

The Diffusion Approximation of Stochastic Evolutionary Game Dynamics: Mean Effective Fixation Time and the Significance of the One-Third Law

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Abstract The one-third law introduced by Nowak et al. (Nature 428:646–650, 2004) for the Moran stochastic process has proven to be a robust criterion to predict when weak selection will favor a strategy invading a finite population. In this paper, we investigate fixation probability, mean effective fixation time, and average and expected fitnesses in the diffusion approximation of the stochastic evolutionary game. Our main results show that in two-strategy games with strict Nash equilibria A and B : (i) the one-third law means that, if selection favors strategy A when a single individual is using it initially, then one-third of the opponents one meets before fixation are A -individuals; and (ii) the average fitness of strategy A about the mean effective fixation time is larger than that of strategy B . The analysis reinforces the universal nature of the one-third law as of fundamental importance in models of selection. We also connect risk dominance of strategy A to its larger expected fitness with respect to the stationary distribution of the diffusion approximation that includes a small mutation rate between the two strategies.

Keywords One-third law · Average fitness · Mean effective fixation time · Fixation probability

1 Introduction

Evolutionary game theory has been successfully applied since its introduction by Maynard Smith and Price [13] to explain many aspects of the evolution of animal behavior. One of the basic assumptions in the by now classic approach to deterministic evolutionary game dynamics [7] is that population size is large enough that stochastic fluctuations in the evolution

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of phenotypic frequencies due to finite population size can be ignored. On the other hand, it has long been recognized (e.g. [3, 10]) that stochastic effects of finite populations are biologically significant in standard models of population genetics (e.g. models that assume natural selection is weak or there is neutral drift).

Stochastic effects due to small errors in strategy choice have also been used as an equilibrium selection technique in game-theoretic models to predict (long-run) human behavior through such concepts as stochastic stability [4, 9]) (see also [19]). More recently, Nowak et al. [16] investigated a stochastic process for games with two (pure) strategies, denoted by A and B , when total population size is fixed at N . They introduced the one-third law into this model by analyzing when selection favors a single mutant using strategy A replacing a resident population using the other pure strategy B . In its basic form, the one-third law connects Nash equilibrium (NE) concepts of this two-strategy game to stochastic properties of the birth-death Markov system known as the Moran process.¹ Specifically, Nowak et al. [16] showed that (when A and B are both strict NE, population size is large, and selection is weak) the probability this replacement occurs under the Moran process is higher than that obtained from neutral drift if the completely mixed NE of this game plays strategy A less than one-third of the time (see also [15, 20]).

The basic one-third law has been generalized to other Markov processes, such as the Wright-Fisher process [8], that satisfy the mild condition that the Kingman coalescent method [12] of ancestral patterns can be used. Moreover, the dependence of this result on the assumption of weak selection in general birth-death processes has been analyzed [25] and extensions found for multi-player two-strategy games [11].

Of more importance for us, the one-third law also emerges from the continuous-time diffusion approximations of the Moran² and Wright-Fisher processes [23]. In other generalizations, Ohtsuki et al. [17] showed that the one-third property of the mixed NE corresponds to several different evolutionarily significant characteristics of the Moran process; namely, the average relative fitness of A players, the average proportion of each type encountered until fixation along a stochastic path, and the mean effective fixation time (see also [21]). In this paper, these properties are developed through the diffusion approximation method. Our main goal is to show that the one-third law is a general phenomenon of weak selection modeled by two-strategy evolutionary games based on a population with a fixed finite size. A by-product of the analysis in Sects. 3 to 5 used to connect the diffusion approximation to different interpretations of the one-third law for the Moran process is that we are also able to re-interpret risk dominance (also called half-dominance [14]) in terms of the (long-run) expected fitness of A compared to B (Sect. 6).

2 The Moran Process and Diffusion Approximation

The two-strategy stochastic evolutionary game with finite population size introduced by Nowak et al. [16] (see also [15, 20]) is based on the payoff matrix

$$\begin{array}{cc}
 & \begin{array}{cc} A & B \end{array} \\
 \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix}
 \end{array} \tag{1}$$

¹The one-third law can also be connected to other game-theoretic properties of this two-strategy game such as the basin of attraction of strategy A under deterministic evolutionary game dynamics that ignore stochastic effects (see the discussion of p^* -dominance at the end of Sect. 3).

²The diffusion approximation for the Moran process is summarized in Sect. 2.

where the entries in this matrix give the payoffs to the row player (e.g. A gets payoff b when interacting with strategy B). The population size, N , is assumed to be fixed and the number of A -individuals is denoted by j . The number of B -individuals is then $N - j$ and, for the frequency-dependent Moran process, the expected fitnesses of A and B in random pairwise interactions, denoted by f_j and g_j , respectively, are taken as

$$\begin{aligned}
 f_j &= (1 - \omega) + \omega \frac{a(j - 1) + b(N - j)}{N - 1}, \\
 g_j &= (1 - \omega) + \omega \frac{cj + d(N - j - 1)}{N - 1}.
 \end{aligned}
 \tag{2}$$

Here the parameter ω (with $\omega \in [0, 1]$) denotes the selection intensity, which represents the contribution of the game to individual fitness [16].

Nowak et al. [16] assumed that, at each time step, an individual is chosen for reproduction proportional to its fitness,³ and that the one identical offspring produced replaces another randomly chosen individual. For this model, selection is said to favor A replacing B if, when there is initially one A individual in the population (i.e. the initial frequency of A is $1/N$), the fixation probability of A (denoted by ρ_A) is bigger than $1/N$, which is this fixation probability under neutral drift (i.e. $\omega = 0$). The main result of Nowak et al. [16] is that, for weak selection (specifically, for $\omega \ll 1$), selection favors A replacing B if and only if $(N - 2)a + (2N - 1)b > (N + 1)c + (2N - 4)d$. For large population size N , this condition can be approximated as $a + 2b > c + 2d$. If both A and B are strict NE of (1) (i.e. $a > c$ and $d > b$), then $\rho_A > 1/N$ if $x^* < 1/3$, where $x^* = (d - b)/[(a - c) + (d - b)]$ is the frequency of A at the completely mixed NE of this game. This is called the one-third law.

