Weak selection can filter environmental noise in the evolution of animal behavior

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Weak selection is an important assumption in theoretical evolutionary biology, but its biological significance remains unclear. In this study, we investigate the effect of weak selection on stochastic evolutionary stability in a two-phenotype evolutionary game dynamics with a random payoff matrix assuming an infinite, well-mixed population undergoing discrete, nonoverlapping generations. We show that, under weak selection, both stochastic local stability and stochastic evolutionary stability in this system depend on the means of the random payoffs but not on their variances. Moreover, although stochastic local stability or instability of an equilibrium may not depend on environmental noise if selection is weak enough, the growth rate near an equilibrium not only depends on environmental noise, but can even be enhanced by environmental noise if selection is weak. This is the case, for instance, when the variances of the random payoffs as well as the covariances are equal. These results suggest that natural selection could be able to filter (or resist) the effect of environmental noise on the evolution of animal behavior if selection is weak.

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I. INTRODUCTION

Weak selection is an important assumption in theoretical evolutionary biology. It is the assumption that there is little difference between the individuals in reproductive success, or fitness, so that the effects of natural selection are small. Weak selection has a long-standing history in population genetics [1,2]. In infinitely large populations in a constant environment, however, increasing the intensity of selection often results in a mere rescaling of time which does not actually affect the final outcome of the deterministic dynamics [3,4]. On the opposite, in finite populations, changing the intensity of selection may have an important effect on the stochastic dynamics [1,5]. In some situations, results under weak selection have been shown to stay valid as the intensity of selection increases [6]. In general, however, the evolutionary significance of weak selection in finite populations remains unclear.

The assumption of weak selection has already been considered in evolutionary game theory to analyze the stochastic dynamics in finite populations [7]. Here, weak selection means that the expected payoff of an individual has only a very small effect on its fitness so that the evolutionary dynamics is mainly driven by random fluctuations [5,8]. Under the assumption of weak selection, Nowak *et al.* [5] deduced the "one-third law" for the fixation probability in a two-phenotype game-theoretic model and used it to provide an explanation for the evolution of cooperation (see also [9–14]). In order to show the robustness of outcomes in finite populations under weak selection, Wu *et al.* [15,16] investigated some properties of weak selection in the Fermi and Moran processes, where the environment is assumed to be fixed so that the payoff matrix remains constant.

Environmental conditions in the real world are changing and uncertain, and stochastic fluctuations in the surroundings of a population may cause changes in the occurrence of interactions between individuals and, more importantly, changes in the payoffs received by the interacting individuals [17,18]. As pointed out by May [19], the birth rates, carrying capacities, competition coefficients, and other ecological parameters which characterize natural biological systems all, to a greater or lesser degree, exhibit random fluctuations. Therefore, a very challenging question is whether natural selection is able to filter (or resist) the effect of environmental noise on the evolution of animal behavior.

Recently, in order to develop the concept of evolutionary stability in a randomly fluctuating environment, Zheng *et al.* [17,18] investigated conditions for stochastic local stability of the fixation states and constant interior equilibria in a two-phenotype model with random payoffs and developed the concepts of stochastic evolutionary stability and stochastic convergence stability. The results obtained show that stochastic local stability depends not only on the averages of the random payoffs but also on the variances of these random payoffs. Note that Stollmeier and Nagler [20] considered also an evolutionary game dynamics with two phenotypes and time-dependent payoffs in an infinite population undergoing discrete, nonoverlapping generations, but they focused on the unfair coexistence of strategies.

Extending the analysis of stochastic local stability and stochastic evolutionary stability, we are interested in this paper in what determines the characteristics of the evolutionary game dynamics in the presence of environmental noise if

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selection is weak. Our main goal is to reveal the fundamental importance of weak selection in the evolution of animal behavior, or the evolutionary biological significance of weak selection, in a stochastic environment.

It may be useful to recall that stochastic fluctuations in evolutionary game dynamics may be due to either intrinsic noise (i.e., demographic stochasticity), or extrinsic noise (i.e., environmental stochasticity), or a combination of both. Demographic stochasticity mainly involves the occurrence of interactions between individuals, random events of birth and death of individuals, etc. Demographic stochasticity in evolutionary game dynamics due to a finite population size has received a lot of attention as already mentioned [5–14]). On the other hand, stochastic fluctuations in the population state due to a finite population size can be much smaller than those caused by changes in the environment, and then ignored, if the population size is large enough. This assumption is current in evolutionary game theory [3,21,22] and deserves as much attention as the assumption of a population size whose inverse is of order larger than, or equal to, the order of random differences in payoffs. Weak selection, however, another current assumption in evolutionary game theory, may come into play in the short-term as well as the long-term effects of random fluctuations in the environment. This is the question addressed in the present paper, which has not been addressed in previous studies.

II. BASIC MODEL AND DEFINITIONS

Consider an evolutionary game in an infinite population with discrete, nonoverlapping, generations. There are two phenotypes or pure strategies, S_1 and S_2, and the payoffs in pairwise interactions at time step $t \geqslant 0$ are given by the game matrix

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

where $a_{ij}(t)$ is the payoff to strategy S_i against strategy S_j for $i, j = 1, 2$. These payoffs are assumed to be positive random variables that are uniformly bounded below and above by some positive constants. Therefore, there exist real numbers $A, B > 0$ such that $A \leqslant a_{ij}(t) \leqslant B$ for $i, j = 1, 2$ and all $t \geqslant 0$ [17]. Moreover, the probability distributions of $a_{ij}(t)$ for $i, j = 1, 2$ do not depend on $t \geqslant 0$. The means, variances, and covariances of these random payoffs are given by $\langle a_{ij}(t)\rangle = \bar{a}_{ij}$, $\langle (a_{ij}(t) - \bar{a}_{ij})^2\rangle = \sigma_{ij}^2$ and $\langle (a_{ij}(t) - \bar{a}_{ij})(a_{kl}(t) - \bar{a}_{kl})\rangle = \sigma_{ij,kl}$, respectively, 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 $i, j, k, l = 1, 2$. In general, we also assume that the variances of the random payoffs are small [17,18].

