promote the stochastic local stability of the constant interior equilibrium.

In order to test the above theoretical predictions, three numerical examples are investigated below using computer simulations in the case of a random payoff matrix in the form of Eq. (9) with a constant interior equilibrium $\tilde{x} = \tilde{u}/(1 + \tilde{u})$.

Example 1.—If we take $\tilde{u} = 1$ in Eq. (9), then $\tilde{x} = 1/2$ is a constant interior equilibrium. From our theoretical results, both $\tilde{x} = 0$ and $\tilde{x} = 1$ are SLS if $\bar{z} > 0$, while $\tilde{x} = 1/2$ is SLS if $\sigma_z^2 > (2 + \bar{z})^2 \log(1 + \bar{z}/2)^2$. The simulation results based on Eq. (3) are plotted in Fig. S1 (see Ref. [24]), in which we take $\bar{z} = 0.1$ and $\sigma_z^2 = 4$. These simulations strongly support the theoretical predictions, that is, both boundaries and the constant interior equilibrium can be simultaneously SLS. Notice that in the absence of random environmental noise (σ_z^2), both boundaries and the constant interior equilibrium cannot be simultaneously locally stable.

Example 2.—Similarly to example 1, we take $\tilde{u} = 1$ in Eq. (9) so that $\tilde{x} = 1/2$ is a constant interior equilibrium. If $\bar{z} < 0$, then both $\tilde{x} = 0$ and $\tilde{x} = 1$ are SLU. On the other hand, if $\sigma_z^2 = 0$, then $\tilde{x} = 1/2$ is globally asymptotically stable if $|\bar{z}| < 4$ (with $\bar{z} < 0$), while only one stable periodic two-cycle can exist when $|\bar{z}| > 4$ [15] [see Fig. S2(a) in Ref. [24]]. For $\bar{z} = -6$ and $\sigma_z^2 > 0$, the simulation results show the following: (i) when σ_z^2 is small, the probability distribution of x_t over time is bimodal about $\tilde{x} = 1/2$ [see Fig. S2(b) in Ref. [24]]; and (ii) as σ_z^2 increases, a new peak of probability distribution appears at $\tilde{x} = 1/2$, and the amount of probability near the constant interior equilibrium $\tilde{x} = 1/2$ rapidly increases [see Figs. S2(c) and S2(d) in Ref. [24]]. Obviously, the increase of σ_z^2 promotes the stochastic local stability of $\tilde{x} = 1/2$. However, we can see also that, although the increase of σ_z^2 leads to a new peak of the probability distribution at $\tilde{x} = 1/2$, the period doubling characteristic of the system is not completely destroyed if σ_z^2 is not too large.