The diffusion approximation of this Moran process was first studied by Traulsen et al. [22, 23] (see also [21]). For large N , the frequency of A is denoted by x (i.e. $x = j/N$); the fitnesses of A and B are approximated by

$$\begin{aligned}
 f(x) &\approx (1 - \omega) + \omega[xa + (1 - x)b], \\
 g(x) &\approx (1 - \omega) + \omega[xc + (1 - x)d],
 \end{aligned}
 \tag{3}$$

respectively, with corresponding transition probabilities from x to $x + 1/N$ and from x to $x - 1/N$ given by

$$\begin{aligned}
 \pi^+(x) &= \frac{x(1 - x)f(x)}{xf(x) + (1 - x)g(x)}, \\
 \pi^-(x) &= \frac{x(1 - x)g(x)}{xf(x) + (1 - x)g(x)},
 \end{aligned}
 \tag{4}$$

respectively. Let $\phi(x; t)$ denote the probability density distribution that the frequency of strategy A equals exactly x at time t . When the time step for the Moran process is taken as $1/N$, then

$$\begin{aligned}
 \phi(x; t + 1/N) - \phi(x; t) &= \phi(x - 1/N; t)\pi^+(x - 1/N) + \phi(x + 1/N; t)\pi^-(x + 1/N) \\
 &\quad - \phi(x; t)\pi^-(x) - \phi(x; t)\pi^+(x).
 \end{aligned}
 \tag{5}$$

³If selection is weak (i.e. ω is close to 0), every individual will always have positive fitness and so the probability that the chosen individual uses strategy A is given by $\frac{jf_j}{jf_j + (N-j)g_j}$. Although we only analyze the diffusion approximation under weak selection, we will nevertheless assume all payoff entries in (1) are positive so that the frequency-dependent Moran process is defined for all $\omega \in [0, 1]$.

The diffusion approximation of the Moran process emerges from the Taylor series expansion of $\phi(x \pm 1/N; t)$ and $\pi^\pm(x \mp 1/N)$ about x and t (following, for example, the methods in [24]). Specifically, starting from the discrete-time Moran process, Traulsen and Hauert [21] obtain a continuous-time diffusion equation. The outcome (shown in the Appendix) is the Fokker–Planck equation of $\phi(x; t)$; namely,

$$\frac{\partial \phi(x; t)}{\partial t} = -\frac{\partial}{\partial x} D^{(1)}(x)\phi(x; t) + \frac{\partial^2}{\partial x^2} D^{(2)}(x)\phi(x; t). \tag{6}$$

Here

$$\begin{aligned} D^{(1)}(x) &= \pi^+(x) - \pi^-(x), \\ D^{(2)}(x) &= \frac{\pi^+(x) + \pi^-(x)}{2N}, \end{aligned} \tag{7}$$

where $D^{(1)}(x)$ is called the drift term that is due to fitness differences (i.e. to selection) and $\sqrt{2D^{(2)}(x)}$ is the diffusion term (genetic drift in biology) (see also [21]). From (4) and (7), both $x = 0$ and $x = 1$ are absorbing boundaries. Equation (6) is also called the forward Kolmogorov equation in mathematics.

Of equal importance for us is the backward Kolmogorov equation. If the initial frequency p at $t = 0$ is considered, then the probability density function $\phi(x; t)$ should be rewritten as $\phi(x; p, t)$, i.e. the probability density distribution that the frequency of strategy A equals x at time t if its initial frequency is p . For the backward equation, we regard x as fixed and consider p as a random variable. Then, similar to (5),

$$\begin{aligned} \phi(x; p, t + 1/N) - \phi(x; p, t) &= \pi^+(p)\phi(x; p + 1/N, t) + \pi^-(p)\phi(x; p - 1/N, t) \\ &\quad - \pi^+(p)\phi(x; p, t) - \pi^-(p)\phi(x; p, t) \end{aligned} \tag{8}$$

for the Moran process with time step $1/N$. The Taylor expansions of $\phi(x; p, t + 1/N)$ and $\phi(x; p \pm 1/N, t)$ about t and p in the Appendix (see also [3, 10]) yield

$$\frac{\partial \phi(x; p, t)}{\partial t} = D^{(1)}(p)\frac{\partial \phi(x; p, t)}{\partial p} + D^{(2)}(p)\frac{\partial^2 \phi(x; p, t)}{\partial p^2} \tag{9}$$

as the diffusion approximation, i.e. the backward Kolmogorov equation.

Traulsen and Hauert [21] emphasized that the diffusion approximation of the stochastic evolutionary game for large population size can be used to address stochastic properties of the evolutionary dynamics in large populations under weak selection. In this paper, we show that this is indeed the case for the concepts of fixation probability (including both fixation probabilities of A and B), mean effective fixation time and average fitnesses about the mean effective fixation time initially studied for the Moran process (see [17] or [21] for details of the latter concepts). Specifically, we show that each of these concepts has a corresponding property for the diffusion approximation in Sects. 3 to 5, respectively, when population size is large and selection is weak.

3 Fixation Probability of Strategy A

Let $u(p, t)$ denote the probability that strategy A is fixed at time t if its initial frequency is p (i.e. the fixation probability of strategy A at time t with initial frequency p). For the Moran

process, this probability satisfies (8) with $x = 1$ and so its diffusion approximation is given by

$$\frac{\partial u(p, t)}{\partial t} = D^{(1)}(p) \frac{\partial u(p, t)}{\partial p} + D^{(2)}(p) \frac{\partial^2 u(p, t)}{\partial p^2} \tag{10}$$

with the boundary conditions $u(0, t) = 0$ and $u(1, t) = 1$. Consider the ultimate probability $u(p)$ of fixation of strategy A , defined by $u(p) = \lim_{t \rightarrow \infty} u(p, t)$. Since $x = 1$ is an absorbing boundary of (6), this limit exists and $u(p)$ is the stationary solution of (10). That is,

$$D^{(1)}(p) \frac{du(p)}{dp} + D^{(2)}(p) \frac{d^2u(p)}{dp^2} = 0. \tag{11}$$

Furthermore, since the fixation probability of a single individual under neutral drift is $1/N$, the extension of the one-third law to the diffusion equation would then be the statement that, when selection is weak and population size is large, $u(1/N) > 1/N$. To examine this statement, we follow Traulsen et al. [23], who show that the solution of (11) is given by

$$u(p) = \frac{\int_0^p \tilde{S}(s) ds}{\int_0^1 \tilde{S}(s) ds}, \tag{12}$$

where

$$\begin{aligned} \tilde{S}(s) &\equiv \exp\left(-\int_0^s \frac{D^{(1)}(z)}{D^{(2)}(z)} dz\right) \\ &= \exp\left(-\int_0^s 2N \frac{f(z) - g(z)}{f(z) + g(z)} dz\right) \\ &= \exp\left(-\int_0^s 2N\omega \frac{z(a - c) + (1 - z)(b - d)}{2 - 2\omega + \omega z(a + c) + (1 - z)(b + d)} dz\right). \end{aligned}$$