Let x_t be the frequency of strategy S_1 at time step $t \geqslant 0$ and, similarly, $1 - x_t$ the frequency of strategy S_2. Then the expected payoffs of strategies S_1 and S_2 at time step $t \geqslant 0$ 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. Furthermore, in order to show the effect of selection intensity on the evolutionary dynamics of strategies S_1 and S_2, and without loss of generality, the fitnesses of S_1 and S_2 at time step $t \geqslant 0$ are simply defined as $(1 - w) + w\pi_{1,t}$ and $(1 - w) + w\pi_{2,t}$, respectively, where w with $0 \leqslant w \leqslant 1$ represents the selection intensity [5,7]. So, the number of replicates of a strategy from one step to the next is proportional to its fitness, and the frequency of strategy S_1 at time step $t + 1$ is given by the recurrence equation

$$x_{t+1} = \frac{x_t((1 - w) + w\pi_{1,t})}{x_t((1 - w) + w\pi_{1,t}) + (1 - x_t)((1 - w) + w\pi_{2,t})} \tag{2}$$

for $t \geqslant 0$. This model can be viewed as a Wright-Fisher model in the limit of a large population size (see, e.g., [3]), but with fitness differences of order larger than the inverse of the population size and subject to stochastic fluctuations. Defining $u_t = x_t/(1 - x_t)$, the recurrence equation takes the simple form

$$u_{t+1} = u_t \left[\frac{u_t((1 - w) + wa_t) + ((1 - w) + wb_t)}{u_t((1 - w) + wc_t) + ((1 - w) + wd_t)} \right]. \tag{3}$$

Let $\hat{x}$ represent a constant (nonrandom) equilibrium of (2) that does not depend on the randomness of the payoff matrix $\mathbf{A}(t)$. This is clearly the case for both $\hat{x} = 0$ and $\hat{x} = 1$, called the *fixation states* or the *boundary equilibria*. This may also be the case for a constant equilibrium $\hat{x}$ with $0 < \hat{x} < 1$, called a constant interior equilibrium. A constant equilibrium $\hat{x}$ is said to be *stochastically locally stable* (SLS) if for every $\epsilon > 0$ there exists $\delta_0 > 0$ such that $\mathbb{P}(x_t \to \hat{x}) \geqslant 1 - \epsilon$ as soon as $|x_0 - \hat{x}| < \delta_0$ [17,23,24]. This means that x_t tends to $\hat{x}$ as $t \to \infty$ with probability arbitrarily close to 1 (but different from 1) if the initial state x_0 is sufficiently near $\hat{x}$. On the other hand, a constant equilibrium $\hat{x}$ can be said to be *stochastically locally unstable* (SLU) if $\mathbb{P}(x_t \to \hat{x}) = 0$ as soon as $|x_0 - \hat{x}| > 0$ [17,23,24]. If this is the case, then $\hat{x}$ cannot be reached with probability 1 from any initial state different from $\hat{x}$. Based on these definitions, we present some simplified mathematical arguments for the stochastic local stability of a constant equilibrium (the more rigorous mathematical proofs are similar to those in [17]).

III. EFFECT OF WEAK SELECTION ON THE STOCHASTIC LOCAL STABILITY OF AN EQUILIBRIUM

Consider first the stochastic local stability of the fixation state $\hat{x} = 0$ in (2), which corresponds to the equilibrium $\hat{u} = \hat{x}/(1 - \hat{x}) = 0$ in (3). Note that (3) can be rewritten in the form

$$\frac{u_{t+1}}{u_t} = \left[\frac{(1 - w) + wb_t}{(1 - w) + wd_t} \right] R_t\ , \tag{4}$$

where

$$R_t = 1 + \frac{u_t[((1 - w) + wa_t)((1 - w) + wd_t) - ((1 - w) + wb_t)((1 - w) + wc_t)]}{u_t((1 - w) + wb_t)((1 - w) + wc_t) - ((1 - w) + wb_t)((1 - w) + wd_t)}\ . \tag{5}$$

Then, iterating this recurrence equation leads to

$$\frac{1}{n}[\log u_n - \log u_0] = \frac{1}{n}\sum_{t=0}^{n-1}\log\left[\frac{(1-w)+wb_t}{(1-w)+wd_t}\right] + \frac{1}{n}\sum_{t=0}^{n-1}\log R_t \tag{6}$$

for $n \geqslant 1$. Therefore, if $u_t \to 0$ (which compels $\log R_t \to 0$), then the strong law of large numbers guarantees that

$$\lim_{n\to\infty}\frac{1}{n}\Big[\log u_n - \log u_0\Big] \approx \left\langle \log\left[\frac{(1-w)+wb_t}{(1-w)+wd_t}\right]\right\rangle . \tag{7}$$

Using Egorov's theorem, it can be shown that the fixation state $\hat{x} = 0$ is SLS if

$$\left\langle \log\left[\frac{(1-w)+wb_t}{(1-w)+wd_t}\right]\right\rangle = \langle \log[(1-w)+wb_t]\rangle - \langle \log[(1-w)+wd_t]\rangle < 0\,, \tag{8}$$

and $\hat{x} = 0$ is SLU if the inequality is reversed [17]. The mean geometric growth rate on the left-hand side in (8) represents the rate of convergence to 0 if 0 is SLS and the rate of divergence from 0 if 0 is SLU.

