

Game theory and evolution: finite size and absolute fitness measures

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Abstract

This article is concerned with the characterization and existence of evolutionarily stable strategies (ESS) in Games against Nature, a class of models described by finite size populations and absolute fitness measures. We address these problems in terms of a new formalism which revolves around the concept evolutionary entropy, a measure of the diversity of options associated with a strategy – pure strategies have zero entropy, mixed strategies positive entropy. We invoke this formalism to show that ESS are characterized by extremal states of entropy. We illustrate this characterization of ESS by an analysis of the evolution of the sex ratio and the evolution of seed size. © 2000 Elsevier Science Inc. All rights reserved.

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1. Introduction

Evolutionary game theory, as proposed by Maynard Smith and Price [1], is a mathematical formalism which aims to explain in evolutionary terms how conflicting interests can lead to stable behavioral traits within a population of organisms. In this game-theoretic model, individuals in the population are said to adopt *strategies*, which represent any genetically programmed behavioral action. The *payoff* associated with a strategy is described by the *Darwinian fitness* of the individuals that adopt it. A strategy is said to be *evolutionarily stable* if it has the property that if all members of the population adopt it, no mutant phenotype could invade the population under the influence of natural selection.

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The notion of an evolutionarily stable strategy (ESS) represents the cornerstone of evolutionary game theory: the concept has been given mathematical formalizations in several different contexts (cf. [2–6]) and attempts have been made to characterize its properties and explicitly specify the strategy in a large class of examples.

The mathematical representation of the model rests on two main assumptions:

A(1) Population size is large – effectively infinite. This condition ensures that fluctuations in population numbers due, for example, to small perturbations in the individual payoffs can be neglected – a situation which ensures that conditions for the invasion of a mutant strategy will be a deterministic process.

A(2) The fitnesses ascribed to individual strategies refer to *relative* values, such as the change in the mean number of offspring that survive for reproduction, rather than *absolute* values, such as the net reproduction rate.

In the analysis of models based on the assumptions of infinite size and relative fitness measures, strategies are parametrized in terms of the distribution $p = (p_i)$, where p_i represents the frequency of individuals adopting the i th strategy. The notion of an evolutionarily stable strategy is characterized in terms of the selective advantage s of the incumbent population with respect to the mutant type, which is given by

$$s = \Delta W, \tag{1.1}$$

where, W , the index of Darwinian fitness, is measured in terms of numbers of surviving offspring. This notion of selective advantage has been invoked by Maynard Smith [2], Hofbauer and Sigmund [3], Zeeman [4], Hines [5] and Lessard [6] to show that an ESS satisfies two properties:

B(1) *An equilibrium condition – the Nash solution concept.* This refers to the strategy $p = (p_i)$, where each player holds the correct expectation about the others behavior and acts to maximize his fitness.

B(2) *A stability criterion.* The incumbent strategy is evolutionarily stable if given that the population is at a Nash equilibrium, the fitness of the incumbent always exceeds the fitness of any rare mutant.

The class of games considered by Maynard Smith and Price are distinguished by two main features: (a) they deal with local competition within a population, (b) they pertain to situations in which the success of a strategy depends on its frequency. The mathematical formalism, in particular the measure of fitness invoked, is adapted to analyze an evolutionary dynamics which refers to interactions of individuals within populations.

As emphasized, however, in [7], a complete evolutionary theory must also address itself to problems which arise from the interaction of the population with the external environment. The questions which arise in this context are: what is the probability of extinction of a population in the given environment? Under what conditions will a mutant, that is, a population whose phenotypic composition differs slightly from the incumbent population, invade the existing type and replace it. Lewontin [7] seems to have been the first to recognize that these problems can be formalized in a game theory context, which is now called Games against Nature. In this class of models, the selective unit is a population which is defined by a certain behavioral feature or strategy, and the central problem concerns the invulnerability of the population to invasion by populations adopting mutant strategies. Games against Nature deals with interactions between populations rather than interactions within populations. This class of games and the evolutionarily

stable strategies (ESS) they generate have been studied recently by several authors, in particular Metz, Nisbet and Geritz [8], Rand et al. [9], Geritz [10], Rees and Westoby [11]. The analytical representation of this class of models revolves around two main conditions:

C(1) Population size is large, effectively infinite – a condition identical to A(1) and ensuring similar effects.

C(2) The fitness assigned to strategies refers to *absolute* values such as net-reproduction rate, rather than *relative* values such as the change in the mean number of offspring that survive for reproduction.

The selective advantage s , in this class of models is given by

$$s = \Delta r, \quad (1.2)$$

where r represents the rate of increase in total population numbers, given by the Malthusian parameter in constant environment models, and the dominant Lyapunov exponent in random environment contexts. The derivation of (1.2) can be shown to rest implicitly on the assumption that the population size of the incumbent is effectively infinite.

This article will relax the infinite size condition and analyze Games against Nature on the assumption that size is finite. We will appeal to a statistical mechanics formalism, elaborated in other population dynamics contexts in [12,13], to show that in this new class of models, the selective advantage s of the incumbent strategy with respect to the mutant strategy will now be represented in terms of two demographic variables, the population growth rate r , the rate of increase of total population numbers, and the demographic variance σ^2 , which represents the variance in the contribution of the different strategists to the total payoff.

Analytically, selective advantage s will be shown to be described by

$$s = \Delta r - \frac{1}{N} \Delta \sigma^2, \quad (1.3)$$

where N denotes the total population size. The derivation of (1.3) will be based on a stochastic model which considers the invasion condition of new mutants in the resident population to be determined by a diffusion process, on account of the fluctuations due to the finite size condition. We refer to [14], where stochastic elements are introduced in the analysis of the mutation process in models distinct from the cases considered in this paper.

In our analysis of this new family of models we will parametrize the population in terms of the distribution $\mu = (\mu_i)$, where μ_i represents the relative contribution of the i th strategy to the total payoff. We will denote by \mathcal{M} the collection of such distributions and appeal to the new characterization of selective advantage to show that ESS in this new context satisfies the following analogues of B(1) and B(2).

D(1) An equilibrium condition, which we call thermodynamic equilibrium, is described in terms of the function evolutionary entropy H defined by

$$H = - \sum_i \mu_i \log \mu_i. \quad (1.4)$$

Evolutionary entropy H is a measure of the diversity of options associates with a strategy – pure strategies have zero entropy, mixed strategies positive entropy. Thermodynamic equilibria refer to

strategies which are extremal states (minima or maxima) of entropy, within a natural class of strategies known as demographic equilibria.

D(2) A stability criterion, which will be expressed in terms of two demographic parameters, the reproductive potential Φ and the correlation index γ . The parameter Φ measures the net-payoff, averaged over all strategy classes; whereas γ is an index of the correlation, with respect to the different strategy classes, of the net payoff function.

We will appeal to this depiction of ESS in terms of the equilibrium condition and stability criteria to establish the following set of criteria for ESS.

Theorem 1.1. *Evolutionary stable strategies are characterized by extremal states of entropy.*

There exist only finitely many strategies for which entropy becomes extremal. If there are no ecological constraints restricting strategies to subsets \mathcal{M}_c of \mathcal{M} , the extremal strategies are global and described by the pure strategies, which minimize entropy, and the equidistribution on Ω which maximizes entropy. In the case of constraints, extremal strategies will be local and defined on the boundary of the subset \mathcal{M}_c . Hence the evolutionarily stable strategies constitute a subset of these three classes of strategies: the equidistributed strategy, pure strategies and non-equidistributed extremal strategies.

In the case of strategies that are global maxima or minima, we will show that the existence criterion can be expressed in terms of a single parameter, the reproductive potential.

Theorem 1.2. *An equidistributed strategy is an ESS if and only if it yields a negative reproductive potential.*

Theorem 1.3. *A pure strategy is an ESS if and only if it yields a positive reproductive potential.*

In the case of constraints limiting the number of strategies for which entropy becomes extremal, the excluded global maximum or minima, respectively, can be replaced by local maxima or minima appearing on the boundary of the set \mathcal{M}_c . Then the existence criteria will be expressed in terms of the two variables, the reproductive potential, and the correlation index.

Theorem 1.4. *A non-equidistributed extremal strategy is an ESS if and only if either of the following conditions holds:*

- (i) $\Phi \leq 0$, $\gamma > 0$,
- (ii) $\Phi \geq 0$, $\gamma < 0$.

Our analysis will establish that non-equidistributed extremal strategies are local maxima if and only if the reproductive potential is negative and the index is positive, whereas, they describe local minima if and only if the reproductive potential is positive and the index is negative.

This article is organized as follows. In Section 2 we describe in detail the concepts and formalism we have introduced to analyze the game theoretic models in which the notions of finite size and absolute fitness measures are considered. In particular, we provide a motivation for the notion thermodynamic equilibrium. In Section 3 we present a perturbation analysis of such equilibria which forms the basis for our analysis of the mutation event and our investigations of

ESS. We exploit the notions of Section 2 and the results of Section 3 to derive our main results, namely Theorem 1.1 (Section 4) and Theorems 1.2–1.4 (Section 5). Section 6 contrasts the formalism of the classical models (infinite size, relative fitness) with the new set of models (finite size, absolute fitness). We illustrate the significance of our new formalism by a study of the evolution of the sex ratio, see [15], and the evolution of polymorphism in seed size, see [10,11]. Studies of the sex ratio in the context of classical game theory models predict a 1–1 sex ratio is the ESS. Our analysis based on evolutionary entropy as the measure of fitness predicts that a 1–1 sex ratio is evolutionarily stable if and only if the population has stationary size. Our analysis thus indicates that in exponentially growing populations departures from a 1–1 sex ratio may occur. Studies of seed size polymorphism [10], in terms of game theory models invoking growth rate as fitness predict that there is no stable seed size monomorphism: the polymorphic condition is the unique ESS. We will appeal to the entropy formalism to generate a larger repertoire of ESS. We will delineate three classes of ESS, each class being defined by the ecological condition the plants experience. The three classes of ESS are described as follows:

- (a) Equal number of seeds of different sizes.
- (b) All seeds of the same size.
- (c) Variable number of seeds of different sizes.

The polymorphic strategy (a) and the monomorphic strategy (b), both require the stringent condition that seed size and reproductive yield are uncorrelated. We will show that strategy (a) is an ESS if the total net-reproductive yield is bounded by the number of distinct seed sizes, whereas strategy (b) is an ESS if the net seed production increases exponentially. The polymorphic strategy (c) requires that seed size and reproductive yield are correlated.