For $N\omega \ll 1$ and $\alpha \equiv a - b - c + d$ (recall that $x^* \equiv \frac{d-b}{a-c+d-b}$),

$$\tilde{S}(s) \approx \exp\left(-\int_0^s N\omega(\alpha z + (b - d)) dz\right) = \exp\left(-\frac{N\omega\alpha}{2}(s^2 - 2sx^*)\right). \tag{13}$$

Clearly, if there is no selection (i.e. $\omega = 0$), then $u(p) = p$ since $\tilde{S}(s)|_{\omega=0} = 1$. In particular, if there is initially exactly one A individual in the population (i.e. $p = 1/N$), then $u(1/N) = 1/N$ (the same result holds for the Moran process under neutral selection [3, 15]). For $\omega \neq 0$ but $N\omega \ll 1$, we consider the Taylor expansion of $u(p)$ about $\omega = 0$. Since $\frac{\partial u(p)}{\partial \omega} = \frac{\int_0^p \frac{\partial \tilde{S}(s)}{\partial \omega} ds \cdot \int_0^1 \tilde{S}(s) ds - \int_0^p \tilde{S}(s) ds \cdot \int_0^1 \frac{\partial \tilde{S}(s)}{\partial \omega} ds}{[\int_0^1 \tilde{S}(s) ds]^2}$ and $\frac{\partial \tilde{S}(s)}{\partial \omega}|_{\omega=0} = -\frac{N\alpha}{2}(s^2 - 2sx^*)\tilde{S}(s)|_{\omega=0} = -\frac{N\alpha}{2}(s^2 - 2sx^*)$,

$$\begin{aligned} \frac{\partial u(p)}{\partial \omega} \Big|_{\omega=0} &= -\frac{N\alpha}{2} \int_0^p (s^2 - 2sx^*) ds + p \frac{N\alpha}{2} \int_0^1 (s^2 - 2sx^*) ds \\ &= -\frac{N\alpha}{2} \left[\frac{p^3}{3} - p^2x^* \right] + p \frac{N\alpha}{2} \left[\frac{1}{3} - x^* \right] \end{aligned}$$

$$\begin{aligned}
 &= p \frac{N\alpha}{2} \left[-\frac{p^2}{3} + px^* + \frac{1}{3} - x^* \right] \\
 &= p \frac{N\alpha}{2} \left[-x^*(1-p) + \frac{1}{3}(1-p)(1+p) \right] \\
 &= p(1-p) \frac{N\alpha}{2} \left[-x^* + \frac{1}{3}(1+p) \right].
 \end{aligned} \tag{14}$$

Thus, the Taylor expansion of $u(p)$ about $\omega = 0$ is

$$\begin{aligned}
 u(p) &= u(p)|_{\omega=0} + \omega \left. \frac{\partial u(p)}{\partial \omega} \right|_{\omega=0} \\
 &= p + p(1-p) \frac{N\omega\alpha}{2} \left[-x^* + \frac{1}{3}(1+p) \right].
 \end{aligned} \tag{15}$$

If A and B are both strict NE, then $\alpha > 0$ and so $u(p) > p$ if $x^* < (1+p)/3$ (and $u(p) < p$ if $x^* > (1+p)/3$). For large population size, we have $u(1/N) > 1/N$ if $x^* < 1/3$. This result corresponds to the one-third law of Nowak et al. [16] (see also [15]). That is, under weak selection and large population size satisfying $N\omega \ll 1$,⁴ the probability that a single A -individual takes over the population that otherwise consists of B -individuals is greater than $1/N$ if $x^* < 1/3$ (see also [21, 22]).

Similarly, let $u'(q)$ be the ultimate fixation probability of B if its initial frequency is q . From the above method applied to strategy B ,

$$u'(q) = q + q(1-q) \frac{N\omega\alpha}{2} \left[-y^* + \frac{1}{3}(1+q) \right], \tag{16}$$

where $y^* = 1 - x^*$. This result also follows directly from (15) since the absorbing states of our one-dimensional diffusion process are the two endpoints. Thus, the population will eventually be in a monomorphic fixation state of either all A individuals or all B individuals (i.e. $u(p) + u'(q) = 1$ when $q = 1 - p$). From (15), (16) and $\alpha > 0$, $u(1/N) > u'(1/N)$ if $x^* < 1/2$, and $u(1/N) < u'(1/N)$ if $x^* > 1/2$. This is another interpretation of selection favoring A more than B . It corresponds more directly to the observation by Nowak [15] that, if both A and B are strict NE, then the risk-dominant equilibrium will also have a higher fixation probability when comparing the two Moran processes starting with only one individual using a particular strategy.

Both risk dominance and the one-third law are connected to the concept of p^* -dominance when both pure strategies are strict NE. By definition, strategy A is p^* -dominant in a two-strategy game if the expected payoff to A is greater than that of B from a random pairwise interaction whenever the frequency of strategy A is at least p^* [14].⁵ It is well known that A is risk dominant if and only if it is half dominant. From this perspective, the one-third law states that selection favors strategy A if it is one-third dominant. Furthermore, the basin of attraction of a p^* -dominant strategy under deterministic evolutionary dynamics contains all mixed strategies with frequency of A at least p^* . That is, a strict NE that satisfies the

⁴To avoid repetition, weak selection will mean $N\omega \ll 1$ from now on.

⁵ p^* -dominant is equivalent to p^* -superior for two-strategy games [2] in that strategy A has higher than average expected payoff if the frequency of strategy A is at least p^* .

one-third law must attract all initial populations whose frequency of strategy A is at least one-third.

From the above discussion, it would be reasonable to call properties of the Moran process (and its diffusion approximation) that correspond to risk dominance the one-half law of stochastic evolutionary dynamics based on finite population size. On the other hand, risk dominance (and half dominance) are already well-established concepts studied in other contexts (e.g. [1, 6]). For this reason, it may be more appropriate to continue to refer to these properties of the Moran process as consequences of risk dominance rather than to speak of the one-half law.

4 Mean Effective Fixation Time

In this section, we consider the mean time until one of the boundaries (i.e. $x = 0$ or $x = 1$) is reached. Let $\vartheta(t; p)$ denote the density function of the time t until absorption occurs given the initial frequency p . Similar to the analysis of fixation probability in the previous section, $\vartheta(t; p)$ also satisfies the backward equation [3]

$$\frac{\partial \vartheta(t; p)}{\partial t} = D^{(1)}(p) \frac{\partial \vartheta(t; p)}{\partial p} + D^{(2)}(p) \frac{\partial^2 \vartheta(t; p)}{\partial p^2}$$

where the boundary conditions are now $\vartheta(t, 0) = \vartheta(t, 1) = 0$.