In the case where the payoffs have small enough variances, we have the approximation

$$\langle \log[(1-w)+wa_{ij}(t)]\rangle \approx \log[(1-w)+w\bar{a}_{ij}] - \frac{w^2\sigma_{ij}^2}{2((1-w)+w\bar{a}_{ij})^2} \tag{9}$$

for $i, j = 1, 2$ [17]. Then, the inequality in (8) can be rewritten as

$$\log\left[\frac{(1-w)+w\bar{b}}{(1-w)+w\bar{d}}\right] + \frac{w^2\sigma_d^2}{2\big((1-w)+w\bar{d}\big)^2} - \frac{w^2\sigma_b^2}{2\big((1-w)+w\bar{b}\big)^2} < 0\,. \tag{10}$$

Furthermore, when w is small enough, we have the approximation

$$\log\left[\frac{(1-w)+w\bar{b}}{(1-w)+w\bar{d}}\right] \approx w(\bar{b}-\bar{d})\,. \tag{11}$$

Therefore, if selection is weak enough, then the fixation state $\hat{x} = 0$ is SLS if $\bar{b} - \bar{d} < 0$ and SLU if $\bar{b} - \bar{d} > 0$. This implies that the stochastic local stability of $\hat{x} = 0$ depends on the means of the random payoffs b_t and d_t but does not depend on their variances. An example of the stochastic local stability of fixation state $\hat{x} = 0$ under weak selection is shown in Fig. 1. By symmetry, under weak enough selection, the fixation state $\hat{x} = 1$ is SLS if $\bar{c} - \bar{a} < 0$ and SLU if $\bar{c} - \bar{a} > 0$. On the other hand, in the degenerate case where $b_t = d_t$ (or $a_t = c_t$) for all $t \geqslant 0$, and under weak enough selection, the fixation state $\hat{x} = 0$ (or $\hat{x} = 1$) is SLS if $\bar{a} - \bar{c} < 0$ (or $\bar{d} - \bar{b} < 0$) and SLU if $\bar{a} - \bar{c} > 0$ (or $\bar{d} - \bar{b} > 0$). (The mathematical proofs are given in the Appendix.)

Moreover, as a special case, if $\hat{u}(a_t - c_t) = d_t - b_t$ for all $t \geqslant 0$ where $\hat{u}$ is a positive constant, then the random payoff matrix $\mathbf{A}(t)$ in (1) can be rewritten as

$$\begin{pmatrix} a_t & b_t \\ c_t & d_t \end{pmatrix} = \begin{pmatrix} c_t + z_t & b_t \\ c_t & b_t + \hat{u}z_t \end{pmatrix} = \begin{pmatrix} a_t & d_t - \hat{u}z_t \\ a_t - z_t & d_t \end{pmatrix}, \tag{12}$$

where $z_t = a_t - c_t$ for all $t \geqslant 0$. For this random payoff matrix, $\hat{x} = \hat{u}/(1+\hat{u})$ is a constant interior equilibrium of (2). Similarly to the the stochastic local stability analysis of the fixation state $\hat{x} = 0$, it can be shown that under weak selection, the constant interior equilibrium $\hat{x} = \hat{u}/(1+\hat{u})$ is SLS if $\bar{c} - \bar{a} > 0$ and SLU if $\bar{c} - \bar{a} < 0$ (the mathematical proofs are given in the Appendix). This result shows that, if a constant interior equilibrium exists, then its stochastic local stability under weak selection depends on the means of the random payoffs but not on their variances. However, we have to point out that even if selection is weak, whether or not a constant interior equilibrium exists cannot in general be determined only by the means of the random payoffs.

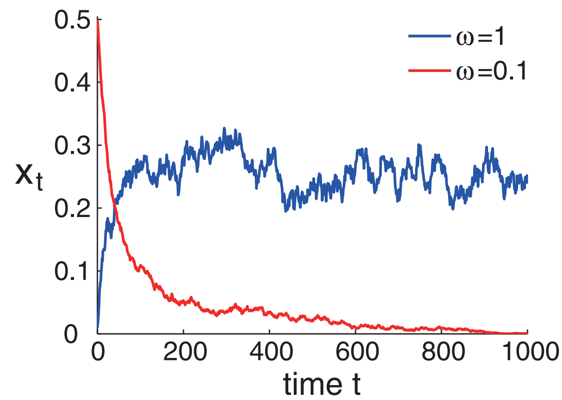

FIG. 1. Effect of selection intensity on the stochastic local stability of fixation state $\hat{x} = 0$. Consider a random payoff matrix $\mathbf{A}(t) = \begin{pmatrix} 7 & 9+\eta_t \\ 8 & 10+\xi_t \end{pmatrix}$, where η_t and ξ_t are uniform random variables with $\bar{\eta} = \bar{\xi} = 0$, $\sigma_\eta^2 = 5.3$, and $\sigma_\xi^2 = 30$ for all $t \geqslant 0$. Simulation results illustrate the stochastic local stability or instability of $\hat{x} = 0$ for two intensities of selection. When $w = 1$, then $\hat{x} = 0$ is SLU and the population state is driven away from 0 even from an initial state close to 0 such as $x_0 = 0.01$. When $w = 0.1$, then $\hat{x} = 0$ is SLS and the population state tends to 0. Each curve represents an average of 100 simulated trajectories starting from the same initial state. Note that each trajectory in the case $w = 1$ fluctuates between 0 and 1 without any convergence.

IV. EFFECT OF ENVIRONMENTAL NOISE ON THE GROWTH RATE NEAR AN EQUILIBRIUM UNDER WEAK SELECTION

A further challenging question concerns the rate of convergence (or divergence) near an equilibrium in (2) with the random payoff matrix $\mathbf{A}(t) = (a_{ij}(t))_{2\times 2}$ in (1) at time step $t \geqslant 0$, compared to the deterministic dynamics with the constant mean payoff matrix $\bar{\mathbf{A}} = (\bar{a}_{ij})_{2\times 2}$: Does this rate increase or decrease as the variance in the payoffs increases?