We should remark at this point that the notion of entropy has been applied in other population dynamics contexts, see for example the work of Bomze [16], Iwasa [17] and Ginzburg [18]. In these studies, entropy is interpreted primarily in terms of the Kullback–Lieber distance and the properties which form a central part of our work were not exploited by these authors. The entropy concept used in this paper is embedded in ergodic theory and statistical mechanics, a formalism which was introduced in a population biology context in [19]. The thermodynamic methods we exploit, invoke besides entropy, a large family of related macroscopic variables – reproductive potential, demographic variance. The power of the application of the thermodynamic formalism to game theory resides in the pertinence of these concept to characterize the complexities generated by problems of finite size and absolute measures of fitness.

2. Games against Nature

We consider a large but finite population of individuals. We assume that the behavior of the individuals in the population can be described in terms of a set of choices $\Omega := \{x_1, \dots, x_d\}$. These elements x_i represent the different options which are available to the individuals in the population. The *payoff* associated with the set Ω should depend on the choices of the x_i only, in particular it should be independent of the time the choice is made. Hence it is represented by a function φ which assigns to each $x_i \in \Omega$ a real non-negative number $\varphi(x_i)$, a measure of the net-offspring production associated with the option x_i .

The quantity $Z(\varphi) = \sum_{i=1}^d \varphi(x_i)$ represents the total net-offspring production of a given individual in the population. Let $N(n)$ denote the number of individuals in the population at time n . Then

$$N(n+1) = Z(\varphi)N(n).$$

Hence

$$N(n+1) = Z(\varphi)^n N(0).$$

The net reproduction rate, that is, the growth rate per generation, denoted $r(\varphi)$ is given by

$$r(\varphi) = \lim_{n \rightarrow \infty} \frac{1}{n} \log N(n),$$

hence

$$r(\varphi) = \log Z(\varphi). \tag{2.1}$$

2.1. Demographic equilibria

We consider a population of organisms parametrized in terms of behavioral options x_1, \dots, x_d for a game. The net-offspring production associated with the option x_i is $\varphi(x_i)$. From (2.1) we observe that subject to the process defined by $\varphi(x_i)$, the population will increase per generation at the rate $r(\varphi)$.

Now let \mathcal{M} denote the set of probability distributions μ on Ω . An element $\mu \in \mathcal{M}$ ascribes to each x_i a number μ_i , with $0 \leq \mu_i \leq 1$, $\sum_{i=1}^d \mu_i = 1$. The quantity $\mu = (\mu_i)$ is called a *strategy*. It refers to the preference of certain options in the populations and not to individual action; i.e. we consider the class of strategies $\mu \in \mathcal{M}$ as the expression of a demographic program which assigns $\varphi(x_i)$ to each behavioral option $x_i \in \Omega$. Hence a game can be described by the mathematical object (Ω, μ, φ) , where $\mu \in \mathcal{M}$.

We now introduce the notion of a *demographic equilibrium* by showing that the parameter $r(\varphi)$ satisfies a variational principle analogous to the principle of the minimization of free energy in statistical mechanics, see [13,20]. We define for any strategy $\mu \in \mathcal{M}$, the evolutionary entropy H given by (1.4), and the reproductive potential Φ given by

$$\Phi := \mu(\log \varphi) = \sum_{i=1}^d \mu_i \log \varphi(x_i). \tag{2.2}$$

We introduce for any $\mu \in \mathcal{M}$, the quantity

$$P(\mu, \varphi) = H(\mu) + \mu(\log \varphi)$$

and call it the *power* of the strategy μ corresponding to the payoff φ . Then a probability distribution $\hat{\mu} \in \mathcal{M}$ is said to be a *demographic equilibrium state* if

$$P(\hat{\mu}, \varphi) = \sup_{\mu \in \mathcal{M}} P(\mu, \varphi).$$

Thus at demographic equilibrium the strategy maximizes the sum of the entropy and reproductive potential. We will now show that the maximum $P(\hat{\mu}, \varphi)$ is precisely $r(\varphi)$, the growth rate given by

(2.1). In view of this property, the concept demographic equilibrium characterizes the state of a population which is increasing exponentially at the rate $r(\varphi)$.

By appealing to [20, 0.2], we can formalize these observations and characterize the demographic equilibrium condition in terms of the following well-known proposition.

Proposition 2.1. *A strategy $\hat{\mu}$ is a demographic equilibrium state corresponding to the payoff φ if one of the following two equivalent conditions is satisfied:*

(i) $\hat{\mu}$ satisfies

$$r(\varphi) = H(\hat{\mu}) + \hat{\mu}(\log \varphi), \tag{2.3}$$

where $r(\varphi)$ is the population growth rate.

(ii) $\hat{\mu} = (\hat{\mu}_i)$ is given by

$$\hat{\mu}_i = \frac{\varphi(x_i)}{Z(\varphi)}. \tag{2.4}$$

Proof. By the definitions of power and entropy we have for any strategy μ

$$P(\mu, \varphi) = - \sum_{i=1}^d \mu_i \log \mu_i + \sum_{i=1}^d \mu_i \log \varphi(x_i) = \sum_{i=1}^d \mu_i \log \frac{\varphi(x_i)}{\mu_i}.$$

In order to make comparisons between $\varphi(x_i)$ and μ_i easier let us normalize φ by setting $\tilde{\varphi}(x_i) := \varphi(x_i)/Z(\varphi)$ such that $\tilde{\varphi}(x_i) \leq 1$ and $\sum_i \tilde{\varphi}(x_i) = 1$. Then

$$P(\mu, \varphi) = \sum_{i=1}^d \mu_i \log \frac{\tilde{\varphi}(x_i)}{\mu_i} + \log Z(\varphi)$$

and the first term on the right-hand side becomes maximal if and only if the fraction is constant for all i , i.e. identical to 1 because of the normalization. This yields $\hat{\mu}_i = \varphi(x_i)/Z(\varphi)$. \square

Let us summarize that the setup for a game is completely described by the payoff function φ defined on the space of options Ω . Our model and analysis then shows that a demographic equilibrium represents a biological meaningful state where the three parameters r , H , Φ characterize the game. In the evolutionary studies we develop, we will assume that the population is at demographic equilibrium. The system can therefore be represented by the mathematical object $(\Omega, \hat{\mu}, \varphi)$ with the macroscopic parameters defined at the state $\hat{\mu}$. The relation between the three parameters r , H , Φ from (2.3) given by

$$r = H + \Phi.$$

We note from the above identity that

$$\Phi < 0 \Rightarrow r < H, \quad \Phi > 0 \Rightarrow r > H.$$

Accordingly, we will use the parameter Φ to classify populations according to prevailing constraints on their growth rate: $\Phi < 0$ (bounded growth), $\Phi > 0$ (unbounded growth).

2.2. Evolutionarily stable strategies (ESS)

The incumbent population can be described in terms of the triple $(\Omega, \hat{\mu}, \varphi)$. In fact, $\hat{\mu}$ is given by (2.4) and thus completely determined by φ , as are the demographic parameters $r(\varphi)$, H and Φ due to Proposition 2.1.

We will consider a mutation to be represented by a change in the distribution of net-offspring production. Such a change in distribution, which we denote by φ^* will induce a new demographic equilibrium strategy $\hat{\mu}^*$. Hence the mutant population can be represented by the triple $(\Omega, \hat{\mu}^*, \varphi^*)$.

Mathematically we think of φ^* as a small perturbation of φ . Smallness is expressed in terms of a parameter δ of small absolute value such that $\varphi^* = \varphi(\delta)$. We postulate that the simplest equation describing the potential $\varphi(\delta)$ generated by a mutation in a gene that defines a phenotype with potential φ , will assume the form

$$\log \varphi^* = \log \varphi(\delta) = \log \varphi + \delta \log \psi. \quad (2.5)$$

Expression (2.5) simply asserts that $\log \varphi(\delta)$ is a sum of two components: (a) the first, $\log \varphi$ due to the ancestral type, (b) the second, $\delta \log \psi$ due to some deviation δ of small absolute value from the ancestral type. The natural generalization of (2.5) is

$$\log \varphi(\delta) = \log \varphi + \delta \log \psi, \quad (2.6)$$

that means

$$\varphi^* = \varphi \psi^\delta, \quad (2.7)$$

where

$$\int \log \varphi \, d\hat{\mu} = \int \log \psi \, d\hat{\mu} \quad (2.8)$$

and

$$\frac{d}{d\delta} \left(\int \log \varphi \, d\hat{\mu}^* \right)_{\delta=0} = \frac{d}{d\delta} \left(\int \log \psi \, d\hat{\mu}^* \right)_{\delta=0}. \quad (2.9)$$

Condition (2.8) asserts that the rates $\log \varphi$ and $\log \psi$ averaged over the different strategies coincide, while (2.9) asserts that the perturbation mainly changes intensities of the rates. The generalization (2.6) thus states that the component $\delta \log \psi$ which characterizes the mutation is now represented by a deviation δ from a type with the same average growth rate as the ancestral type.

The notion of an *evolutionarily stable strategy* $\hat{\mu}$ for the resident population $(\Omega, \hat{\mu}, \varphi)$ requires that the population $(\Omega, \hat{\mu}^*, \varphi^*)$ described by any deviant strategy $\hat{\mu}^*$ will be displaced in competition, by the one described by $\hat{\mu}$. This condition can be analytically expressed as follows.

Let $N^*(n)$ and $N(n)$ denote the total payoff up to time $n \in \mathbb{Z}_+$ for the mutant and incumbent strategy, respectively. As we intend to consider in the selection procedure $N(n)$ and $N^*(n)$ not only as deterministic, but also as stochastic processes due to fluctuations, we rather work with general $N(n)$ and $N^*(n)$ and not just with $N(n) = Z(\varphi)^n$ and $N^*(n) = Z(\varphi \psi^\delta)^n$. Due to the finite sizes of

both payoffs, in particular the small size of the mutant payoff, fluctuations in their values will occur. We identify the total payoffs of the incumbent and mutant with their population size. Hence the frequency $p(n)$ of the mutant is given by

$$p(n) = \frac{N^*(n)}{N^*(n) + N(n)}. \tag{2.10}$$

We assume that the mutant population is initially rare, i.e. $N^*(n) \ll N(n)$ for small n . Then $\hat{\mu}$ is an ESS if $p(n) \rightarrow 0$ as $n \rightarrow \infty$ for any mutant population.

We should emphasize at this point that this new criterion for an ESS rests critically on the assumption that population size is finite (as a condition for the use of the stochastic model), and that fitness is described by absolute population properties. We will appeal to this characterization of ESS to show that ESS are given by extremal states of entropy.

Example. We will illustrate the concepts we have introduced by a reformulation of the sex-ratio game. A complete analysis of the game will be described in Section 7.