Since the mean fixation time $\bar{t}(p) = \int_0^\infty t \vartheta(t; p) dt$ is finite [3, p. 140], we have $t \vartheta(t; p) \rightarrow 0$ as $t \rightarrow \infty$. Thus,

$$\begin{aligned} -1 &= - \int_0^\infty \vartheta(t; p) dt \\ &= -[t \vartheta(t; p)]_0^\infty + \int_0^\infty t \frac{\partial \vartheta(t; p)}{\partial t} dt \\ &= 0 + \int_0^\infty t \left(D^{(1)}(p) \frac{\partial \vartheta}{\partial p} + D^{(2)}(p) \frac{\partial^2 \vartheta}{\partial p^2} \right) dt. \end{aligned}$$

This can be rewritten as

$$-1 = D^{(1)}(p) \frac{d\bar{t}(p)}{dp} + D^{(2)}(p) \frac{d^2 \bar{t}(p)}{dp^2}. \tag{17}$$

From Ewens [3, pp. 140 to 145], the solution of (17), subject to the boundary condition $\bar{t}(0) = \bar{t}(1) = 0$, can be expressed in terms of the notation introduced in Sect. 3. Specifically,

$$\bar{t}(p) = \int_0^1 t(x; p) dx,$$

where

$$t(x; p) = \frac{u'(1-p)}{D^{(2)}(x)\tilde{S}(x)} \int_0^x \tilde{S}(s) ds$$

for $0 \leq x \leq p$, and

$$t(x; p) = \frac{u(p)}{D^{(2)}(x)\tilde{S}(x)} \int_x^1 \tilde{S}(s) ds$$

for $p \leq x \leq 1$. When $N\omega \ll 1$, $\tilde{S}(x) \approx 1$ and $D^{(2)}(x) \approx x(1 - x)/2N$. Thus, for weak selection, $\bar{t}(p)$ is approximated by

$$\begin{aligned} \bar{t}(p) &= \int_0^p t(x; p) dx + \int_p^1 t(x; p) dx \\ &= 2Nu'(1 - p) \int_0^p \frac{1}{1 - x} dx + 2Nu(p) \int_p^1 \frac{1}{x} dx \\ &= -2N[(1 - p) \ln(1 - p) + p \ln(p)]. \end{aligned} \tag{18}$$

The integral $\int_{x_1}^{x_2} t(x; p) dx$ represents the mean time that the frequency of A , x , spends in the interval (x_1, x_2) before absorption. It approximates the average amount of time spent before absorption in those states of the Moran process that are in this interval (i.e. those j for which $x_1 < j/N < x_2$), which is called the “mean sojourn time” by Ohtsuki et al. [17]. Furthermore, $\int_{x_1}^{x_2} \pi^+(x)t(x; p) dx$ represents the mean time that the system state jumps from x to $x + 1/N$ when x is in the interval (x_1, x_2) , and, similarly, $\int_{x_1}^{x_2} \pi^-(x)t(x; p) dx$ the mean time that the system state jumps from x to $x - 1/N$ when x is in the interval (x_1, x_2) . Notice that $\int_{x_1}^{x_2} \pi^+(x)t(x; p) dx + \int_{x_1}^{x_2} \pi^-(x)t(x; p) dx < \int_{x_1}^{x_2} t(x; p) dx$ since the system state does not always jump from state x to $x \pm 1/N$. We call

$$\int_{x_1}^{x_2} (\pi^+(x) + \pi^-(x))t(x; p) dx$$

the mean effective time that x spends in the interval (x_1, x_2) (see the corresponding concept of “mean effective sojourn time” introduced by Ohtsuki et al. [17] for the Moran process). Moreover, let $\bar{\tau}(p)$ denote the mean effective fixation time until one or the other absorbing boundary is reached when the initial frequency of A is p . Then,

$$\bar{\tau}(p) = \int_0^1 (\pi^+(x) + \pi^-(x))t(x; p) dx.$$

For weak selection,

$$\begin{aligned} \bar{\tau}(p) &= \int_0^p (\pi^+(x) + \pi^-(x))t(x; p) dx \\ &\quad + \int_p^1 (\pi^+(x) + \pi^-(x))t(x; p) dx \\ &= \int_0^p 2Nu'(1 - p)x dx + \int_p^1 2Nu(p)(1 - x) dx \\ &\approx 2N(1 - u(p)) \int_0^p x dx + 2Nu(p) \int_p^1 (1 - x) dx \\ &= N(p^2 + u(p) - 2pu(p)). \end{aligned} \tag{19}$$

In particular, for $p = 1/N$, $\bar{\tau}(p) \approx 1 - \frac{1}{N}$.

By dividing $\bar{\tau}(p)$ into two parts, we can now approximate the mean effective time $\bar{\tau}_1(p)$ of meeting A -individuals and the mean effective time $\bar{\tau}_2(p)$ of meeting B -individuals before absorption. Specifically, $\bar{\tau}_1(p) = \int_0^1 x(\pi^+(x) + \pi^-(x))t(x; p) dx$ and $\bar{\tau}_2(p) = \int_0^1 (1 -$

$x)(\pi^+(x) + \pi^-(x))t(x; p) dx$ and so $\bar{\tau}(p) = \bar{\tau}_1(p) + \bar{\tau}_2(p)$. Extending the calculations in (19) for $N\omega \ll 1$ and $p = 1/N$ (see the Appendix)

$$\bar{\tau}_1(p) \approx \frac{1}{3} - \frac{1}{3N^2} \quad \text{and} \quad \bar{\tau}_2(p) \approx \frac{2}{3} - \frac{1}{N} + \frac{1}{3N^2}. \tag{20}$$

Thus, for weak selection and large population size, the ratio (mean effective fixation time meeting A -individuals)/(mean effective fixation time) is about $1/3$ when $p = 1/N$ (i.e. $\bar{\tau}_1(p)/\bar{\tau}(p) \approx 1/3$ for $p = 1/N$). Equivalently, the ratio (mean effective fixation time meeting B -individuals)/(mean effective fixation time) is about $2/3$ (i.e. $\bar{\tau}_2(p)/\bar{\tau}(p) \approx 2/3$ for $p = 1/N$). That is, as stated by Ohtsuki et al. [17] for the Moran process, “one-third of the opponents that one meets (in interactions leading to state changes) until either extinction or fixation are A -players and two-thirds are B -players”. The above calculations show the same result is true for the diffusion equation corresponding to the Moran process, yielding another version of the one-third law.