Example 3.—In this example, we take $\tilde{u} = 1/2$ in Eq. (9) so that $\tilde{x} = 1/3$ is a constant interior equilibrium. If $\bar{z} < 0$, then both $\tilde{x} = 0$ and $\tilde{x} = 1$ are SLU. On the other hand, if $\sigma_z^2 = 0$, then $\tilde{x} = 1/3$ is globally asymptotically stable if $|\bar{z}| < 6$ (with $\bar{z} < 0$), while an increase of $|\bar{z}|$ (with $|\bar{z}| > 6$) leads to period-doubling bifurcation and chaos [15] [see Fig. 1(a)]. Here, we take $\bar{z} = -9$ so that the system exhibits a stable periodic four-cycle if $\sigma_z^2 = 0$ [see also Fig. 1(a)]. Similarly to the results in example 2, we notice that (i) when σ_z^2 is small (but $\sigma_z^2 \neq 0$), the probability distribution of x_t over time shows four peaks (this phenomenon exactly matches the nonlinear dynamical characteristics of the system) [see Fig. 1(b)], and (ii) with the increase of σ_z^2,
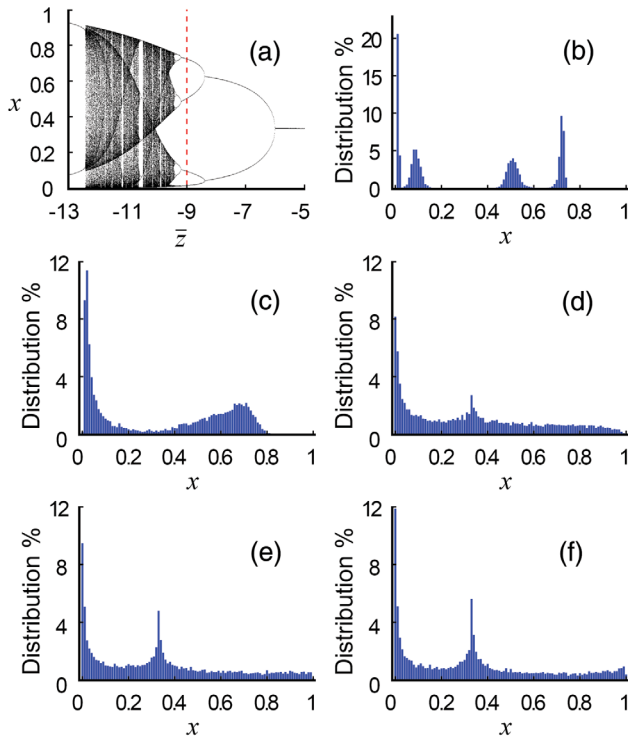
FIG. 1. An increase of σ_z^2 promotes the stochastic local stability of $\tilde{x} = 1/3$. (a) For the random payoff matrix $\begin{pmatrix} 1+z_t & 1 \\ 1 & 1+z_t/2 \end{pmatrix}$ with $\bar{z} = -9$, if $\sigma_z^2 = 0$, both boundaries and the constant interior equilibrium $\tilde{x} = 1/3$ are unstable and there is a stable periodic four-cycle (red dash line). (b) For $\sigma_z^2 = 0.01$, the probability distribution of x_t exhibits four peaks, characteristic of a stable periodic four-cycle, when σ_z^2 is small (but $\sigma_z^2 \neq 0$). (c)–(f) For $\sigma_z^2 = 0.25, 9, 16, 25$ in panels (c)–(f), respectively, we can see that increasing σ_z^2 not only leads to the appearance of a new peak of probability distribution of x_t at $\tilde{x} = 1/3$, but also to an increase in the amount of probability near $\tilde{x} = 1/3$.

a new peak of the probability distribution appears at $\tilde{x} = 1/3$ and the amount of probability near $\tilde{x} = 1/3$ is also positively related to the size of σ_z^2 [see Figs. 1(c)–1(f)].

Conclusion and discussion.—Our theoretical results and simulations on evolutionary games with a random payoff matrix clearly show that stochastic fluctuations in the payoffs as a result of random noise in the environment make the dynamical system much more complex, namely, that an increase in the level of environmental noise could promote stochastic local stability of a constant interior equilibrium. Although it may look at first glance that the matrix games considered in this Letter have totally uncertain outcomes, this is not the case. The payoffs in pairwise interactions are not assumed to be independent identically distributed random variables. In particular, they are not assumed to have the same expected value. The structure of the game is determined by the expected payoffs which in turn determine the dynamical properties of fixation states as well as interior equilibria if they exist in the absence of variability. The local stability properties and conditions have to be extended when random

perturbations on the payoffs are introduced. These extensions for fixation states can be used to define stochastic evolutionary concepts such as stochastic evolutionary stability and stochastic convergence stability [21].

In this Letter, we have focused on the existence of a stochastically locally stable interior equilibrium in a discrete-time two-phenotype model with an exponential function of the payoff as fitness to best approximate a continuous-time model. The three examples allow us to address the global dynamics of the system and make evolutionary predictions in the most interesting cases, namely, when the fixation states are both stochastically locally stable or both stochastically locally unstable. As shown, an increase in the variance of environmental noise (σ_z^2) favors the stochastic local stability of an interior equilibrium even in the former case, which is rather surprising. In our simulations, a gradual increase in the environmental noise intensity leads to a gradual increase in the probability distribution of the population state over a long period of time near the constant interior equilibrium at which all individuals have the same average fitness. Moreover, this is in agreement with the mathematical condition for a constant interior equilibrium [Eq. 14] to be SLS, so that the population state tends to wander around it. Notice that the stochastic local stability of the constant interior equilibrium depends not only on the averages of the payoffs but also on their variances and covariances contrary to the boundary equilibria. This is a characteristic of the stochastic model compared to the deterministic model that can make possible the coexistence of a SLS interior equilibrium with two SLS boundary equilibria as environmental noise intensity increases.