The set of choices is given by $\Omega = \{x_1, x_2\}$, where x_1, x_2 represent the pure strategies of producing male or female offspring. Let N_1 and N_2 denote the population size in the daughter and grand daughter generation, respectively. The payoffs $\varphi(x_1)$ and $\varphi(x_2)$ are given by

$$\varphi(x_1) = \frac{p}{m} \frac{N_2}{N_1}, \quad \varphi(x_2) = \frac{1-p}{1-m} \frac{N_2}{N_1}. \tag{2.11}$$

Here m denotes the average sex ratio in the population and the ratio $p : 1 - p$ represents the distribution of male and female offsprings produced by an individual. The total net-offspring production is given by $Z(\varphi) = \varphi(x_1) + \varphi(x_2)$, hence

$$Z(\varphi) = \frac{p}{m} \frac{N_2}{N_1} + \frac{1-p}{1-m} \frac{N_2}{N_1}. \tag{2.12}$$

The state $\mu = (\mu_1, \mu_2)$ which defines demographic equilibrium is given by

$$\mu_1 = \frac{\varphi(x_1)}{Z(\varphi)}, \quad \mu_2 = \frac{\varphi(x_2)}{Z(\varphi)},$$

where $\varphi(x_1), \varphi(x_2)$ are given by (2.11) and $Z(\varphi)$ is given by (2.12). The parameters reproductive potential Φ and evolutionary entropy are defined at demographic equilibrium by

$$\Phi = \frac{p(1-m)}{p+m-2mp} \log \left(\frac{p}{m} \frac{N_2}{N_1} \right) + \frac{m(1-p)}{p+m-2mp} \log \left(\frac{1-p}{1-m} \frac{N_2}{N_1} \right), \tag{2.13}$$

$$H = - \frac{p(1-m)}{p+m-2mp} \log \frac{p(1-m)}{p+m-2mp} - \frac{m(1-p)}{p+m-2mp} \log \frac{m(1-p)}{p+m-2mp}. \tag{2.14}$$

The state $\hat{\mu} = (\hat{\mu}_1, \hat{\mu}_2)$ which defines what we call the thermodynamic equilibrium is given by an extremal state of the entropy function, defined by (2.14).

We will show that there is a unique extremum – it corresponds to the state which maximizes H . Indeed, the analysis of (2.14) will show that the maximum value of H is attained when $p = m$. This condition corresponds to the thermodynamic equilibrium,

$$\hat{\mu} = (1/2, 1/2). \quad (2.15)$$

The state defined by (2.15) is equidistributed. Accordingly, we will exploit the condition $\Phi < 0$, where Φ is defined by (2.13), to show that the equidistribution (2.15) is an ESS if and only if $N_2/N_1 = 1$, a condition which corresponds to a stationary size constraint.

These observations indicate that the $(\frac{1}{2}, \frac{1}{2})$ sex ratio can be realized in terms of a simple optimality principle, namely the maximization of evolutionary entropy.

3. Perturbation analysis

An incumbent population at demographic equilibrium is described by the mathematical object $(\Omega, \hat{\mu}, \varphi)$, where $\hat{\mu}$ denotes the demographic equilibrium which corresponds to the payoff φ . At demographic equilibrium, the population is described by the parameters r , H , Φ and σ^2 . The latter is called *demographic variance* and will be introduced shortly. The deviants derived by mutation in a small subset of the incumbent population will be assumed to be also at demographic equilibrium. This population will be represented by the object $(\Omega, \hat{\mu}_\delta, \varphi(\delta))$ for δ of small absolute value, where $\varphi(\delta)$ is a perturbation of the payoff φ and $\hat{\mu}_\delta$ the demographic equilibrium corresponding to the payoff $\varphi(\delta)$. The mutants will be described by the parameters $r(\delta)$, $H(\delta)$, $\Phi(\delta)$ and $\sigma^2(\delta)$. We will now exploit the perturbation analysis described in [13], in order to evaluate the change Δr , ΔH , $\Delta \sigma^2$ which are induced by the mutation event.

We consider mutations defined by (2.7) satisfying conditions (2.8) and (2.9). We obtain for the mutation process, for fixed ψ satisfying Eqs. (2.8) and (2.9), the new function

$$\tilde{r}(\delta) := r(\varphi\psi^\delta) = \log Z(\varphi\psi^\delta) = \log \sum_{i=1}^d e^{\log \varphi(x_i)} e^{\delta \log \psi(x_i)}. \quad (3.1)$$

This function is clearly analytic in δ and we have

$$\begin{aligned} \tilde{r}'(\delta) &= \frac{1}{Z(\varphi\psi^\delta)} \frac{d}{d\delta} Z(\varphi\psi^\delta) \\ &= \frac{1}{Z(\varphi\psi^\delta)} \sum_{i=1}^d \varphi(x_i) \psi(x_i)^\delta \log \psi(x_i) \\ &= \sum_{i=1}^d \log \psi(x_i) \hat{\mu}_\delta(x_i), \end{aligned}$$

$$\begin{aligned}
 \tilde{r}''(\delta) &= \sum_{i=1}^d \log \psi(x_i) \frac{d}{d\delta} \hat{\mu}_\delta(x_i) \\
 &= -\frac{1}{Z(\varphi\psi^\delta)^2} \left(\frac{d}{d\delta} Z(\varphi\psi^\delta) \right)^2 + \frac{1}{Z(\varphi\psi^\delta)} \frac{d^2}{d\delta^2} Z(\varphi\psi^\delta) \\
 &= -\frac{1}{Z(\varphi\psi^\delta)^2} \sum_{i=1}^d \varphi(x_i)\psi(x_i)^\delta \log \psi(x_i) \sum_{k=1}^d \varphi(x_k)\psi(x_k)^\delta \log \psi(x_k) \\
 &\quad + \frac{1}{Z(\varphi\psi^\delta)} \sum_{i=1}^d \varphi(x_i)\psi(x_i)^\delta (\log \psi(x_i))^2 \\
 &= -\left(\sum_{i=1}^d \log \psi(x_i) \hat{\mu}_\delta(x_i) \right)^2 + \sum_{i=1}^d (\log \psi(x_i))^2 \hat{\mu}_\delta(x_i), \\
 \tilde{r}'''(\delta) &= \frac{2}{Z(\varphi\psi^\delta)^3} \left(\frac{d}{d\delta} Z(\varphi\psi^\delta) \right)^3 - 3 \frac{1}{Z(\varphi\psi^\delta)^2} \left(\frac{d}{d\delta} Z(\varphi\psi^\delta) \right) \left(\frac{d^2}{d\delta^2} Z(\varphi\psi^\delta) \right) + \frac{1}{Z(\varphi\psi^\delta)} \frac{d^3}{d\delta^3} Z(\varphi\psi^\delta) \\
 &= 2 \left(\sum_{i=1}^d \log \psi(x_i) \hat{\mu}_\delta(x_i) \right)^3 - 3 \sum_{i=1}^d \log \psi(x_i) \hat{\mu}_\delta(x_i) \sum_{k=1}^d (\log \psi(x_k))^2 \hat{\mu}_\delta(x_k) \\
 &\quad + \sum_{i=1}^d (\log \psi(x_i))^3 \hat{\mu}_\delta(x_i),
 \end{aligned}$$

in particular

$$\tilde{r}'(0) = \frac{1}{Z(\varphi)} \sum_{i=1}^d \varphi(x_i) \log \psi(x_i) = \int \log \psi \, d\hat{\mu}, \tag{3.2}$$

where $\hat{\mu}$ is the demographic equilibrium state for φ . We note that when $\varphi = \psi$, then we have

$$r'(0) = \int \log \varphi \, d\hat{\mu}. \tag{3.3}$$

Furthermore,

$$\begin{aligned}
 \tilde{r}''(0) &= \int (\log \psi)^2 \, d\hat{\mu} - \left(\int \log \psi \, d\hat{\mu} \right)^2 \\
 &= \int \left(\log \psi - \int \log \psi \, d\hat{\mu} \right)^2 \, d\hat{\mu} =: \sigma^2(\psi) \geq 0.
 \end{aligned} \tag{3.4}$$

Analogously, it follows that

$$\begin{aligned}
 \tilde{r}'''(0) &= 2 \left(\int \log \psi \, d\hat{\mu} \right)^3 - 3 \int (\log \psi)^2 \, d\hat{\mu} \int \log \psi \, d\hat{\mu} + \int (\log \psi)^3 \, d\hat{\mu} \\
 &= \int \left(\log \psi - \int \log \psi \, d\hat{\mu} \right)^3 \, d\hat{\mu} =: \kappa(\psi).
 \end{aligned} \tag{3.5}$$

Note that from the variational principle (2.3) and (3.1) we can deduce that $\tilde{r}(\delta) = H(\mu_\delta) + \mu_\delta(\log(\varphi\psi^\delta))$, i.e.

$$\tilde{r}(\delta) = H(\mu_\delta) + \mu_\delta(\log \varphi) + \delta\mu_\delta(\log \psi)$$

and hence

$$\tilde{r}'(0) = H'(\hat{\mu}) + \frac{d}{d\delta}\mu_\delta(\log \varphi)|_{\delta=0} + \hat{\mu}(\log \psi). \quad (3.6)$$

Comparing (3.2) and (3.6) we obtain

$$H'(\hat{\mu}) = -\frac{d}{d\delta}\mu_\delta(\log \varphi)|_{\delta=0}$$

and consequently

$$\frac{\partial^2}{\partial \varepsilon \partial \delta} r(\varphi^{1+\varepsilon}\psi^\delta)|_{\varepsilon=\delta=0} = \frac{d}{d\delta}\mu_\delta(\log \varphi)|_{\delta=0} = -H'(\hat{\mu}). \quad (3.7)$$

Let us remark that $\sigma^2(\psi)$, as defined in (3.4), is the variance of the random variable $\log \psi$ with respect to the equilibrium state $\hat{\mu}$ for φ .

We note that

$$\sigma^2(\varphi) = \int (\log \varphi)^2 d\hat{\mu} - \left(\int \log \varphi d\hat{\mu} \right)^2 \quad (3.8)$$

and we have $\sigma^2(\varphi) = 0 \iff H = 0$ or $H = H_{\max}$, where H_{\max} denotes the maximal entropy given by $\log d$ and realized by the equidistribution (see for example [21, Corollary 4.2.1]). We call $\sigma^2(\varphi)$ the *demographic variance of the strategy* μ , and for fixed φ we denote by $\sigma^2(\delta)$ the demographic variance of the equilibrium state μ_δ for $\varphi^{1+\delta}$. Note that

$$\sigma^2(\delta) = (1 + \delta)^2 \left[\int (\log \varphi)^2 d\hat{\mu}_\delta - \left(\int \log \varphi d\hat{\mu}_\delta \right)^2 \right].$$

So, if we choose $\psi = \varphi$, then

$$\sigma^2(\delta) = (1 + \delta)^2 \tilde{r}''(\delta)$$

and therefore we obtain via differentiation with the help of (3.5) that

$$\frac{d\sigma^2}{d\delta}(0) = 2\sigma^2(\varphi) + \kappa(\varphi) =: \gamma. \quad (3.9)$$

Moreover we deduce from (3.7) that

$$\sigma^2 := \sigma^2(0) = r''(0) = H'(\hat{\mu}). \quad (3.10)$$

We call γ given by (3.9) the *correlation index* of the strategy. The parameter γ is a measure of the correlation with respect to the different strategy classes of the net-payoff function. This quantity γ is 0 for both pure strategies and equidistributed mixed strategies.