5 Average Fitness About the Mean Effective Fixation Time

Ohtsuki et al. [17] also emphasized that the one-third law is equivalent to the positivity of the average Malthusian fitness⁶ of A (i.e. $\int_0^1 (1-x)(f(x) - g(x)) dx > 0$ if and only if $x^* < 1/3$). They then relate this result, which is based on the deterministic game dynamics of infinite population size, to the fixation probability of A under the Moran process. In this section, we develop a more direct link between average fitnesses of strategies A and B using the diffusion approximation when selection is weak.

For this purpose, define the average fitness of strategy A about the mean effective fixation time $\bar{\tau}(p)$, denoted by $\bar{f}_{\bar{\tau}(p)}$, as $\frac{1}{\bar{\tau}(p)} \int_0^1 f(x)(\pi^+ + \pi^-)t(x; p) dx$. Similarly, $\bar{g}_{\bar{\tau}(p)} \equiv \frac{1}{\bar{\tau}(p)} \int_0^1 g(x)(\pi^+ + \pi^-)t(x; p) dx$ is the average fitness of strategy B about the mean effective fixation time. We have

$$\begin{aligned} \bar{f}_{\bar{\tau}(p)} &= \frac{1}{\bar{\tau}(p)} \left[\int_0^p f(x)(\pi^+ + \pi^-)t(x; p) dx \right. \\ &\quad \left. + \int_p^1 f(x)(\pi^+ + \pi^-)t(x; p) dx \right] \\ &= \frac{2N}{\bar{\tau}(p)} \left[\int_0^p xf(x)(1-u(p)) dx + \int_p^1 (1-x)f(x)u(p) dx \right] \\ &= \frac{2N}{\bar{\tau}(p)} \left[(1-u(p)) \left(\frac{1}{2}(1-\omega)p^2 + \frac{1}{3}\omega(a-b)p^3 + \frac{1}{2}\omega bp^2 \right) \right. \\ &\quad \left. + u(p) \left(\frac{1}{2} - \frac{1}{2}\omega + \frac{1}{6}\omega a + \frac{1}{3}\omega b - (1-\omega + \omega b)p \right) \right. \\ &\quad \left. + \frac{1}{2}(1-\omega - \omega(a-2b))p^2 + \frac{1}{3}\omega(a-b)p^3 \right] \\ &\approx 1 - \omega + \omega b + \frac{\omega(a-b)}{3} \cdot \frac{2p^3 + u(p)(1-3p^2)}{p^2 + u(p)(1-2p)}. \end{aligned} \tag{21}$$

⁶The Malthusian fitness of A when the population is in state x (i.e. $(1-x)(f(x) - g(x))$) is also called the relative advantage of A [5] since it is the difference between the fitness of A and the average population fitness (i.e. $f(x) - (xf(x) + (1-x)g(x))$).

The final step above results from substituting (19) for the mean effective time $\bar{\tau}(p)$. Similarly,

$$\bar{g}_{\bar{\tau}(p)} \approx 1 - \omega + \omega d + \frac{\omega(c-d)}{3} \cdot \frac{2p^3 + u(p)(1-3p^3)}{p^2 + u(p)(1-2p)}. \tag{22}$$

Thus, for weak selection and large population size,

$$\bar{f}_{\bar{\tau}(1/N)} - \bar{g}_{\bar{\tau}(1/N)} \approx \omega(b-d) + \frac{\omega(a-b-(c-d))}{3} = \omega\alpha \left(\frac{1}{3} - x^* \right)$$

when $p = 1/N$.

Assume that A and B are both strict NE (i.e. $\alpha > 0$ and $0 < x^* < 1$). Clearly, $\bar{f}_{\bar{\tau}(1/N)} - \bar{g}_{\bar{\tau}(1/N)} > 0$ if and only if $x^* < 1/3$. This result yields another interpretation of the one-third law of Nowak et al. [16] that provides a possible theoretical explanation why the one-third law should be considered a natural result of frequency-dependent selection. That is, the one-third law can be equivalently stated as follows: under weak selection and large population size, if the average fitness of A is greater than the average fitness of B about the mean effective fixation time $\bar{\tau}(1/N)$, then the fixation probability of A , $u(1/N)$, is greater than $1/N$.

In particular, the one-third law implies that the difference between the average fitnesses of A and B about the mean effective fixation time is positive when a single A -individual is initially present in a large population that consists otherwise of B -individuals. The positivity of the average Malthusian fitness of A considered by Ohtsuki et al. [17] assumes a uniform distribution of the strategy frequency x , whereas average fitnesses about the mean effective fixation time are based directly on the (non uniform) frequency distribution of the diffusion process.

6 Expected Fitness and Risk dominance

As discussed in Sect. 3, although Nowak et al. [16] emphasized the one-third law, they also pointed out that, when A and B are strict NE, $\rho_A > \rho_B$ (i.e. A is more likely to replace B than vice versa) under the Moran process with weak selection and large population size if and only if A is risk dominant (i.e. $x^* < 1/2$). Using the results of Sect. 5, a similar connection can be made between risk dominance and average fitness differences about the mean effective fixation time when A is initially rare to when B is initially rare. In this section, we show instead that risk dominance of A implies that the expected fitness of A is larger than that of B under the stationary distribution of the diffusion approximation that includes a small mutation term used to eliminate the absorbing boundaries.

Assume that μ is the mutation rate from A to B as well as from B to A . Following the approach of Traulsen et al. [22], the transition probabilities in (4) are changed to

$$\begin{aligned} \pi^+(x) &= (1-x) \frac{xf(x)(1-\mu) + (1-x)g(x)\mu}{xf(x) + (1-x)g(x)}, \\ \pi^-(x) &= x \frac{xf(x)\mu + (1-x)g(x)(1-\mu)}{xf(x) + (1-x)g(x)}, \end{aligned} \tag{23}$$

while the drift and diffusion terms in (6) become

$$\begin{aligned}
 D^{(1)}(x) &= x(1-x) \frac{f(x) - g(x)}{xf(x) + (1-x)g(x)} + \mu \frac{-xf(x) + (1-x)g(x)}{xf(x) + (1-x)g(x)}, \\
 D^{(2)}(x) &= \frac{1}{2N} \left[x(1-x) \frac{f(x) + g(x)}{xf(x) + (1-x)g(x)} + (2x-1)\mu \frac{xf(x) - (1-x)g(x)}{xf(x) + (1-x)g(x)} \right].
 \end{aligned}
 \tag{24}$$

Moreover, the stationary distribution of (6) is given by⁷

$$\phi(x) = \frac{C}{D^{(2)}(x)} e^{\int_0^x \frac{D^{(1)}(s)}{D^{(2)}(s)} ds}, \tag{25}$$

where $C = [\int_0^1 \frac{1}{D^{(2)}(x)} e^{\int_0^x (D^{(1)}(s)/D^{(2)}(s)) ds} dx]^{-1}$ is the normalization constant [18].