Consider first the situation where the fixation state $\hat{x} = 0$ is SLS in the stochastic dynamics under weak selection. Owing

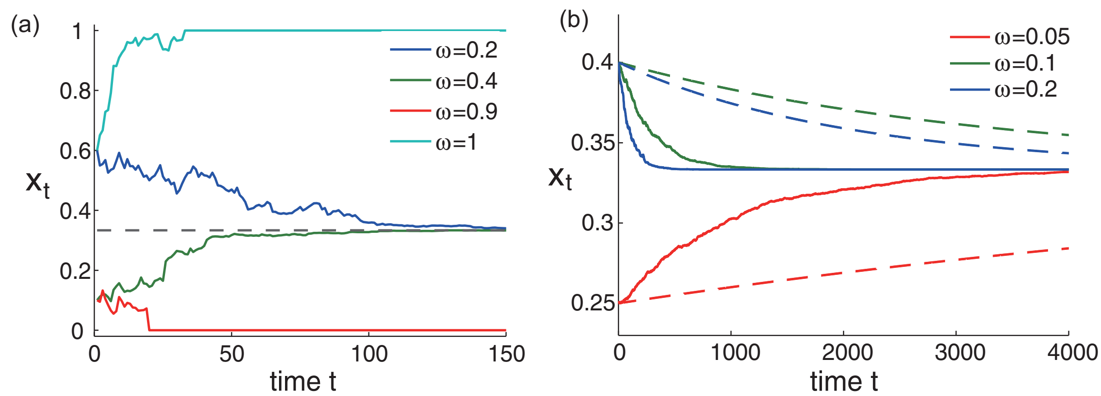

FIG. 2. Simulations for the stochastic local stability of a constant interior equilibrium under weak selection. We consider the random payoff matrix $\binom{4+z_t \quad 3}{4 \quad 3+\hat{u}z_t}$, where $\hat{u} = 1/2$ is a positive constant and z_t is taken as a normal random variable with mean $\bar{z} = -0.01$ and variance $\sigma_z^2 = 4$ at time step $t \geqslant 0$. In this case, $\hat{x} = \hat{u}/(1+\hat{u}) = 1/3$ is a constant interior equilibrium. Moreover, (i) if $w = 1$ (i.e., strong selection), then $\hat{x} = 1/3$ is SLU with respect to the stochastic dynamics, while (ii) $\hat{x} = 1/3$ is a globally asymptotically stable equilibrium with respect to the deterministic dynamics with payoff matrix $\binom{4+\bar{z} \quad 3}{4 \quad 3+\hat{u}\bar{z}}$. The simulations show in (a) that a decrease in the selection intensity w results in $\hat{x} = 1/3$ becoming SLS and in (b) that the system state x_t tends to $\hat{x} = 1/3$ when the selection intensity is small enough. Here, each of the solid curves represents an average of 100 simulated curves starting at the same initial state, and the dashed curves represent the deterministic dynamics with the payoff matrix given by the mean payoff matrix in the stochastic dynamics.

to (10) and (11), the rate of convergence to 0 is approximated as

$$\left\langle \log\left[\frac{(1-w)+wb_t}{(1-w)+wd_t}\right]\right\rangle \approx \begin{cases} w(\bar{b}-\bar{d}) + \frac{w^2(\sigma_d^2-\sigma_b^2)}{2} & \text{if} \quad \sigma_b^2 \neq \sigma_d^2\,, \\ w(\bar{b}-\bar{d}) + w^3\sigma^2(\bar{b}-\bar{d}) & \text{if} \quad \sigma_b^2 = \sigma_d^2 = \sigma^2\,, \end{cases} \tag{13}$$

where $w(\bar{b}-\bar{d}) < 0$ approximates the rate of convergence in the deterministic mean-field dynamics with payoff matrix $\bar{\mathbf{A}}$. Therefore, the rate of convergence in the stochastic dynamics is faster (or slower) than the rate of convergence in the deterministic mean-field approximation if $\sigma_b^2 \geqslant \sigma_d^2$ (or $\sigma_b^2 < \sigma_d^2$). Note that these inequalities have to be reversed for the rate of divergence from 0 to be faster (or slower) in the stochastic dynamics than that in the mean-field approximation in the case where 0 is SLU with $w(\bar{b}-\bar{d}) > 0$. In particular, the growth rate is always faster in the stochastic dynamics when $\sigma_b^2 = \sigma_d^2$. Analogous conclusions can be drawn for the fixation state $\hat{x} = 1$.

Similarly, in the situation where $\hat{u}(a_t - c_t) = d_t - b_t$ for all $t \geqslant 0$ with $\hat{u}$ being a positive constant corresponding to an SLS interior equilibrium $\hat{x} = \hat{u}/(1+\hat{u})$ in the stochastic dynamics under weak selection (that is, $\bar{c} > \bar{a}$), it can be shown that the rate of convergence to $\hat{x}$ in the stochastic dynamics is faster (or slower) than that in the deterministic mean-field approximation if $\hat{u}(\sigma_c^2 - \sigma_a^2) + 2(\sigma_{c,d} - \sigma_{a,d}) \leqslant 0$ (or $\hat{u}(\sigma_c^2 - \sigma_a^2) + 2(\sigma_{c,d} - \sigma_{a,d}) > 0$) (see the Appendix for a proof). Moreover, the same is true for the rate of divergence from an SLU $\hat{x}$ in the stochastic dynamics under weak selection (that is, $\bar{c} < \bar{a}$) if the inequalities are reversed. Note that, in the special case where $\sigma_c^2 = \sigma_a^2$ and $\sigma_{c,d} = \sigma_{a,d}$, the growth rate is always faster in the stochastic dynamics.