So, for δ of small absolute value we have the following approximations by the linearizations (3.3), (3.9) and (3.10):

$$\Delta r \approx \Phi \delta, \quad \Delta H \approx -\sigma^2 \delta, \quad \Delta \sigma^2 \approx \gamma \delta.$$

In particular, we obtain for δ of small absolute value the following so-called *mutation relations*:

$$\Phi < 0 \Rightarrow \Delta r \Delta H > 0, \quad (3.11)$$

$$\Phi > 0 \Rightarrow \Delta r \Delta H < 0, \quad (3.12)$$

$$\gamma < 0 \Rightarrow \Delta H \Delta \sigma^2 > 0, \quad (3.13)$$

$$\gamma > 0 \Rightarrow \Delta H \Delta \sigma^2 < 0. \quad (3.14)$$

Let us remark that in contrast to σ^2 , which is always non-negative, γ can assume negative and positive values.

We will illustrate the values assumed by H , σ^2 and γ with an example which will play an important role in the analysis of the sex-ratio model, namely any two-option game with strategies $\mu = (p, 1-p)$ for $p \in (0, 1)$ and normalized payoffs, i.e. $\varphi = \mu$. It can easily be checked that the normalization $\varphi(x_i) \mapsto \varphi(x_i)/(\varphi(x_1) + \varphi(x_2))$, $i = 1, 2$ can be done without loss of generality, as this procedure does not change the quantities of interest.

Any way, in this (and thus in the general two-option game) case we have

$$H = -p \log p - (1-p) \log(1-p),$$

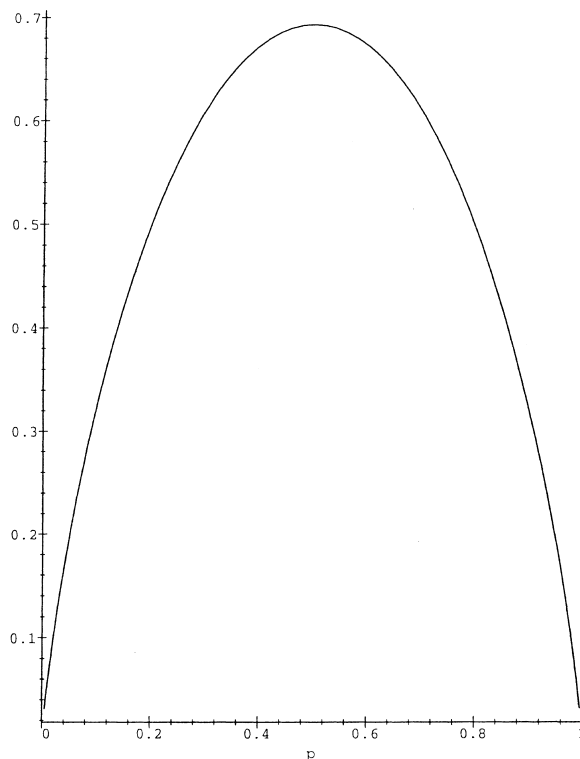


Fig. 1. Entropy for two-option games.

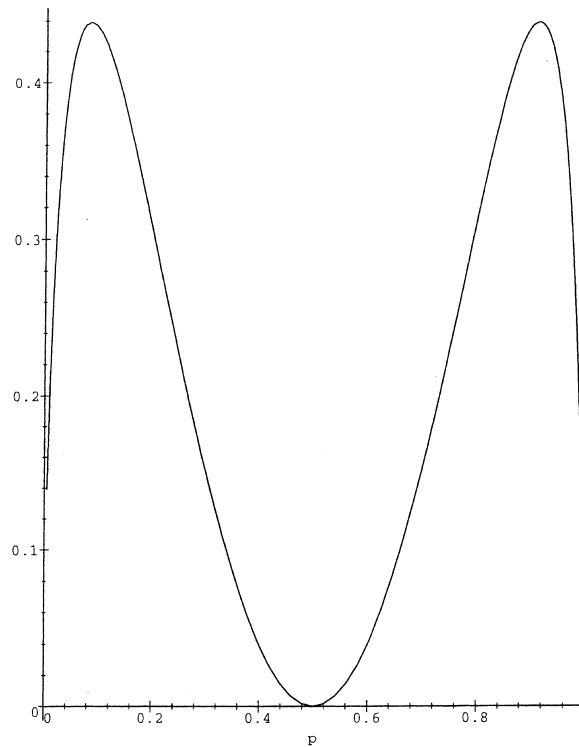


Fig. 2. Demographic variance for two-option games.

$$\sigma^2 = (1-p)p \left(\log \frac{p}{1-p} \right)^2,$$

$$\gamma = (1-p)p \left(\log \frac{p}{1-p} \right)^2 \left[2 + (1-2p) \log \frac{p}{1-p} \right].$$

Fig. 1 shows the population entropy for a two-option game as a function of p , while Fig. 2 presents the demographic variance and Fig. 3 the evolutionary index as a function of p .

4. Evolutionarily stable strategies: characterization

In this section we derive necessary and sufficient conditions for the existence of an ESS. Our analysis revolves around the assumption that population sizes are finite and the idea that owing to statistical fluctuations the quantities $N(n)$ and $N^*(n)$ described in Section 2 are random variables. Consequently, invasion of the mutant strategy will be a stochastic event.

Our treatment of this stochastic analysis invokes three elements:

1. An investigation of $N(n)$ on the microscopic level by studying sample paths and stochastic processes;

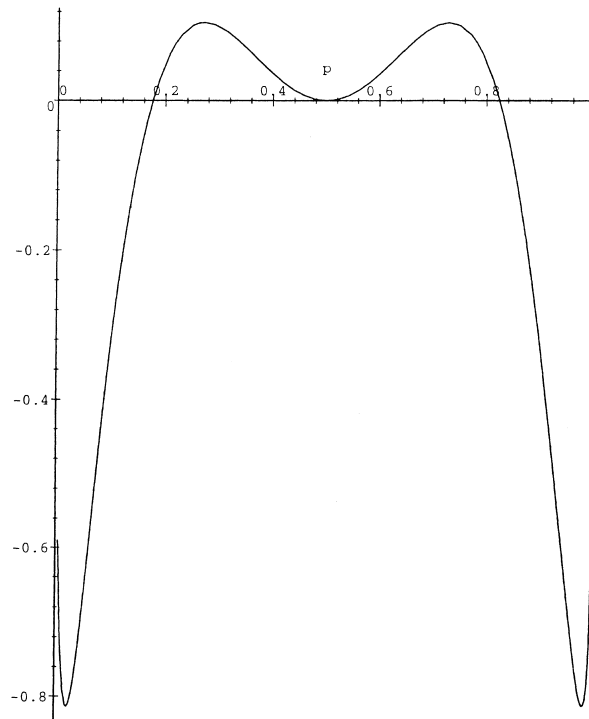


Fig. 3. Correlation index for two-option games.

2. The introduction of a stochastic model for $N(n)$ induced by fluctuations caused by the stochastic behavior on the microscopic level and the approximation of the probability density function of $N(n)$ in terms of solutions of diffusion equations.
3. A study of the invasion–extinction dynamics of the mutant strategy in terms of a pair of coupled Fokker–Planck equations.

The effect of statistical fluctuations due to finite population size has an extensive literature which goes back to the pioneering studies of Wright and Fisher, see for example [22,23] and the review article by Feller [24]. For other developments which invoke the Fokker–Planck equation we refer to [25–27].

Statistical fluctuations in population numbers have two main sources:

1. *Demographic stochasticity*. Sampling effects due to the condition of finite size. This randomness arises because of chance realizations of individual probabilities of birth and death. Since independent individual events tend to average out in large populations, the effects of demographic stochasticity decreases with increasing population size.
2. *Environmental stochasticity*. Randomness in the case is ascribable to temporal environmental changes. The magnitude of the population fluctuations induced is set by the degree of environmental variance, independent of the absolute population size.

Each of these mechanisms engender different kinds of variance of the fluctuations induced. Hence, although the Fokker–Planck equations which emerge from the models describing the different

mechanisms are formally similar, the parameter spaces in which they operate are unique to the model system investigated.

In the studies we undertake, the stochasticity derives from sampling effects due to finite size. Thus our description can be subsumed under demographic stochasticity. The variance which this stochasticity generates will be given by what we call the demographic variance as expressed by (3.4).

Fluctuations induced by demographic stochasticity is analogous to the internal variations observed in certain physical processes and our analysis in Section 4.1 draws from the ideas reviewed in [28]. The development in Sections 4.2 and 4.3 has analogues in the work of Feller [24] and Gillespie [25] who analyzed related models.

Feller's work gives a general review of diffusion theory in genetics and studies in particular a two-dimensional branching process as a genetic model. Our formulation in Section 4.2, in particular, is inspired by this work. Gillespie [25] exploited Feller's ideas to analyze the dynamics of selection in finite populations. The expressions we derive in Section 4.3 have their analogues in [25]. The mathematical models, however, are quite distinct. Our models are game theoretic systems with individuals adopting mixed strategies. The variance in these systems corresponds to demographic variance, as defined by (3.8); growth rate refers to the asymptotic rate of increase of the total payoff as defined by (2.1). The models described in [25] are Wright–Fisher models in population genetics. The variance parameter refers to the variance in the number of offspring of a given genotype; the growth rate parameter pertains to the mean number of offspring.

4.1. Microscopic analysis of payoff and growth rate

Let us recall the definition of the total payoff up to time n as

$$N(n) = Z(\varphi)^n = \sum_{i_1, \dots, i_n=1}^d \varphi(x_{i_1})\varphi(x_{i_2}) \cdots \varphi(x_{i_n}).$$

Thus $N(n)$ consists of all possible payoffs for options played in n consecutive games. Since there exist d^n different options for such n games, it might become intractable to describe them completely. As in statistical mechanics we can give up this microscopic description and work with macroscopic quantities which can be obtained by a probabilistic description of the single payoffs. The natural probabilistic description of our situation is guaranteed by the use of the equilibrium strategy μ . The n th product of μ defines a probability measure on Ω^n equipped with its power-set as σ -algebra and the n th product of φ becomes a random variable on that probability space.