Our conclusion may seem counterintuitive and has important biological implications. There is an analogy, however, between our results on SLS equilibria in an evolutionary game model as a function of noise intensity and noise-induced transitions in the number of peaks in stationary probability densities of diffusion processes for stochastic differential equations models in physics, chemistry, and biology [25]. On the other hand, May [26] found that a simple deterministic logistic difference equation can lead to periodic limit cycles and chaos. This discovery led people to believe that nonlinear biological systems could result in the emergence of complex dynamics, and that such dynamics (especially chaos) should be easily observable in natural populations. Nevertheless, the majority of attempts to find chaos in nature have either drawn a blank or remained controversial. Since then, several studies have aimed to explain why natural populations do not exhibit chaos [27]. Our results on the effects of random noise on evolutionary game dynamics can provide some clues for addressing this question, mainly, that stochastic fluctuations in the environment may play a role in impeding the emergence of complex dynamical behaviors in natural populations. The explanation might be that a random

environment favors the evolution of more robust equilibrium population strategies but this remains to be confirmed by further studies.

*Corresponding author.
lessards@dms.umontreal.ca
†Corresponding author.
yitao@ioz.ac.cn

[1] J. Maynard Smith and G. Price, Nature (London) **246,** 15 (1973).
[2] J. Maynard Smith, *Evolution and the Theory of Games* (Cambridge University Press, Cambridge, England, 1982).
[3] R. Axelrod, *The Evolution of Cooperation* (Basic Books, New York, 1984).
[4] S. Lessard, Theor. Popul. Biol. **25,** 210 (1984).
[5] J. Hofbauer and K. Sigmund, *The Theory of Evolution and Dynamical Systems* (Cambridge University Press, Cambridge, England, 1988).
[6] M. A. Nowak, *Evolutionary Dynamics* (Harvard University Press, Cambridge, MA, 2006).
[7] M. Broom and J. Rychtář, *Game-Theoretical Models in Biology* (CRC Press, London, UK, 2013).
[8] P. D. Taylor and L. B. Jonker, Math. Biosci. **40,** 145 (1978).
[9] E. C. Zeeman, in *Global Theory of Dynamical Systems* (Springer Verlag, Berlin, Heidelberg, 1980), p. 471.
[10] J. W. Weibull, *Evolutionary Game Theory* (MIT Press, Cambridge, MA, 1995).
[11] G. Szabó and C. Hauert, Phys. Rev. Lett. **89,** 118101 (2002).
[12] A. Traulsen, M. A. Nowak, and J. M. Pacheco, Phys. Rev. E **74,** 011909 (2006).
[13] J. C. Claussen and A. Traulsen, Phys. Rev. Lett. **100,** 058104 (2008).
[14] A. Traulsen, N. Shoresh, and M. A. Nowak, Bull. Math. Biol. **70,** 1410 (2008).
[15] Y. Tao, Q.-S. Yang, Z.-G. Jiang, and Z.-W. Wang, J. Theor. Biol. **188,** 21 (1997).
[16] T. L. Vincent and M. E. Fisher, Evol. Ecol. **2,** 321 (1988).
[17] L. E. Blume, Games Econ. Behav. **5,** 387 (1993).
[18] R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton University Press, Princeton, NJ, 1973).
[19] P. Turchin, L. Oksanen, P. Ekerholm, T. Oksanen, and H. Henttonen, Nature (London) **405,** 562 (2000); O. N. Bjornstad and B. T. Grenfell, Science **293,** 638 (2001); X.-D. Zheng, L.-L. Deng, W.-Y. Qiang, R. Cressman, and Y. Tao, Phys. Rev. E **95,** 042404 (2017).
[20] R. Lande, S. Engen, and B.-E. Sæther, *Stochastic Population Dynamics in Ecology and Conservation* (Oxford University Press, New York, 2003).
[21] X.-D. Zheng, C. Li, S. Lessard, and Y. Tao, Phys. Rev. E **96,** 032414 (2017).
[22] S. Karlin and U. Liberman, Theor. Popul. Biol. **6,** 355 (1974).
[23] S. Karlin and U. Liberman, J. Math. Biol. **2,** 1 (1975).
[24] See Supplemental Material at http://link.aps.org/supplemental/10.1103/PhysRevLett.120.218101 for additional figures.
[25] W. Horsthemke and R. Lefever, *Noise-Induced Transitions: Theory and Applications in Physics, Chemistry, and Biology* (Springer-Verlag, Berlin, 2006).
[26] R. M. May, Nature (London) **261,** 459 (1976).
[27] T. N. Sherratt and D. M. Wilkinson, *Big Questions in Ecology and Evolution* (Oxford University Press, New York, 2009).