For weak selection,

$$\begin{aligned}
 D^{(1)}(x) &\approx x(1-x)\omega\alpha(x-x^*) + (1-2x)\mu, \\
 D^{(2)}(x) &\approx \frac{1}{2N} [2x(1-x) + (1-2x)^2\mu].
 \end{aligned}$$

Thus, the stationary distribution is approximated by

$$\phi(x) \approx \frac{2CN}{2x(1-x) + (1-2x)^2\mu} \exp \left[\int_0^x 2N \frac{s(1-s)\omega\alpha(s-x^*) + (1-2s)\mu}{2s(1-s) + (1-2s)^2\mu} ds \right]. \tag{26}$$

In particular, when $\omega = 0$, $\phi(x)$ is symmetric about $x = \frac{1}{2}$ (i.e. $\phi(\frac{1}{2} + t) = \phi(\frac{1}{2} - t)$ for $0 \leq t \leq \frac{1}{2}$) since the skew-symmetry of $\frac{(1-2s)\mu}{2s(1-s) + (1-2s)^2\mu}$ implies that

$$\int_{t-\frac{1}{2}}^{t+\frac{1}{2}} 2N \frac{(1-2s)\mu}{2s(1-s) + (1-2s)^2\mu} ds = 0.$$

This result also follows from the classical theory of neutral selection [10] and is illustrated by Traulsen et al. [22, Fig. 1] who show that $\phi(x)$ has its maximum at $x = 1/2$ if the mutation rate μ is large and its minimum there if μ is small. More important for us is that, by the same reasoning, $\phi(x)$ is symmetric about $x = \frac{1}{2}$ when $x^* = \frac{1}{2}$. Thus, this stationary distribution's expected value $\langle x \rangle \equiv \int_0^1 x\phi(x) dx$ (i.e. the expected frequency of strategy A) satisfies $\langle x \rangle = \frac{1}{2}$.

Now assume that A and B are strict NE and that A is risk dominant (i.e. $\alpha > 0$ and $0 < x^* < \frac{1}{2}$). For weak selection,

$$\begin{aligned}
 \phi(x) &\approx \frac{2CN}{2x(1-x) + (1-2x)^2\mu} \\
 &\times \exp \left[\int_0^x 2N \frac{s(1-s)\omega\alpha((s-\frac{1}{2}) + (\frac{1}{2}-x^*)) + (1-2s)\mu}{2s(1-s) + (1-2s)^2\mu} ds \right] \\
 &= \frac{2CN}{2x(1-x) + (1-2x)^2\mu} \exp \left[\int_0^x 2N \frac{s(1-s)\omega\alpha(s-\frac{1}{2}) + (1-2s)\mu}{2s(1-s) + (1-2s)^2\mu} ds \right] \\
 &\times \exp \left(\frac{1}{2} - x^* \right) \left[\int_0^x \frac{2Ns(1-s)\omega\alpha}{2s(1-s) + (1-2s)^2\mu} ds \right].
 \end{aligned} \tag{27}$$

⁷The Fokker–Planck equation (6) with $D^{(1)}(x)$ and $D^{(2)}(x)$ given in (24) has a unique stationary distribution since this diffusion process no longer has absorbing boundaries.

That is, the stationary distribution when $0 < x^* < \frac{1}{2}$ is (the renormalization of) the symmetric stationary distribution for $x^* = \frac{1}{2}$ multiplied by the positive function

$$\exp\left(\frac{1}{2} - x^*\right) \left[\int_0^x \frac{2Ns(1-s)\omega\alpha}{2s(1-s) + (1-2s)^2\mu} ds \right]$$

that increases in x . This implies that $\langle x \rangle > \frac{1}{2}$ when $0 < x^* < \frac{1}{2}$.

The last result can be restated in terms of the difference between the expected fitnesses of A and B under weak selection. From (3), this is

$$\langle f(x) - g(x) \rangle \approx \omega\alpha(\langle x \rangle - x^*).$$

Since $\langle x \rangle > x^*$ and $\alpha > 0$, $\langle f(x) - g(x) \rangle > 0$ when $x^* < 1/2$. The corresponding analysis when $x^* > 1/2$ shows $\langle f(x) - g(x) \rangle < 0$. That is, A has higher expected fitness than B if and only if it is the risk-dominant NE.

The same conclusion can be made when expected fitness with respect to the stationary distribution is replaced by average fitness with respect to the uniform distribution used by Ohtsuki et al. [17]. Specifically, the average fitness of strategy A is greater than B if and only if $x^* < 1/2$ since $\int_0^1 (f(x) - g(x)) dx \approx \omega\alpha \int_0^1 (\langle x \rangle - x^*) dx = \omega\alpha(\frac{1}{2} - x^*)$. However, our result based on the nonuniform stationary distribution is more relevant to the stochastic process underlying the diffusion approximation. For example, the strategy with higher expected fitness is also known as the stochastically stable NE that is selected in models that incorporate small errors in strategy choice [9, 19].

7 Conclusion

In this paper, following Traulsen and Hauert [21] and Ohtsuki et al. [17], properties of the fixation probability and mean effective fixation time for the Moran process are investigated using the diffusion approximation. The analysis leads to several new interpretations of selection favoring strategy A under weak selection. In the following summary of our results, we assume that A and B are both strict Nash equilibria of the two-strategy game.

The first property (Sect. 3) confirms the weak selection result that Nowak et al. [16] obtained for the Moran process (i.e. selection favors strategy A when population size is large if this strategy satisfies the one-third law) remains valid for the diffusion approximation. In Sect. 4, we show that the mean effective fixation time $\bar{\tau}(p)$ (here, p is the initial frequency of strategy in the finite population) can be divided into two parts, $\bar{\tau}_1(p)$ and $\bar{\tau}_2(p)$, where $\bar{\tau}_1(p)$ represents the mean effective fixation time meeting A -individuals and $\bar{\tau}_2(p)$ the mean effective fixation time meeting B -individuals. Then, for weak selection (i.e. $N\omega \ll 1$) and large population size, the ratio $\bar{\tau}_1(1/N)/\bar{\tau}(1/N)$ is about $1/3$, and the ratio $\bar{\tau}_2(1/N)/\bar{\tau}(1/N)$ is about $2/3$. This result provides a new perspective on the calculation for the Moran process done by Ohtsuki et al. [17] who emphasized that, in one invasion attempt by strategy A , an individual interacts on average with B -individuals twice as often as with A -individuals, which yields the one-third law.