Now let us note that with respect to μ the function $\log \varphi$ also defines a random variable with finite state space and with mean Φ and variance σ^2 according to the last section. So, let us consider the n th partial sum of independent and identically distributed (namely according to μ) random variables $Y_i := \log \varphi$ and denote it by S_n . This defines a sample path $S_n : \Omega^n \rightarrow \mathbb{R}$ of length n for $\log \varphi$, the time mean ($n \rightarrow \infty$) of which tends to Φ by the ergodic theorem for almost all $x \in \Omega^{\mathbb{N}}$ with respect to the product measure \mathbb{P} of μ on $\Omega^{\mathbb{N}}$. To the time fluctuations $(1/n)S_n - \Phi$ we can apply the *central limit theorem* to obtain that

$$\lim_{n \rightarrow \infty} \mathbb{P} \left\{ \frac{S_n - n\Phi}{\sigma\sqrt{n}} \leq x \right\} = \mathcal{N}(x), \tag{4.1}$$

where \mathcal{N} denotes the standard normal distribution. If we define a family of stochastic processes by

$$X_n(t) = \frac{S_{[nt]} - [nt]\Phi}{\sqrt{n}},$$

where $[\cdot]$ denotes the Gauß bracket, then it is known (see for example [29, 7.3]) that X_n converges in distribution as $n \rightarrow \infty$ to Brownian motion X with variance σ^2 .

Thus we can conclude that asymptotically the deviations of the sample path S_n from the mean for $n \rightarrow \infty$ for \mathbb{P} – almost all $x \in \Omega^{\mathbb{N}}$ can be approximated by Brownian motion with variance $\sigma^2 t$, if we consider a continuous time evolution $S_t, t \in \mathbb{R}_+$. In the following we will adopt this continuous time approximation.

4.2. The diffusion equation

We have just seen that our deterministic model is related to certain stochastic processes on a microscopic level. Due to our assumptions that population sizes are finite and fitness is described by absolute measures, fluctuations should also be present at the macroscopic level. Therefore, it is more realistic to replace the deterministic model given by $N(n) = Z(\varphi)^n$ by a stochastic one, which in fact is not a diffusion approximation, but makes use of the results of our approximations and yields the deterministic model for infinite population size. Though it might be a bit confusing, we will denote the new stochastic process by $N(t)$ and the old deterministic system by $N(n)$.

On the basis of the last section we could think of $N(n) = Z(\varphi)^n$ as a quantity built out of random variables (according to the equilibrium state $\hat{\mu}$) asymptotically fluctuating around a mean value approximately like a Brownian particle. We assume that these internal fluctuations on the microscopic level cause fluctuations of the same stochastic nature on the macroscopic level thus transforming the total payoff in a stochastic process. Since we made a continuous time approximation of the fluctuations, we could also describe the time evolution of $N(n)$ into a continuous process. As the time-one mapping of the differential equation

$$\frac{dN}{dt} = r(\varphi)N, \quad N(0) = 1$$

yields $N(n) = Z(\varphi)^n$ and since we assume that the fluctuations should have mean 0, we obtain for the resulting stochastic process $N(t)$

$$\lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} \mathbb{E}\{N(t + \Delta t) - N(t) | N(t) = N\} = r(\varphi)N,$$

where we denote by \mathbb{E} the expectation induced by μ . This gives the first infinitesimal moment of the process. In order to derive the second infinitesimal moment of the process we have to specify the intensity of the variance of the fluctuations. As the influence of microscopical fluctuation on the macroscopic level decreases with the size $N(t)$, we assume according to the central limit result of the last section that the change in $\log N(t)$ in the time interval Δt due to fluctuations is caused by Brownian motion with variance $\sigma^2(\varphi)\Delta t/N(t)$ being a non-trivial function of time. This form of

the variance also guarantees that for infinite population size the process $N(t)$ is just the continuous time version of $N(n)$. Thus we obtain for the second infinitesimal moment of the process

$$\lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} \mathbb{E}\{(N(t + \Delta t) - N(t))^2 | N(t) = N\} = N^2 \lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} \frac{\sigma^2 \Delta t}{N} = \sigma^2 N.$$

Consequently we can deduce from [30, II] that the solution of the Fokker–Planck equation

$$\frac{\partial f}{\partial t} = -r \frac{\partial(fN)}{\partial N} + \frac{\sigma^2}{2} \frac{\partial^2(fN)}{\partial N^2}$$

yields the density $f(N, t)$ for the process $N(t)$, which can be viewed as the solution of the stochastic differential equation

$$dN = rN dt + \sigma\sqrt{N} dW_t.$$

Note that we could also describe the evolution of $N^*(n)$ corresponding to the mutant population in an analogous way. Indeed, the density $f^*(N^*, t)$ for the process $N^*(t)$ becomes

$$\frac{\partial f^*}{\partial t} = -r \frac{\partial(f^*N^*)}{\partial N^*} + \frac{\sigma^{*2}}{2} \frac{\partial^2(f^*N^*)}{\partial N^{*2}}.$$

It will be our goal to compare the stochastic processes $N(t)$ and $N^*(t)$, in particular we want to analyze the process $p(t) = N^*(t)/(N(t) + N^*(t))$. The result will in general be different from the one derived from a deterministic approach, where the limit of $p(t)$ as $t \rightarrow \infty$ can be completely determined in terms of Δr and hence Φ only. In the deterministic approach, the selective advantage is evidently given by

$$s = \Delta r.$$

As we have argued before, such a deterministic consideration would have to be based on infinite population size (for $t \rightarrow \infty$) and would not take care of fluctuations, which should be present. In the stochastic representation, size is finite and the selective advantage will be shown to be determined by

$$s = \Delta r - \frac{1}{M} \Delta \sigma^2,$$

where $M = N + N^*$, the total population size.

We note that when M tends to ∞ , the selective advantage for the stochastic representation coincides with that for the deterministic representation. Moreover, our stochastic process would coincide for discrete time with the original deterministic system, if the population size were infinite. Therefore we propose that the more suitable process to consider for evolutionary phenomena is the stochastic one, which is not a diffusion approximation of the original system anymore, but which presents in our view an improved model for the evolutionary dynamics of interest.

4.3. The invasion condition

We are looking now at the stochastic model just developed and consider the evolutionary dynamics of the mutant and incumbent populations when the mutant is rare. During this phase,

the numbers N and N^* of the incumbent and mutant population are assumed to be separately regulated. Let $\psi(N, N^*, t)$ denote the bivariate density of the pair $(N(t), N^*(t))$. Invoking the statistical independence condition, it follows that the density ψ is given by $\psi(N, N^*, t) = f(N, t)f^*(N^*, t)$, where f^* is the density function corresponding to the mutant population. Since $f(N, t)$ and $f^*(N^*, t)$ are solutions of Fokker–Planck equations, we have that ψ satisfies the equation

$$\frac{\partial \psi}{\partial t} = -r \frac{\partial(\psi N)}{\partial N} + \frac{\sigma^2}{2} \frac{\partial^2(\psi N)}{\partial N^2} - r^* \frac{\partial(\psi N^*)}{\partial N^*} + \frac{\sigma^{*2}}{2} \frac{\partial^2(\psi N^*)}{\partial N^{*2}}.$$

Recalling (2.10) and defining $M(t) = N(t) + N^*(t)$, we obtain

$$\frac{\partial \psi}{\partial t} = -\frac{\partial[\alpha(p, M)\psi]}{\partial p} + \frac{1}{2} \frac{\partial^2[\beta(p, M)\psi]}{\partial p^2} - \frac{\partial[\zeta(p, M)\psi]}{\partial M} + \frac{1}{2} \frac{\partial^2[\delta(p, M)\psi]}{\partial M^2} + \frac{\partial^2[\Omega(p, M)\psi]}{\partial p \partial M},$$

where

$$\alpha(p, M) = p(1 - p) \left[\Delta r - \frac{1}{M} \Delta \sigma^2 \right], \tag{4.2}$$

$$\beta(p, M) = \frac{p(1 - p)}{M} [\sigma^2 p + \sigma^{*2}(1 - p)], \tag{4.3}$$

$$\zeta(p, M) = M[pr^* + (1 - p)r],$$

$$\delta(p, M) = M(p\sigma^{*2} + (1 - p)\sigma^2),$$

$$\Omega(p, M) = p(1 - p)\Delta\sigma^2.$$

We are mainly interested in the problem of invasion or extinction of the mutant population. This decision is taken for small $N^* \ll M$ and N close to equilibrium. Consequently, the changes in N^* and N will be very small and mainly at the expense of the other. This implies that the changes in M will be negligibly small, in particular in effecting the result of the invasion–extinction problem. Thus we restrict our attention to the case where we can neglect the derivatives of ψ with respect to M . We set $\alpha(p, M) \equiv \alpha(p)$, $\beta(p, M) \equiv \beta(p)$, and now consider

$$\frac{\partial \psi}{\partial t} = -\frac{\partial[\alpha(p)\psi]}{\partial p} + \frac{1}{2} \frac{\partial^2[\beta(p)\psi]}{\partial p^2}. \tag{4.4}$$

The problem of extinction–fixation can be analyzed by considering the Kolmogorov backward equation

$$\frac{\partial \psi}{\partial t} = \alpha(p) \frac{\partial \psi}{\partial t} + \frac{1}{2} \beta(p) \frac{\partial^2 \psi}{\partial p^2}$$

with the boundary conditions

$$\psi(0, t) = 1, \quad \psi(1, t) = 0.$$

Let $P(y)$ denote the ultimate probability that the mutant becomes extinct, when y denotes the initial frequency of the mutant, i.e. $P(y) = \lim_{t \rightarrow \infty} \psi(y, t)$. Then $P(y)$ satisfies the ordinary differential equation

$$\alpha(y) \frac{dP}{dy} + \frac{1}{2} \beta(y) \frac{d^2P}{dy^2} = 0 \quad (4.5)$$

with boundary conditions $P(0) = 1$, $P(1) = 0$. Write

$$G(x) = \exp \left[-2 \int_0^x \frac{\alpha(y)}{\beta(y)} dy \right].$$

Then, from (4.5), we obtain

$$P(y) = \frac{\int_y^1 G(x) dx}{\int_0^1 G(x) dx}.$$

Write

$$s = \Delta r - \frac{1}{M} \Delta \sigma^2. \quad (4.6)$$

Then using the expressions for $\alpha(p)$ and $\beta(p)$ given in (4.2) and (4.3), $G(x)$ becomes

$$G(x) = \left[1 - \frac{\Delta \sigma^2}{\sigma^{*2}} x \right]^{2Ms/\Delta \sigma^2}$$

and hence

$$P(y) = \left(1 - \frac{\Delta \sigma^2}{\sigma^{*2}} \right)^{(2Ms/\Delta \sigma^2)+1} - \left(1 - \frac{\Delta \sigma^2}{\sigma^{*2}} y \right)^{(2Ms/\Delta \sigma^2)+1} \bigg/ \left(1 - \frac{\Delta \sigma^2}{\sigma^{*2}} \right)^{(2Ms/\Delta \sigma^2)+1} - 1. \quad (4.7)$$

