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The dynamical attainability of ESS in evolutionary games

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Abstract. In this paper, the attainability of ESS of the evolutionary game among n players under the frequency-independent selection is studied by means of a mathematical model describing the dynamical development and a concept of stability (strongly determined stability). It is assumed that natural selection and small mutations cause the phenotype to change gradually in the direction of fitness increasing. It is shown that (1) the ESS solution is not always evolutionarily attainable in the evolutionary dynamics, (2) in the game where the interaction between two species is completely competitive, the Nash solution is always attainable, and (3) one of two species may attain the state of minimum fitness as a result of evolution. The attainability of ESS is also examined in two game models on the sex ratio of wasps and aphids in light of our criterion of the attainability of ESS.

Key words: Evolutonary game – Dynamical attainability of ESS – Strongly determined stability

1. Introduction

A useful tool to calculate a goal of phenotypic evolution is an evolutionarily stable strategy (ESS), which is a strategy such that, if most of the members of a population adopt it, then no mutant could increase its abundance [16]. It is sometimes called an "uninvadable" or "unbeatable" strategy.

In a constant environment, suppose the fitness of a phenotype x, denoted by $F(x)$, depends only on the strategy of its own, x. Then the optimal strategy x^* is the one which maximizes the fitness:

$$F(x^*) = \max_{x \in D} F(x),$$

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** *Present address*: Division of System Science, Graduate School of Science & Technology, Kobe University, Kobe, Japan where D is a strategy set. Many authors [4, 5, 10, 20, 23] assume that the optimal strategy x^* is an evolutionary goal. Certainly, if a mutant type with the strategy x different from x^* invades the population with most members taking strategy x^*, it will be selected out because of it having a lower fitness than the wild type.

On the other hand, evolutionary stable strategy for the coevolution game is not so simple as in the former case. This is because, in a coevolution game, a species' fitness changes as an opponent species evolves. Thus the fitness of the first species, F_1, is not only a function of its own strategy (x_1) but also a function of an opponent species' strategy (x_2):

$$F_1 \equiv F_1(x_1, x_2)$$

Similarly the fitness of the second species, F_2, can be written:

$$F_2 \equiv F_2(x_1, x_2).$$

Suzuki and Iwasa [21] and Yamaguchi [24] constructed game models, to explain the sex ratio of wasps and aphids respectively, using n person games. In their paper they assumed the Nash solution [17, 19] in the game theory was a goal of coevolution.

The Nash solution is an uninvadable strategy, which is easily understood by the definition of the Nash solution (Eq. (2) in the next section). However, whether the strategy attains the Nash solution in the evolutionary dynamics is a separate question. To illustrate it, we consider a simple example in which the fitness functions are quadratic as:

$$F_1 = -x_1^2 + 4x_1x_2 + x_2^2,$$

$$F_2 = x_1^2 + 4x_1x_2 - x_2^2,$$

where we note that the origin $(x_1, x_2) = (0, 0)$ is the Nash equilibrium.

Now we assume that the evolutionary change of the strategy always occurs in the direction of the increase of its own fitness; i.e. x_1 changes in the direction of F_1 increasing and so on. F_1 is the maximum on the line $\partial F_1/\partial x_1 = 0$ for fixed x_2 because the second derivative is negative (see Fig. 1). Thus in the regions A and B, x_1 changes to the right (x_1 increases) and in the regions C and D it changes to the left (x_1 decreases). We can write down only the direction that x_1 changes (Fig. 1). Similarly, F_2 is the maximum on the line $\partial F_2/\partial x_2 = 0$ for fixed x_1. We can also write down the direction of change in x_2. As shown in Fig. 1, in the region A or C, the set of strategies of species 1 and 2 evidently goes away from the origin (i.e. the Nash equilibrium), and does not attain the origin. Therefore it is a serious question under what conditions we can assume the Nash solution as an evolutionary goal, as Suzuki and Iwasa or Yamaguchi assume. If the strategies of species 1 and 2 attain the Nash solution dynamically, we can consider that the Nash solution is an actual goal of evolution.