All these results show that, although stochastic local stability or instability of an equilibrium state may become unaffected by environmental noise as the intensity of selection diminishes, the rate of convergence or divergence of the system near equilibrium not only depends on environmental noise, but can even be enhanced by environmental noise. These findings are supported by simulation results presented in Fig. 2.

V. EFFECT OF WEAK SELECTION ON STOCHASTIC EVOLUTIONARY STABILITY

Evolutionary stability, or the *evolutionarily stable strategy* (ESS), is the key concept in evolutionary game theory [3,21,22]. Recently, Zheng *et al.* [17] extended the standard definition of an ESS in a constant environment [21] to a variable environment. A *stochastically evolutionarily stable* (SES) strategy is defined as a strategy such that, if all the members of the population adopt it, then the probability of at least any slight perturbed strategy invading the population under the influence of natural selection is arbitrarily low. More specifically, a strategy represented by a frequency vector $\hat{\mathbf{x}}$ is SES if $\hat{\mathbf{x}}$ fixation is SLS against any other strategy $\mathbf{x} \neq \hat{\mathbf{x}}$ at least nearby enough [17]. Here we mainly focus on the effect of weak selection on stochastic evolutionary stability.

For two mixed strategies $\mathbf{x} = (x, 1-x)$ and $\hat{\mathbf{x}} = (\hat{x}, 1-\hat{x})$ with the payoffs to the pure strategies at time step $t \geqslant 0$ given by $\mathbf{A}(t)$ in (1), the payoff matrix takes the form

$$\begin{pmatrix} \mathbf{xA(t)x} & \mathbf{xA}(t)\hat{\mathbf{x}} \\ \hat{\mathbf{x}}\mathbf{A}(t)\mathbf{x} & \hat{\mathbf{x}}\mathbf{A}(t)\hat{\mathbf{x}} \end{pmatrix}, \tag{14}$$

where $\mathbf{xA}(t)\mathbf{x}$ [respectively, $\mathbf{xA}(t)\hat{\mathbf{x}}$] is the expected payoff to strategy $\mathbf{x}$ against strategy $\mathbf{x}$ [respectively, $\hat{\mathbf{x}}$], and $\hat{\mathbf{x}}\mathbf{A}(t)\mathbf{x}$ [respectively, $\hat{\mathbf{x}}\mathbf{A}(t)\hat{\mathbf{x}}$] the expected payoff to strategy $\hat{\mathbf{x}}$ against strategy $\mathbf{x}$ [respectively, $\hat{\mathbf{x}}$]. Analogously to condition (10) for the fixation state $\hat{x} = 0$ to be SLS, the fixation of strategy $\hat{\mathbf{x}}$ is

SLS if

$$\log\left[\frac{(1-w)+w\langle \mathbf{x}\mathbf{A}(t)\hat{\mathbf{x}}\rangle}{(1-w)+w\langle \hat{\mathbf{x}}\mathbf{A}(t)\hat{\mathbf{x}}\rangle}\right] + \frac{w^2\sigma^2_{\hat{\mathbf{x}}\mathbf{A}(t)\hat{\mathbf{x}}}}{2\big((1-w)+w\langle \hat{\mathbf{x}}\mathbf{A}(t)\hat{\mathbf{x}}\rangle\big)^2} - \frac{w^2\sigma^2_{\mathbf{x}\mathbf{A}(t)\hat{\mathbf{x}}}}{2\big((1-w)+w\langle \mathbf{x}\mathbf{A}(t)\hat{\mathbf{x}}\rangle\big)^2} < 0\,, \tag{15}$$

where $\sigma^2_{\hat{\mathbf{x}}\mathbf{A}(t)\hat{\mathbf{x}}}$ and $\sigma^2_{\mathbf{x}\mathbf{A}(t)\hat{\mathbf{x}}}$ denote the variances of $\hat{\mathbf{x}}\mathbf{A}(t)\hat{\mathbf{x}}$ and $\mathbf{x}\mathbf{A}(t)\hat{\mathbf{x}}$, respectively. Therefore, under weak selection, the fixation of strategy $\hat{\mathbf{x}}$ is SLS if $\langle \hat{\mathbf{x}}\mathbf{A}(t)\hat{\mathbf{x}}\rangle - \langle \mathbf{x}\mathbf{A}(t)\hat{\mathbf{x}}\rangle 0$, that is, $\hat{\mathbf{x}}\bar{\mathbf{A}}\hat{\mathbf{x}} - \mathbf{x}\bar{\mathbf{A}}\hat{\mathbf{x}} > 0$. Similarly, under weak selection, the fixation of strategy $\mathbf{x}$ is SLU if we have $\langle \mathbf{x}\mathbf{A}(t)\mathbf{x}\rangle - \langle \hat{\mathbf{x}}\mathbf{A}(t)\mathbf{x}\rangle < 0$, that is, $\mathbf{x}\bar{\mathbf{A}}\mathbf{x} - \hat{\mathbf{x}}\bar{\mathbf{A}}\mathbf{x} < 0$. Combining these results, we can conclude that, under weak selection, strategy $\hat{\mathbf{x}}$ is SES if and only if

$$\hat{\mathbf{x}}\bar{\mathbf{A}}\hat{\mathbf{x}} - \mathbf{x}\bar{\mathbf{A}}\hat{\mathbf{x}} \geqslant 0 \quad \text{for all} \quad \mathbf{x} \neq \hat{\mathbf{x}} \tag{16}$$

$$\text{and} \quad \hat{\mathbf{x}}\bar{\mathbf{A}}\mathbf{x} - \mathbf{x}\bar{\mathbf{A}}\mathbf{x} > 0 \quad \text{for all} \quad \mathbf{x} \neq \hat{\mathbf{x}} \quad \text{if the equality holds above.} \tag{17}$$

Therefore, under weak selection, an SES strategy is a strategy such that, if all the members of the population adopt it, then the probability for any mutant strategy to invade the population under the influence of natural selection is arbitrarily low.