In order to determine the shape of this function, we take a look at the derivatives

$$P'(y) = \frac{\Delta \sigma^2}{\sigma^{*2}} \left(\frac{2Ms}{\Delta \sigma^2} + 1 \right) \left(1 - \frac{\Delta \sigma^2}{\sigma^{*2}} y \right)^{2Ms/\Delta \sigma^2} \bigg/ \left(1 - \frac{\Delta \sigma^2}{\sigma^{*2}} \right)^{(2Ms/\Delta \sigma^2)+1} - 1,$$

$$P''(y) = - \left(\frac{\Delta \sigma^2}{\sigma^{*2}} \right)^2 \left(\frac{2Ms}{\Delta \sigma^2} + 1 \right) \frac{2Ms}{\Delta \sigma^2} \left(1 - \frac{\Delta \sigma^2}{\sigma^{*2}} y \right)^{(2Ms/\Delta \sigma^2)-1} \bigg/ \left(1 - \frac{\Delta \sigma^2}{\sigma^{*2}} \right)^{(2Ms/\Delta \sigma^2)+1} - 1.$$

Except in the degenerate – and for large M unusual – case of $2Ms/\Delta \sigma^2 = -1$, $P'(y)$ cannot vanish, hence must be negative. In this situation the numerator of $P''(y)$ is always negative, while the denominator is negative for $s > 0$ and positive for $s < 0$. Thus we can conclude the following:

$$s > 0 \Rightarrow P \text{ is convex,}$$

$$s < 0 \Rightarrow P \text{ is concave.}$$

The degree of curvature of P depends on the magnitude of s , i.e. on the values of Δr , $\Delta \sigma^2$ and M , as can be seen from the following graphs, obtained by numerical calculation for some suitable choices of $\Delta \sigma^2/\sigma^{*2}$ and $M_s/\Delta \sigma^2$ and showing the dependence of $P(y)$, the ultimate probability that the mutant becomes extinct, on y , the initial frequency of the mutant.

If $\Delta r \Delta \sigma^2 < 0$, then the sign of s does not depend on M and a reasonable large M leads to an exponent $b := (2Ms/\Delta\sigma^2) + 1 = (2M\Delta r/\Delta\sigma^2) - 1$ sufficiently small to cause the extreme shape shown in Fig. 4. If $\Delta r > 0$, $\Delta\sigma^2 > 0$, we have to distinguish two cases: for $\Delta r > \Delta\sigma^2/M$ we have $s > 0$ with exponent b sufficiently large for reasonable M leading to the extreme shape shown in Fig. 5(a), while for $\Delta r < \Delta\sigma^2/M$ we have $s < 0$ with an exponent that increases in M and hence leads to a probability which is an increasing function of M (cf. Fig. 5(b)). If $\Delta r < 0$, $\Delta\sigma^2 < 0$ (cf. Fig. 6), we have to distinguish two analogous cases leading to the following assertions about the extinction–invasion phenomenon for populations of a size M :

1. $\Delta r > 0$, $\Delta\sigma^2 < 0$: the mutant invades almost surely.
 2. $\Delta r < 0$, $\Delta\sigma^2 > 0$: the mutant becomes extinct almost surely.
 3. $\Delta r > 0$, $\Delta\sigma^2 > 0$:
 - $M > \Delta\sigma^2/\Delta r \approx \gamma/\Phi$: the mutant invades almost surely,
 - $M < \Delta\sigma^2/\Delta r \approx \gamma/\Phi$: the mutant becomes extinct with a probability which decreases as M increases.
 4. $\Delta r < 0$, $\Delta\sigma^2 < 0$:
 - $M > \Delta\sigma^2/\Delta r \approx \gamma/\Phi$: the mutant becomes extinct almost surely,
 - $M < \Delta\sigma^2/\Delta r \approx \gamma/\Phi$: the mutant invades with a probability which increases as M increases.
- We can deduce from (4.6) that for finite population size M invasion can be excluded if

$$\Delta r < 0, \Delta\sigma^2 \geq 0 \quad \text{or} \quad \Delta r \leq 0, \Delta\sigma^2 > 0 \tag{4.8}$$

with respect to any mutant strategy. We will in Section 4.4, exploit the mutation relations given in Section 3 to show that the criteria (4.8) can be characterized in terms of the extremal states of entropy.

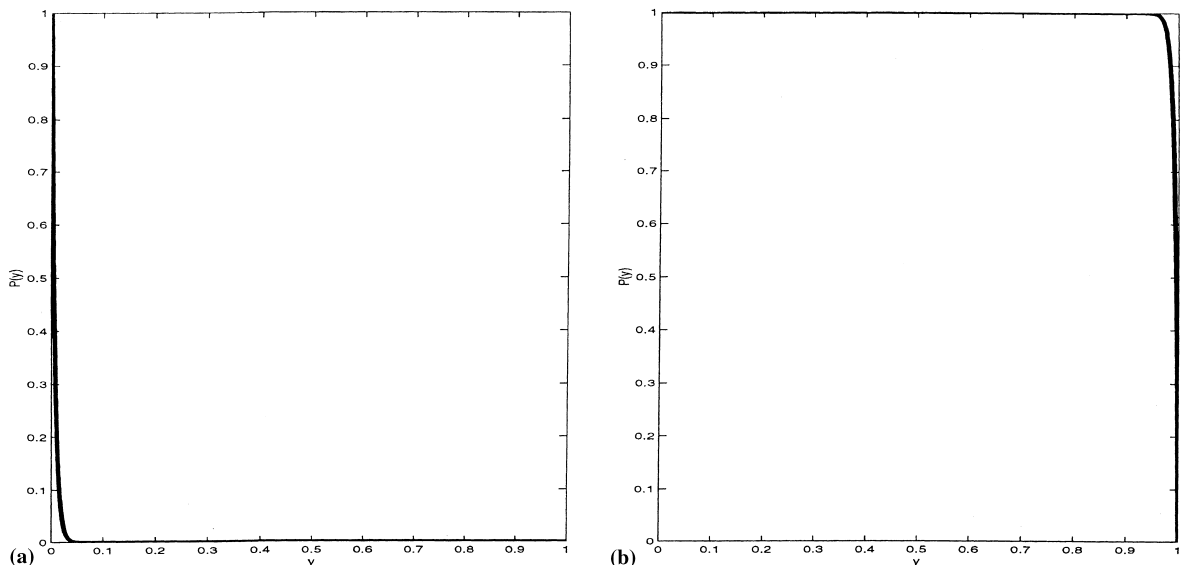


Fig. 4. (a) $\Delta r > 0$, $\Delta\sigma^2 < 0$ and (b) $\Delta r < 0$, $\Delta\sigma^2 > 0$.

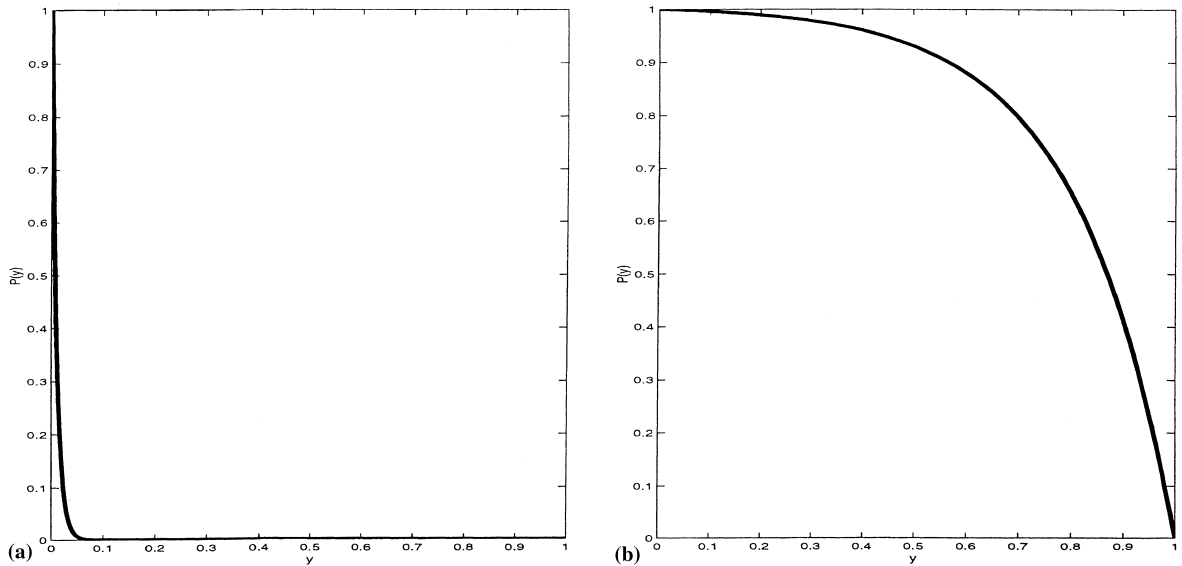


Fig. 5. $\Delta r > 0$, $\Delta\sigma^2 > 0$ and (a) $M > \Delta\sigma^2/\Delta r$, (b) $M < \Delta\sigma^2/\Delta r$.

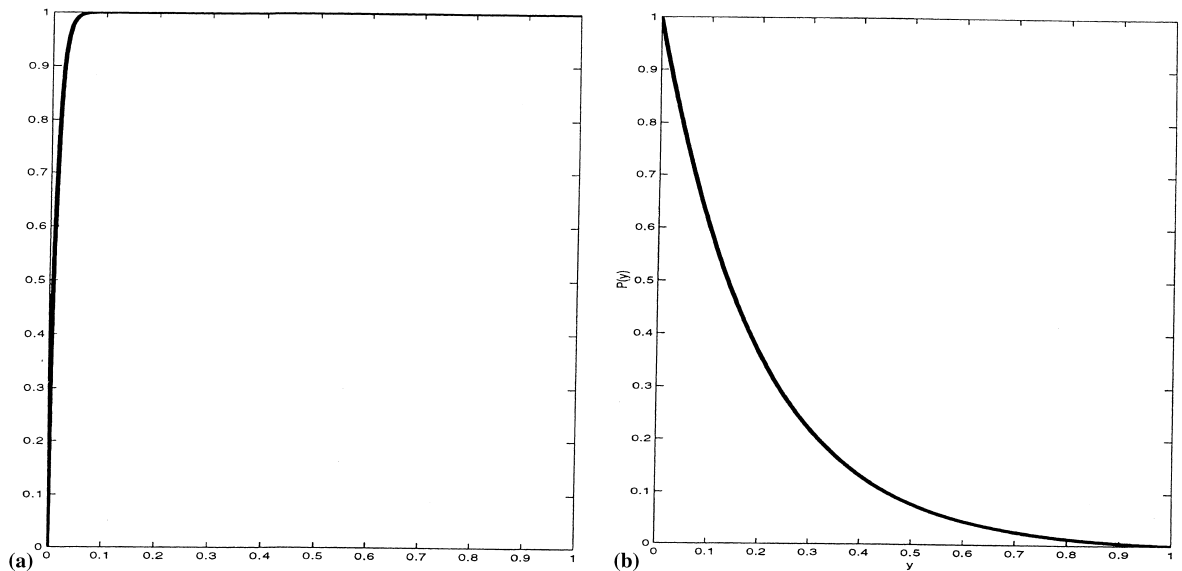


Fig. 6. $\Delta r < 0$, $\Delta\sigma^2 < 0$ and (a) $M > \Delta\sigma^2/\Delta r$, (b) $M < \Delta\sigma^2/\Delta r$.