On the other hand, in the weak selection limit with $p = 1/N$, the average fitness of A about the mean effective fixation time is bigger than the average fitness of B about the mean effective fixation time if $x^* < 1/3$ (Sect. 5). This gives a natural interpretation of the one-third law as a means to predict when selection favors A . Ohtsuki et al. [17] instead emphasized that the one-third law implies that the average Malthusian fitness of A under the

uniform distribution is positive. In our model, this comparison is directly connected to the stochastic process in that the one-third law implies that the difference between the average fitnesses of A and B about the mean effective fixation time is positive. In Sect. 6, we show that the expected fitness of A under the stationary distribution of the diffusion approximation with small mutation is larger than the expected fitness of B if strategy A is risk dominant. This result gives an alternative meaning to the notion of selection favoring A more than B originally considered in terms of their fixation probabilities by Nowak et al. [16].

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Appendix A

A.1 The Fokker–Planck Equation

First, we derive the Fokker–Planck equation (6) from (5). For large N , the probability densities, $\phi(x; t + 1/N)$ and $\phi(x \pm 1/N; t)$, and the transition probabilities, $\pi^\pm(x \mp 1/N)$ have Taylor series expansions at x and t given by

$$\begin{aligned} \phi(x; t + 1/N) &\approx \phi(x; t) + \frac{\partial}{\partial t} \phi(x; t) \frac{1}{N}, \\ \phi(x \pm 1/N; t) &\approx \phi(x; t) \pm \frac{\partial}{\partial x} \phi(x; t) \frac{1}{N} + \frac{\partial^2}{\partial x^2} \phi(x; t) \frac{1}{2N^2}, \\ \pi^\pm(x \mp 1/N) &\approx \pi^\pm(x) \mp \frac{\partial}{\partial x} \pi^\pm(x) \frac{1}{N} + \frac{\partial^2}{\partial x^2} \pi^\pm(x) \frac{1}{2N^2}. \end{aligned} \tag{28}$$

From the first (linear) expansion, the left-hand side of (5) is $\phi(x; t + 1/N) - \phi(x; t) \approx \frac{\partial}{\partial t} \phi(x; t) \frac{1}{N}$. The other two expansions, the second order approximations of terms on the right-hand side of (5) are

$$\begin{aligned} \phi(x - 1/N; t) \pi^+(x - 1/N) &\approx \phi(x; t) \pi^+(x) + \phi(x; t) \left[-\frac{\partial}{\partial x} \pi^+(x) \frac{1}{N} + \frac{\partial^2}{\partial x^2} \pi^+(x) \frac{1}{2N^2} \right] \\ &\quad - \pi^+(x) \frac{\partial}{\partial x} \phi(x; t) \frac{1}{N} + \left(\frac{\partial}{\partial x} \phi(x; t) \right) \left(\frac{\partial}{\partial x} \pi^+(x) \right) \frac{1}{N^2} \\ &\quad + \pi^+(x) \frac{\partial^2}{\partial x^2} \phi(x; t) \frac{1}{2N^2}, \\ \phi(x + 1/N; t) \pi^-(x + 1/N) &\approx \phi(x; t) \pi^-(x) + \phi(x; t) \left[\frac{\partial}{\partial x} \pi^-(x) \frac{1}{N} + \frac{\partial^2}{\partial x^2} \pi^-(x) \frac{1}{2N^2} \right] \\ &\quad + \pi^-(x) \frac{\partial}{\partial x} \phi(x; t) \frac{1}{N} + \left(\frac{\partial}{\partial x} \phi(x; t) \right) \left(\frac{\partial}{\partial x} \pi^-(x) \right) \frac{1}{N^2} \\ &\quad + \pi^-(x) \frac{\partial^2}{\partial x^2} \phi(x; t) \frac{1}{2N^2}. \end{aligned}$$

That is, the right-hand side of (5) up to second order terms becomes

$$\begin{aligned}
 & \phi(x; t) \left[-\frac{\partial}{\partial x} \pi^+(x) \frac{1}{N} + \frac{\partial^2}{\partial x^2} \pi^+(x) \frac{1}{2N^2} \right] - \pi^+(x) \frac{\partial}{\partial x} \phi(x; t) \frac{1}{N} \\
 & + \left(\frac{\partial}{\partial x} \phi(x; t) \right) \left(\frac{\partial}{\partial x} \pi^+(x) \right) \frac{1}{N^2} \\
 & + \pi^+(x) \frac{\partial^2}{\partial x^2} \phi(x; t) \frac{1}{2N^2} + \phi(x; t) \pi''(x) \\
 & + \phi(x; t) \left[\frac{\partial}{\partial x} \pi^-(x) \frac{1}{N} + \frac{\partial^2}{\partial x^2} \pi^-(x) \frac{1}{2N^2} \right] \\
 & + \pi^-(x) \frac{\partial}{\partial x} \phi(x; t) \frac{1}{N} + \left(\frac{\partial}{\partial x} \phi(x; t) \right) \left(\frac{\partial}{\partial x} \pi^-(x) \right) \frac{1}{N^2} \\
 & = \phi(x; t) \left[\frac{\partial(\pi^-(x) - \pi^+(x))}{\partial x} \frac{1}{N} \right] + (\pi^-(x) - \pi^+(x)) \frac{1}{N} \frac{\partial \phi(x; t)}{\partial x} \\
 & + \frac{\partial^2(\pi^-(x) + \pi^+(x))}{\partial x^2} \frac{1}{2N^2} \\
 & + \left(\frac{\partial}{\partial x} \phi(x; t) \right) \left(\frac{\partial}{\partial x} (\pi^-(x) + \pi^+(x)) \right) \frac{1}{N^2} + (\pi^-(x) + \pi^+(x)) \frac{1}{2N^2} \frac{\partial^2 \phi(x; t)}{\partial x^2} \\
 & = \frac{1}{N} \frac{\partial \phi(x; t) (\pi^-(x) - \pi^+(x))}{\partial x} + \frac{1}{2N^2} \frac{\partial^2 \phi(x; t) (\pi^-(x) + \pi^+(x))}{\partial x^2}.
 \end{aligned}$$

Equating the left and right hand approximations of (5) results in (6).