The above conclusion shows that the conditions for strategy $\hat{\mathbf{x}}$ to be SES under weak selection depends only on the average payoff matrix $\bar{\mathbf{A}}$ and that they exactly match the standard conditions for an ESS with the payoff matrix $\bar{\mathbf{A}}$ [21]. So, under weak selection: (i) the pure strategy $\hat{\mathbf{x}} = (0, 1)$ is SES if $\bar{d} > \bar{b}$; (ii) the pure strategy $\hat{\mathbf{x}} = (1, 0)$ is SES if $\bar{a} > \bar{c}$; and (iii) if $\bar{a} > \bar{c}$ and $\bar{d} > \bar{b}$, or $\bar{a} < \bar{c}$ and $\bar{d} < \bar{b}$, then the mixed strategy $\hat{\mathbf{x}} = (\hat{x}, 1-\hat{x})$ with $\hat{x} = (\bar{b}-\bar{d})/(\bar{b}-\bar{d}+\bar{c}-\bar{a})$ is SES if $\bar{b} > \bar{d}$ and $\bar{c} > \bar{a}$ [3,21]. Moreover, even if no constant interior equilibrium exists in (2), it is still possible for a mixed strategy to be SES. For example, consider a random payoff matrix $\binom{1+\xi_t \;\; 3}{3 \;\; 2+\xi_t}$, where ξ_t is a random variable with mean $\langle \xi_t\rangle = 0$ and variance $\langle \xi_t^2\rangle = \sigma_\xi^2$ at time step $t \geqslant 0$, where σ_ξ^2 is small but $\sigma_\xi^2 \neq 0$ such that both $1+\xi_t$ and $2+\xi_t$ are positive random payoffs for $t \geqslant 0$. With this random payoff matrix, although no constant interior equilibrium exists, the mixed strategy $\hat{\mathbf{x}} = (\hat{x}, 1-\hat{x})$ with $\hat{x} = 1/3$ is SES with respect to the stochastic dynamics.

VI. DISCUSSION

How natural selection can reduce the impact of environmental stochastic fluctuations on the evolution of animal behavior is a very challenging question. In this study, we have considered the effects of weak selection on a two-phenotype evolutionary game dynamics in an infinite population with a random payoff matrix. The results show that, under weak selection, both stochastic local stability and stochastic evolutionary stability in this system depend only on the means of the random payoffs and not at all on their variances. However, although stochastic local stability or instability of an equilibrium may not be affected by environmental noise, the rate of convergence or divergence near an equilibrium not only depends on environmental noise, but can even be enhanced by environmental noise. This is the case, for instance, when the variances of the random payoffs as well as the covariances are equal. These predictions are supported by analytical approximations and computer simulations.

Our analysis is based on the concept of stochastic evolutionary stability through the analysis of stochastic local stability that was developed in a previous paper of ours [17] to predict the results of long-term evolution of strategies in a stochastic environment. This is actually an extension of the classic concept of an evolutionarily stable strategy to take into account random payoffs as a result of environmental noise. These have been approximated in the case of weak selection to show that stochastic evolutionary stability can be unaffected, and evolution can even occur faster, in the presence of environmental noise when selection is weak enough. It might be worth stressing that weak selection is not equivalent to weak noise. Actually, it is almost the opposite, since selection would often appear strong when noise is weak. It may be obvious that the effects of weak noise can be counteracted by the pressure of strong selection. That the effects of noise can be counteracted by the pressure of weak selection is less obvious, not to mention that weak selection can increase the rate of evolution in the presence of noise. These findings have biological implications, since they reveal an unexpected role of weak selection in the evolution of biological populations in a random environment.

Previous studies on the impact of environmental noise on biological evolution involved such mechanisms as the storage effect and the bet-hedging strategy in populations with overlapping generations [25–28]. Such mechanisms concern the trade-off between adult survival and reproduction but can involve, in principle, any life history trait. They have been used to explain the coexistence of competitors and are somehow related to the notion of protected polymorphism in structured populations under the effects of spatially or temporally varying selection regimes [29]. Our study takes the opposite view of looking at a general condition, namely, weak selection, which could counteract the effects of random noise. That the same condition can enhance the rate of evolution in the presence of random noise is an unexpected bonus. And that the results are obtained under minimal assumptions, namely, a matrix game with random payoffs in a well-mixed population, suggests that they might be of general validity.

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APPENDIX

1. Stochastic local stability of fixation state $\hat{x} = 0$ in degenerate cases

In the degenerate case where $b_t = d_t$ for all $t \geqslant 0$, let $v_t = 1/u_t = (1 - x_t)/x_t$. From Eq.(3), we have the recurrence equation

$$v_{t+1} = v_t \left[\frac{\big((1-w) + wc_t\big) + v_t\big((1-w) + wd_t\big)}{\big((1-w) + wa_t\big) + v_t\big((1-w) + wd_t\big)} \right]. \tag{A1}$$

Iterating this recurrence equation leads to

$$\frac{1}{n}(v_n - v_0) = \frac{1}{n}\sum_{t=0}^{n-1}\left[\frac{(1-w)+wc_t}{(1-w)+wd_t} - \frac{(1-w)+wa_t}{(1-w)+wd_t}\right] - \frac{1}{n}\sum_{t=0}^{n-1}\frac{\frac{(1-w)+wa_t}{(1-w)+wd_t}\left(1 - \frac{(1-w)+wa_t}{(1-w)+wc_t}\right)}{\frac{(1-w)+wa_t}{(1-w)+wc_t} + \frac{(1-w)+wd_t}{(1-w)+wc_t}v_t}. \tag{A2}$$

Therefore, if $u_t \to 0$ (that is, $v_t \to \infty$), then the strong law of large numbers guarantees that

$$\lim_{n\to\infty}\frac{1}{n}\big(v_n - v_0\big) \approx \left\langle \frac{(1-w)+wc_t}{(1-w)+wd_t} - \frac{(1-w)+wa_t}{(1-w)+wd_t} \right\rangle. \tag{A3}$$

Then, using Egorov's theorem, the fixation state $\hat{x} = 0$ is SLS if

$$\left\langle \frac{(1-w)+wc_t}{(1-w)+wd_t} \right\rangle - \left\langle \frac{(1-w)+wa_t}{(1-w)+wd_t} \right\rangle > 0 \tag{A4}$$

(the more rigorous mathematical proofs are similar to those in [17]).