4.4. ESS as extremal states of entropy

We recall that a strategy is an ESS if it is invulnerable to invasion by any deviant strategy. We have seen that such an ESS is guaranteed under condition (4.8) with respect to any mutant strategy. We can specify such situations as follows.

Proposition 4.1. *Relations (4.8) can hold only for any deviant strategy if and only if one of the following two cases occurs:*

- (i) $\Phi < 0$, $\gamma \geq 0$ or $\Phi \leq 0$, $\gamma > 0$,
- (ii) $\Phi > 0$, $\gamma \leq 0$ or $\Phi \geq 0$, $\gamma < 0$.

In the first case (4.8) is equivalent to $\Delta H \leq 0$, in the second to $\Delta H \geq 0$.

Proof. We recall from (3.11) and (3.12) that $\Phi < 0$ implies $\Delta r \Delta H > 0$; and $\Phi > 0$ implies $\Delta r \Delta H < 0$. We also recall from (3.13) and (3.14) that $\gamma < 0$ entails $\Delta H \Delta \sigma^2 > 0$ and $\gamma > 0$ implies $\Delta H \Delta \sigma^2 < 0$. Hence in the case $\Phi < 0$ we have that $\Delta r < 0$ implies $\Delta H \leq 0$. In addition, when $\gamma \geq 0$, we have that $\Delta \sigma^2 \geq 0$ implies $\Delta H \leq 0$. Analogously it follows that in the case of $\Phi > 0$ we have $\Delta r < 0$ entails $\Delta H \geq 0$; and when $\gamma < 0$, we observe that $\Delta \sigma^2 \geq 0$ implies $\Delta H \geq 0$. We also get the respective assertions if we start with the strict inequalities for γ . Hence when (i) holds, (4.8) is equivalent to $\Delta H \leq 0$, and when (ii) holds, (4.8) is equivalent to $\Delta H \geq 0$. \square

This proposition provides not only a nice characterization of ESS, but also a necessary condition for them. Since the conditions $\Delta H \leq 0$ and $\Delta H \geq 0$ assert that the incumbent strategies correspond to maximum and minimum states of entropy, respectively, we immediately obtain from Proposition 4.1 the following result.

Theorem 4.2. *ESS are described by extremal states of entropy.*

Hence every ESS is an extremal state of entropy. However not all extremal states are ESS. In order to delineate the class of extremal states which are ESS, we need to examine the stability criteria as described by the parameters Φ and γ .

5. Evolutionarily stable strategies: existence

We have managed so far to derive a characterization of possible ESS by appealing to entropy. We will now make use of this characterization to obtain an existence result, i.e. conditions for the existence of an evolutionary stable strategy. In deriving these existence criteria we note that evolutionary entropy H is bounded from below and from above, and strategies, where H attains its maximum and minima are well characterized (see for example [21, Corollary 4.2.1]).

Lemma 5.1. *For a set Ω of d choices every game (Ω, μ, φ) satisfies $H(\mu) \leq \log d$, and*

- (i) $H(\mu) = \log d$ if and only if $\mu_i = 1/d$ for all $i = 1, \dots, d$, i.e. μ is the equidistribution,
- (ii) $H(\mu) = 0$ if and only if $\mu_i = 0$ for all $i = 1, \dots, d$ except one j with $\mu_j = 1$, i.e. μ is a pure strategy.

This lemma yields a pre-selection for ESS. Due to constraints some of these candidates for an ESS cannot be realized and have to be replaced by points on the boundary of the set \mathcal{M}_c of possible strategies. Thus we can immediately deduce the following result.

Proposition 5.2. *If there are no constraints on the payoffs the only possible candidates for an ESS are the pure strategies and the equidistribution. In case of constraints excluding any of these candidates, these have to be replaced by strategies which maximize or, respectively, minimize entropy and which necessarily have to lie on the boundary of the set \mathcal{M}_c of admissible strategies.*

We know that the evolutionary stable strategies form a subset of the three extremal strategies: the unique global maximum, the global minima, and the local extrema. This third situation arises when certain constraints on the payoff function obtain. Our existence result can now be expressed in terms of the following theorems.

Theorem 5.3. *The equidistribution on Ω is an ESS if and only if it satisfies $\Phi < 0$.*

The equidistribution constitutes the global maximum. The condition $\Phi < 0$ simply expresses a stability condition. The equidistribution satisfies $\gamma = 0$ – a property which implies that there exists no correlation between the strategy classes and the net-payoff function.

Theorem 5.4. *A pure strategy is an ESS if and only if it satisfies $\Phi > 0$.*

Pure strategies represent global minima: the relation $\Phi > 0$ expresses a stability criterion. Pure strategies also satisfy the condition $\gamma = 0$, which, as we observed, defines the case where the strategy classes and net-payoff function are uncorrelated.

Theorem 5.5. *In the case of constraints, a local maximum can replace the excluded global maximum if and only if*

$$\Phi < 0, \quad \gamma > 0,$$

and a local minimum can replace an excluded global minimum if and only if

$$\Phi > 0, \quad \gamma < 0,$$

Non-equidistributed mixed strategies can represent local maxima or minima: since these extremal states are local, the index γ which describes the stability property may have arbitrary sign. In the case of a local maximum, the condition $\gamma < 0$ describes a negative correlation between the strategy classes and the net-payoff function, the condition $\gamma > 0$ represents a positive correlation.

At first sight, the result of Theorem 4.2 might not look very interesting, as it yields rather strange looking ESS. This is due to the formal character of our approach, in particular the general setup of our games. In general, our ESS contain implicitly more conventional information about the evolutionarily stable strategy, in particular if there exist constraints for the payoffs, a situation described by the condition $\gamma \neq 0$. We are going to illustrate this in the analysis of two well-studied games, see Section 7.

6. Games within populations, Games against Nature: a contrast

It is of some interest at this point to contrast the classical models based on games within populations with the new class of models based on Games against Nature developed in this paper.

6.1. Games within populations: infinite size, relative fitness

The models proposed by Maynard Smith and Price [1] are concerned with pairwise conflicts within a population. The game can be described in terms of a set of options $\Omega = \{x_1, \dots, x_d\}$. The state of the population is described by the vector $p = (p_i)$, where p_i is the frequency of i -strategists. If an i -strategist contends with a j -strategist in a pairwise conflict, the payoff to the former is a_{ij} , where a_{ij} is measured in terms of an increase in fitness (the expected number of surviving offspring). An i -strategist will encounter a j -strategist with frequency p_j and then receive a payoff a_{ij} . The expected payoff to the i -strategist is $\sum_{j=1}^d a_{ij}p_j$. The expected payoff to a population $p = (p_i)$ against itself is

$$E(p, p) = \sum_{i,j} p_i a_{ij} p_j.$$

The expected payoff to population $q = (q_i)$ against $p = (p_i)$ is

$$E(q, p) = \sum_{i,j} q_i a_{ij} p_j.$$

A state p is said to be an ESS if, when all individuals in the population adopt this strategy, no mutant can invade. To characterize this analytically, we consider a population consisting mainly of individuals playing strategy p , with a small frequency ε of some mutants playing an alternative strategy p^* . The fitness of the population of incumbents $W(p)$ is given by

$$W(p) = (1 - \varepsilon)E(p, p) + \varepsilon E(p, p^*).$$

The fitness of the population of mutants is

$$W(p^*) = (1 - \varepsilon)E(p^*, p) + \varepsilon E(p^*, p^*).$$

Selective advantage s is given by $s = \Delta W$, where $\Delta W = W(p^*) - W(p)$.

The condition that p is an ESS requires $s < 0$. This property holds if the following conditions are satisfied:

(i) $E(p, p) \geq E(p^*, p)$ for all p^* , that is

$$\sum_{i,j} p_i^* a_{ij} p_j \leq \sum_{i,j} p_i a_{ij} p_j, \tag{6.1}$$

an equilibrium condition – the Nash criterion.

(ii) If $E(p, p) = E(p^*, p)$ and $p^* \neq p$, then $E(p^*, p^*) < E(p^*, p)$, that is

$$\sum_{i,j} p_i^* a_{ij} p_j^* < \sum_{i,j} p_i a_{ij} p_j, \tag{6.2}$$

a stability condition.

6.2. Games against Nature: finite size, absolute fitness

The models considered in this article are concerned with games described by payoffs to certain behavioral options which could be interpreted as interactions between the population and an external environment. Thus, the population is parametrized in terms of a set of d options and characterized by a corresponding distribution representing the net-offspring production.

A strategy is the probability distribution $\hat{\mu}$ given by

$$\hat{\mu} = \frac{\varphi(x_i)}{Z(\varphi)}, \quad Z(\varphi) = \sum_{i=1}^d \varphi(x_i).$$

The fitness variables in this class of models are the population growth rate r , the demographic variance σ^2 , and the entropy H . The incumbent population in these models is described by the mathematical object $(\Omega, \hat{\mu}, \varphi)$. A mutant population is represented by the object $(\Omega, \hat{\mu}^*, \varphi^*)$, where φ^* is given by

$$\log \varphi^* = \log \varphi + \delta \log \varphi$$

and $\hat{\mu}^*$ by

$$\hat{\mu}_i^* = \frac{\varphi^*(x_i)}{Z(\varphi^*)}.$$

The selective advantage s in this model is now expressed by (4.6). The condition that $\hat{\mu}$ is an ESS requires that $s < 0$ for all M , where M denotes the population size of the incumbent. This property entails that

$$\Delta r < 0, \Delta \sigma^2 \geq 0 \quad \text{or} \quad \Delta r \leq 0, \Delta \sigma^2 > 0.$$

These conditions hold if the following relations are satisfied:

1. μ is an extremal state of entropy H – an equilibrium condition.
2. μ is evolutionary stable – a stability condition. Stability is expressed in terms of conditions on the reproductive potential Φ and the index γ . When μ is a global maximum, we require $\Phi < 0$; a global minimum $\Phi > 0$. When μ is a local maximum, we require $\Phi < 0, \gamma > 0$; a local minimum, then $\Phi > 0, \gamma < 0$.