A.2 The Backward Equation

Second, we derive the backward equation (9) as the diffusion approximation to

$$\begin{aligned}
 \phi(x; p, t + 1/N) &= \pi^+(p) \phi(x; p + 1/N, t) + \pi^-(p) \phi(x; p - 1/N, t) \\
 &+ [1 - \pi^+(p) - \pi^-(p)] \phi(x; p, t).
 \end{aligned}$$

From the Taylor expansions in above equation applied to the variables p and t in $\phi(x; p, t)$,

$$\begin{aligned}
 \phi\left(x; p, t + \frac{1}{N}\right) - \phi(x; p, t) &\approx \frac{1}{N} \frac{\partial \phi(x; p, t)}{\partial t}, \\
 \pi^+(p) \left(\phi\left(x; p + \frac{1}{N}, t\right) - \phi(x; p, t) \right) &\approx \pi^+(p) \left(\frac{1}{N} \frac{\partial \phi(x; p, t)}{\partial p} + \frac{1}{2N^2} \frac{\partial^2 \phi(x; p, t)}{\partial p^2} \right), \\
 \pi^-(p) \left(\phi\left(x; p - \frac{1}{N}, t\right) - \phi(x; p, t) \right) &\approx \pi^-(p) \left(-\frac{1}{N} \frac{\partial \phi(x; p, t)}{\partial p} + \frac{1}{2N^2} \frac{\partial^2 \phi(x; p, t)}{\partial p^2} \right).
 \end{aligned}$$

Substituting these expressions yields (9). The backward equation can also be obtained directly from the Fokker–Planck equation without going through the discrete-time Moran process [10].

A.3 Derivation of $\bar{\tau}_1(p)$ and $\bar{\tau}_2(p)$

Recall that $\bar{\tau}_1(p)$ denotes the mean effective time of meeting A -individuals and $\bar{\tau}_2(p)$ the mean effective time of meeting B -individuals before absorption. From (19), we have

$$\begin{aligned}\bar{\tau}_1(p) &= \int_0^p x(\pi^+(x) + \pi^-(x))t(x; p) dx \\ &\quad + \int_p^1 x(\pi^+(x) + \pi^-(x))t(x; p) dx \\ &= \int_0^p 2N(1-u(p))x^2 dx + \int_p^1 2Nu(p)x(1-x) dx \\ &= \frac{2Np^3}{3} + Nu(p)(1/3 - p^2) \\ &\approx \frac{1}{3} - \frac{1}{3N^2},\end{aligned}$$

and

$$\begin{aligned}\bar{\tau}_2(p) &= \int_0^p (1-x)(\pi^+(x) + \pi^-(x))t(x; p) dx \\ &\quad + \int_p^1 (1-x)(\pi^+(x) + \pi^-(x))t(x; p) dx \\ &= \int_0^p 2N(1-u(p))x(1-x) dx + \int_p^1 2Nu(p)(1-x)^2 dx \\ &= N(1-u(p))(p^2 - 2p^3/3) + 2Nu(p)(1/3 - p(1-p) - p^3/3) \\ &\approx \frac{2}{3} - \frac{1}{N} + \frac{1}{3N^2}\end{aligned}$$

for weak selection and large population size. These are the expressions given in (20) of the main text.

References

1. Binmore K, Samuelson L, Young P (2003) Equilibrium selection in bargaining models. *Games Econ Behav* 45:296–328
2. Cressman R (2009) Continuously stable strategies, neighborhood superiority and two-player games with continuous strategy space. *Int J Game Theory* 38:221–247
3. Ewens WJ (2004) *Mathematical population genetics*. Springer, New York
4. Foster DP, Young HP (1990) Stochastic evolutionary game dynamics. *Theor Popul Biol* 38:219–232
5. Garay J (2008) Relative advantage and fundamental theorems of natural selection. In: *Mathematical modeling of biological systems*, vol II. Birkhauser, Boston, pp 63–74
6. Harsanyi JC, Selten R (1988) *A general theory of equilibrium selection in games*. MIT Press, Cambridge
7. Hofbauer J, Sigmund K (1998) *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge
8. Imhof LA, Nowak MA (2006) Evolutionary game dynamics in a Wright-Fisher process. *J Math Biol* 52:667–681
9. Kandori M, Mailath GJ, Rob R (1993) Learning, mutation, and long-run equilibria in games. *Econometrica* 61:29–56

10. Kimura M (1964) Diffusion models in population genetics. *J Appl Probab* 1:177–232
11. Lessard S (2011) On the robustness of the extension of the one-third law of evolution to the multi-player game. *Dyn Games Appl* (forthcoming)
12. Lessard S, Ladret V (2007) The probability of fixation of a single mutant in an exchangeable selection model. *J Math Biol* 54:721–744
13. Maynard Smith J, Price GR (1973) The logic of animal conflict. *Nature* 246:15–18
14. Morris S, Rob R, Shin HS (1995) Dominance and belief potential. *Econometrica* 63:145–157
15. Nowak MA (2006) *Evolutionary dynamics*. Harvard University Press, Cambridge
16. Nowak MA, Sasaki A, Taylor C, Fudenberg D (2004) Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428:646–650
17. Ohtsuki H, Bordalo P, Nowak MA (2007) The one-third law of evolutionary dynamics. *J Theor Biol* 249:289–295
18. Risken H (1992) *The Fokker–Planck equation: methods of solution and applications*. Springer, Berlin
19. Sandholm WH (2010) *Population games and evolutionary dynamics*. MIT Press, Cambridge
20. Taylor C, Fudenberg D, Sasaki A, Nowak MA (2004) Evolutionary game dynamics in finite populations. *Bull Math Biol* 66:1621–1644
21. Traulsen A, Hauert C (2009) Stochastic evolutionary game dynamics. In: Schuster HG (ed) *Reviews of nonlinear dynamics and complexity, vol II*. Wiley-VCH, New York
22. Traulsen A, Claussen JC, Hauert C (2006) Coevolutionary dynamics in large, but finite populations. *Phys Rev E* 74:011901
23. Traulsen A, Pacheco JM, Imhof LA (2006) Stochasticity and evolutionary stability. *Phys Rev E* 74:021905
24. van Kampen NG (1992) *Stochastic processes in physics and chemistry*. Elsevier, Amsterdam
25. Wu B, Altrock PM, Wang L, Traulsen A (2010) Universality of weak selection. *Phys Rev E* 82:046106