Note that

$$\left\langle \frac{(1-w)+wc_t}{(1-w)+wd_t} \right\rangle \approx \frac{(1-w)+w\bar{c}}{(1-w)+w\bar{d}} + \frac{((1-w)+w\bar{c})w^2\sigma_d^2}{((1-w)+w\bar{d})^3} - \frac{w^2\sigma_{c,d}^2}{((1-w)+w\bar{d})^2}$$

and

$$\left\langle \frac{(1-w)+wa_t}{(1-w)+wd_t} \right\rangle \approx \frac{(1-w)+w\bar{a}}{(1-w)+w\bar{d}} + \frac{((1-w)+w\bar{a})w^2\sigma_d^2}{((1-w)+w\bar{d})^3} - \frac{w^2\sigma_{a,d}^2}{((1-w)+w\bar{d})^2}.$$

Thus, under weak enough selection (that is, for w small enough), the fixation state $\hat{x} = 0$ is SLS if $\bar{c} - \bar{a} > 0$ and SLU if $\bar{c} - \bar{a} < 0$.

Similarly, in the degenerate case where $a_t = c_t$ for all $t \geqslant 0$, under weak enough selection, the fixation state $\hat{x} = 1$ is SLS if $\bar{b} - \bar{d} > 0$ and SLU if $\bar{b} - \bar{d} < 0$.

2. Stochastic local stability of a constant interior equilibrium

With the random payoff matrix $\mathbf{A}(t)$ in Eq. (12) where $\hat{u} > 0$, the recurrence equation in Eq.(3) can be rewritten in the form

$$u_{t+1} = u_t\left[\frac{u_t[(1-w) + w(c_t + z_t)] + [(1-w) + wb_t]}{u_t[(1-w) + wc_t] + [(1-w) + w(b_t + \hat{u}z_t)]}\right]. \tag{A5}$$

From this equation and the equality $\hat{u}(a_t - c_t) = d_t - b_t$, we have

$$\begin{aligned} u_{t+1} - \hat{u} &= (u_t - \hat{u})\left[\frac{u_t((1-w)+wc_t) + u_t wz_t + \hat{u}wz_t + ((1-w)+wb_t)}{u_t((1-w)+wc_t) + ((1-w)+wb_t) + \hat{u}wz_t}\right] \\ &= (u_t - \hat{u})\left[\frac{u_t((1-w)+wa_t) + ((1-w)+wd_t)}{u_t((1-w)+wc_t) + ((1-w)+wd_t)}\right]. \end{aligned} \tag{A6}$$

In particular, this ensures that $u_{t+1} - \hat{u} > 0$ if $u_t - \hat{u} > 0$, and $u_{t+1} - \hat{u} < 0$ if $u_t - \hat{u} < 0$. Moreover, some algebraic manipulations yield

$$\frac{u_t((1-w)+wa_t) + ((1-w)+wd_t)}{u_t((1-w)+wc_t) + ((1-w)+wd_t)} = \left[\frac{\hat{u}((1-w)+wa_t) + ((1-w)+wd_t)}{\hat{u}((1-w)+wc_t) + ((1-w)+wd_t)}\right]Q_t,$$

where

$$Q_t = 1 - \frac{(u_t - \hat{u})((1-w)+wd_t)wz_t}{D_t} \tag{A7}$$

with

$$\begin{aligned} D_t &= [\hat{u}((1-w)+wa_t) + ((1-w)+wd_t)] \\ &\quad \times [\hat{u}((1-w)+wc_t) + ((1-w)+wd_t) + (u_t - \hat{u})((1-w)+wc_t)]. \end{aligned} \tag{A8}$$

Therefore, iterating Eq. (A6) leads to

$$\lim_{n\to\infty}\frac{1}{n}\log\left[\frac{u_n-\hat{u}}{u_0-\hat{u}}\right]=\lim_{n\to\infty}\frac{1}{n}\sum_{t=0}^{n-1}\log\left[\frac{\hat{u}((1-w)+wa_t)+((1-w)+wd_t)}{\hat{u}((1-w)+wc_t)+((1-w)+wd_t)}\right]+\lim_{n\to\infty}\frac{1}{n}\sum_{t=0}^{n-1}\log Q_t\ . \tag{A9}$$

If $u_t\to\hat{u}$ (which compels $Q_t\to 1$), then the strong law of large numbers guarantees that

$$\lim_{n\to\infty}\frac{1}{n}\log\left[\frac{u_n-\hat{u}}{u_0-\hat{u}}\right]\approx\left\langle\log\left[\frac{\hat{u}((1-w)+wa_t)+((1-w)+wd_t)}{\hat{u}((1-w)+wc_t)+((1-w)+wd_t)}\right]\right\rangle. \tag{A10}$$

Using Egorov's theorem, the constant interior equilibrium $\hat{x}=\hat{u}/(1+\hat{u})$ is SLS if

$$\left\langle\log\left[\frac{\hat{u}((1-w)+wa_t)+((1-w)+wd_t)}{\hat{u}((1-w)+wc_t)+((1-w)+wd_t)}\right]\right\rangle<0 \tag{A11}$$

and SLU if the inequality is reversed.