The contrast between the two classes of models is summarized by the Table 1.

Table 1
Relation between the classical and non-classical models

Game theory properties	Games within populations (infinite size, relative fitness measures)	Games against Nature (finite size, absolute fitness measures)
Measures of fitness	Mean payoff $E(p, p) = \sum_{i,j=1}^d p_i a_{ij} p_j$	Entropy H
Conditions of ESS	Either $E(p, p) > E(p^*, p)$ or $E(p, p) = E(p^*, p), E(p^*, p) > E(p^*, p^*)$	Either $\Delta r < 0, \Delta \sigma^2 \geq 0$ or $\Delta r \leq 0, \Delta \sigma^2 > 0$
Solution concept	Nash equilibria $E(p, p) \geq E(p^*, p)$ for all p^*	Thermodynamic equilibria: extremal states of H
Stability condition	If $E(p, p) = E(p^*, p), p^* \neq p$, then $E(p^*, p^*) < E(p^*, p)$	$\Delta H \leq 0, \Phi < 0, \gamma \geq 0, \Delta H \geq 0, \Phi > 0, \gamma \leq 0$

7. Examples

We illustrate the significance of our new formalism by studies of the evolution of the sex ratio and the evolution of seed size polymorphism, two phenomena that have been studied in the context of classical models of evolutionary game theory.

7.1. Sex-ratio model

In this section we reformulate a classical model, the sex-ratio game, in order to illustrate the applicability of our existence and characterization theorems. We will show that the $(\frac{1}{2}, \frac{1}{2})$ sex ratio observed in many populations can be characterized in terms of an optimality principle, the maximization of evolutionary entropy. Our analysis will show that an ESS exists if and only if the population has a stationary size. The stationary condition which emerges from our study can thus explain departures from $(\frac{1}{2}, \frac{1}{2})$ sex ratios observed in many natural populations. Such departures have often been attributed to genetic or behavioral constraints, see for example [15]. Our model indicates that ecological factors which permit rapid exponential growth can also create anomalous sex ratios.

Let us consider a sexual population of one species and parametrize it by the state space $\Omega = \{M, F\}$. In our context M and F represent the pure strategies of producing just male or just female offspring, respectively. We will assume as in [3] that generations are non-overlapping. We also assume that the population is described by a polymorphic group of individuals. Let m denote the average sex ratio in the population, N_1 the population size in the daughter generation, and N_2 the population size in the granddaughter generation. We will assume $N_2 \geq N_1$ to exclude the trivial case where the population becomes extinct. As shown in [3, 15.4], the expected number of children produced by a male in the first generation is N_2/mN_1 , the expected number of children produced by a female in that generation is $N_2/(1-m)N_1$. Let us assume that the primary sex ratio is determined by genes acting on the homogametic sex. As pointed out by Hamilton [31], a measure of the propagation of the gene will now be measured by the expected number of grandchildren. An individual in the population will produce male and female offspring according to his strategy in the ratio $p : 1 - p$. The payoff function is thus given by (2.11). The expected number of grandchildren $Z(\varphi)$ is given by (2.12) and the thermodynamically stable strategy $\hat{\mu}$ by

$$\hat{\mu}_1 = \frac{p(1-m)}{p+m-2mp}, \quad \hat{\mu}_2 = \frac{m(1-p)}{p+m-2mp},$$

leading to the reproductive potential given by (2.13) and the evolutionary entropy given by (2.14).

Note that p is the primary sex ratio which is a genetically determined quantity, while m represents a secondary sex ratio, which is observed in the population and depends on cultural and environmental factors.

Let us start our investigations of evolutionary stable strategies for the sex-ratio model with the search for candidates on the basis of our characterization via evolutionary entropy. Since the pure strategies correspond only to trivial, i.e. degenerate cases like $p = 0$, $p = 1$, $m = 0$ or $m = 1$, we will restrict our attention to the only non-trivial possible case given by the maximally mixed strategy. In this case, evolutionary entropy becomes maximal for the equilibrium $\hat{\mu}$ if and only if

$\hat{\mu}(M) = \hat{\mu}(F) = 1/2$. Note that the distribution $\hat{\mu} = (\frac{1}{2}, \frac{1}{2})$ represents the demographic strategy. The ratio $p : 1 - p$ which represents the proportion of male and female offspring produced satisfies

$$\frac{p}{1-p} = \frac{m}{1-m}.$$

Since the function $f(x) = x/(1-x)$ is strictly increasing on $(0, 1)$, we can in fact derive that an ESS for the sex-ratio model has to satisfy $p = m$. On the basis of this partial result, we can now analyze the existence of an ESS. Namely, for $p = m$ the reproductive potential is

$$\Phi = \log \frac{N_2}{N_1}$$

and hence non-positive if and only if $N_2/N_1 \leq 1$. Since we assumed $N_2/N_1 \geq 1$, we have the following result.

Corollary 7.1. *The unique non-trivial ESS for the sex-ratio model is obtained for $p = m$, if and only if $N_2/N_1 = 1$.*

Corollary 7.1 has significant implications for human demography. We predict that during episodes of ‘baby boom’, a condition defined by a large positive growth rate, significant departures from the $(\frac{1}{2}, \frac{1}{2})$ sex ratio should occur. The only case we know of where the relation between population growth and sex ratio has been documented is [32]. This study of the Israel population during the period 1943–1953, a period of rapid exponential growth, is consistent with our predictions.

7.2. Seed size polymorphisms

Game theoretic models, based on growth rate as a measure of fitness, have been proposed to explain the enormous variation in seed size which describe plant species. Geritz [10] for example, has shown that a single seed size is never evolutionary stable: there is always selection for some continuous variation in seed size. We will apply the game theoretic models based on evolutionary entropy as fitness to show that there exist three classes of seed size distributions that are evolutionarily stable. Our analysis will show that (i) when correlations between seed size and net-reproductive yield vanishes, there exist two evolutionarily stable seed size patterns: (a) equal number of seeds of different size – when population growth is bounded by the number of seed sizes; (b) all seeds of the same size – when total seed production increases; (ii) when a correlation between seed size and net-reproductive yield is obtained, there exists a unique evolutionarily stable seed size pattern, namely a continuous variation in seed size.

Let Ω denote the set of seed sizes, $\Omega = \{x_1, \dots, x_d\}$. Let $\varphi(x_i)$ denote the net-reproductive yield, that is net production associated with seed size x_i . The quantity $Z(\varphi) = \sum_i \varphi(x_i)$ represents the total net-seed production of an individual. Population growth rate $r(\varphi)$ is given by $r(\varphi) = \log Z(\varphi)$. The strategy $\hat{\mu} = (\hat{\mu}_i)$ that defines demographic equilibrium is given by $\hat{\mu}_i = \varphi(x_i)/Z(\varphi)$, where $\hat{\mu}_i$ represents the proportion of seeds of sizes x_i produced by an individual. The evolutionary stable strategies are extremal states of entropy $H = -\sum_i \hat{\mu}_i \log \hat{\mu}_i$. To characterize these strategies, we consider the reproductive potential $\Phi = \sum_i \hat{\mu}_i \log \varphi(x_i)$. This quantity measures the net-seed production averaged over all the size classes. We observe that

$$\Phi = r - H.$$

Hence $\Phi < 0$ entails $r < H$ and describes a bounded population growth; also $\Phi > 0$ implies $r > H$ and represents unbounded population growth. The expression

$$\sigma^2 = \sum_1^d \mu_i (\log \varphi(x_i))^2 - \left(\sum_1^d \mu_i \log \varphi(x_i) \right)^2$$

is the variance in the net-reproductive yield. The quantity $\gamma = 2\sigma^2 + \kappa$, where κ is given by (3.5) represents the correlation between the seed size and net-reproductive yield. The ESS are characterized by evaluating the extremal states of entropy. We now characterize these extremal states and we appeal to Theorem 5.3–5.5 to determine whether they correspond to ESS.

(i) The distribution $\mu = (1/d, \dots, 1/d)$: *equal number of seeds of different sizes*. This is the global maximum of H . For this distribution we have $\gamma = 0$ and $H = \log d$. The total net reproduction is $Z(\varphi)$. Since $\log Z(\varphi) = H + \Phi$, the reproductive potential Φ is given by

$$\Phi = \log \frac{Z(\varphi)}{d}.$$

From Theorem 5.3 we infer that the equidistribution is an ESS if and only if $\log(Z(\varphi)/d) < 0$, that is, if and only if $Z(\varphi) < d$. We conclude that the equidistribution, equal number of seeds of different sizes, is an ESS, if the following constraints prevail:

- (a) Seed size and individual seed production are uncorrelated ($\gamma = 0$).
- (b) Total net-seed production is bounded by the number of seed sizes ($Z(\varphi) < d$).

(ii) The distribution $\mu = (0, \dots, 0, 1, 0, \dots, 0)$: *all seeds of the same size*. This condition describes a global minimum of H . For this distribution we also have $\gamma = 0$, and $H = 0$. The total net reproduction is $Z(\varphi)$. In view of the identity $\log Z(\varphi) = H + \Phi$, we have $\Phi = \log Z(\varphi)$. From Theorem 5.4 we infer that the pure strategy $\mu = (0, \dots, 0, 1, 0, \dots, 0)$ is an ESS if and only if $\log Z(\varphi) > 0$, that is, if and only if $Z(\varphi) > 1$. We conclude that the pure strategy defined by the property, all seeds of the same size, is an ESS if the following constraints obtain:

- (a) Seed size and individual seed production are uncorrelated ($\gamma = 0$).
- (b) Total net-seed production is greater than unity ($Z(\varphi) > 1$).

(iii) The distribution $\mu = (\mu_i)$ with $\mu_i \neq 1$ for all i and $\mu_i \neq \mu_j$ for some i, j : *a continuous variation in seed size*. This condition describes a local extremum of H . In this case $\gamma \neq 0$, and $0 < H < \log d$. From Theorem 5.5, we infer that the above distribution defines an ESS if one of the following situations obtain:

- (a) A negative correlation between seed size and net-reproductive yield ($\gamma < 0$); unbounded growth ($\Phi > 0$).
- (b) A positive correlation between seed size and net-reproductive yield ($\gamma > 0$); bounded growth ($\Phi < 0$).

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