Note that

$$\langle\log[\hat{u}((1-w)+wa_t)+((1-w)+wd_t)]\rangle\approx\log[\hat{u}((1-w)+w\bar{a})+((1-w)+w\bar{d})]-\frac{\hat{u}^2w^2\sigma_a^2+w^2\sigma_d^2+2\hat{u}w^2\sigma_{a,d}}{2[\hat{u}((1-w)+w\bar{a})+((1-w)+w\bar{d})]^2}$$

and

$$\langle\log[\hat{u}((1-w)+wc_t)+((1-w)+wd_t)]\rangle\approx\log[\hat{u}((1-w)+w\bar{c})+((1-w)+w\bar{d})]-\frac{\hat{u}^2w^2\sigma_c^2+w^2\sigma_d^2+2\hat{u}w^2\sigma_{c,d}}{2[\hat{u}((1-w)+w\bar{c})+((1-w)+w\bar{d})]^2}\ .$$

Thus, under weak enough selection, $\hat{x}=\hat{u}/(1+\hat{u})$ is SLS if $\bar{c}-\bar{a}>0$ and SLU if $\bar{c}-\bar{a}<0$.

3. Convergence rate near an SLS constant interior equilibrium

With the random payoff matrix $\mathbf{A}(t)$ in Eq. (12), we have shown that, under weak enough selection, the constant interior equilibrium $\hat{x}=\hat{u}/(1+\hat{u})$ is SLS if $\bar{c}-\bar{a}>0$. When the system state is near this constant interior equilibrium, the convergence rate of the system to it is given by the right-hand member in Eq. (A10). Under weak selection, the convergence rate is approximated as

$$\left\langle\log\left[\frac{\hat{u}((1-w)+wa_t)+((1-w)+wd_t)}{\hat{u}((1-w)+wc_t)+((1-w)+wd_t)}\right]\right\rangle\approx\log\left[\frac{\hat{u}((1-w)+w\bar{a})+((1-w)+w\bar{d})}{\hat{u}((1-w)+w\bar{c})+((1-w)+w\bar{d})}\right]-\frac{w^2\left(\hat{u}^2\sigma_a^2+\sigma_d^2+2\hat{u}\sigma_{a,d}\right)}{2[\hat{u}((1-w)+w\bar{a})+((1-w)+w\bar{d})]^2}+\frac{w^2\left(\hat{u}^2\sigma_c^2+\sigma_d^2+2\hat{u}\sigma_{c,d}\right)}{2[\hat{u}((1-w)+w\bar{c})+((1-w)+w\bar{d})]^2}\ , \tag{A12}$$

where the term

$$\log\left[\frac{\hat{u}((1-w)+w\bar{a})+((1-w)+w\bar{d})}{\hat{u}((1-w)+w\bar{c})+((1-w)+w\bar{d})}\right]$$

corresponds to the convergence rate of the deterministic system with payoff matrix $\bar{\mathbf{A}}$. Furthermore, if w is small enough, we have the approximations

$$\log\left[\frac{\hat{u}((1-w)+w\bar{a})+((1-w)+w\bar{d})}{\hat{u}((1-w)+w\bar{c})+((1-w)+w\bar{d})}\right]\approx\frac{w(\bar{a}-\bar{c})}{(1+\hat{u})}\ , \tag{A13}$$

$$\frac{w^2\left(\hat{u}^2\sigma_a^2+\sigma_d^2+2\hat{u}\sigma_{a,d}\right)}{2[\hat{u}((1-w)+w\bar{a})+((1-w)+w\bar{d})]^2}\approx\frac{w^2\left(\hat{u}^2\sigma_a^2+\sigma_d^2+2\hat{u}\sigma_{a,d}\right)}{2(1+\hat{u})^2}\ , \tag{A14}$$

$$\frac{w^2\left(\hat{u}^2\sigma_c^2+\sigma_d^2+2\hat{u}\sigma_{c,d}\right)}{2[\hat{u}((1-w)+w\bar{c})+((1-w)+w\bar{d})]^2}\approx\frac{w^2\left(\hat{u}^2\sigma_c^2+\sigma_d^2+2\hat{u}\sigma_{c,d}\right)}{2(1+\hat{u})^2}\ . \tag{A15}$$

Therefore, Eq. (A12) can be rewritten as

$$\left\langle\log\left[\frac{\hat{u}((1-w)+wa_t)+((1-w)+wd_t)}{\hat{u}((1-w)+wc_t)+((1-w)+wd_t)}\right]\right\rangle\approx\frac{w(\bar{a}-\bar{c})}{(1+\hat{u})}+\begin{cases}\frac{\hat{u}w^2}{2(1+\hat{u})^2}\left[\hat{u}\left(\sigma_c^2-\sigma_a^2\right)+2(\sigma_{c,d}-\sigma_{a,d})\right] & \text{if}\quad \hat{u}\left(\sigma_c^2-\sigma_a^2\right)+2(\sigma_{c,d}-\sigma_{a,d})\neq 0\ ,\\ \frac{w^3}{(1+\hat{u})^3}\left(\hat{u}^2\sigma_a^2+\sigma_d^2+2\hat{u}\sigma_{a,d}\right)(\bar{a}-\bar{c}) & \text{if}\quad \hat{u}\left(\sigma_c^2-\sigma_a^2\right)+2(\sigma_{c,d}-\sigma_{a,d})=0\ .\end{cases} \tag{A16}$$

This implies that, under weak enough selection, the convergence rate near the SLS constant interior equilibrium $\hat{u} > 0$ in the stochastic dynamics (with $\bar{c} > \bar{a}$) is faster [or slower] than that in the deterministic mean-field approximation if $\hat{u}(\sigma_c^2 - \sigma_a^2) + 2(\sigma_{c,d} - \sigma_{a,d}) \leqslant 0$ [or $\hat{u}(\sigma_c^2 - \sigma_a^2) + 2(\sigma_{c,d} - \sigma_{a,d}) > 0$].

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