In the present paper, we examine the condition for an ESS to be evolutionary attainable. Firstly, we will propose two candidates of ESS in the coevolution game. Secondly we propose a mathematical model which describes the dynamical development of a set of strategies in the coevolution among n species. In order to examine evolutionary trajectories, we must know not only the sign of movement but also the magnitude of the speed of the evolution, but we cannot know both exactly in most cases. Thirdly, to avoid this difficulty we propose a stability concept, SDS. Next, using the dynamics of evolutionary games and the stability concept we prove several theorems and examine the attainability of ESS.

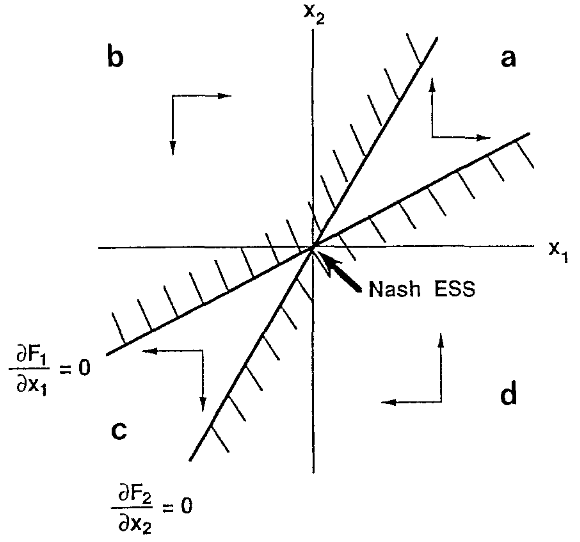

Fig. 1. The direction of evolution. We assume that the change of strategy of a species always occurs in the direction of the increase of its own fitness. F_1 is a maximum on the line $\partial F_1/\partial x_1 = 0$ to a fixed x_2 and F_2 is a maximum on the line $\partial F_2/\partial x_2 = 0$ to a fixed x_1. In the region A or C, strategies of species 1 and 2 seem to go away from the origin (i.e. the Nash point)

In a few examples we demonstrate that the solution with maximum fitness may not be attainable in the course of evolutionary games. Finally we check on the attainability of several simple examples including the sex ratio game models.

2. The dynamics of evolutionary games

Coevolution usually indicates the simultaneous evolution of two or more species which strongly interact with each other, such as host and parasite, prey and predator, and among competitors [7]. We may also consider the coevolution among individuals in the same species if those individuals play different roles, for example, male and female. Hereafter we call both cases, i.e. intra- and inter-specific coevolution, an evolutionary game. In evolutionary games, a fitness of the ith species (or players), F_i $(i = 1, 2, \dots, n)$, depends not only on its own strategy, x_i, but also on the other species' (or players') strategies, x_j $(j \neq i)$, where x_i is assumed to be a continuous variable and n is the number of species:

$$\begin{aligned} F_1 &\equiv F_1(x_1, x_2, \dots) \\ F_2 &\equiv F_2(x_1, x_2, \dots) \\ &\vdots \\ F_n &\equiv F_n(x_1, x_2, \dots). \end{aligned} \tag{1}$$

As mentioned in Sect. 1, our purpose in this paper is to examine whether the ESS of evolutionary games is an actual goal or not. Here we will

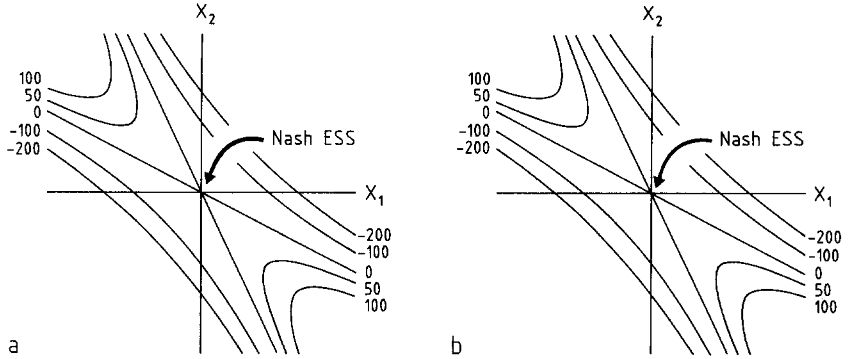

Fig. 2. The contour maps of F_i in Example 1. The numerics attached to the contour lines in the figure represent the values of F_i. The origin is a Nash point and a saddle of the dynamics of Eq. (4) for any k_i's. Thus the Nash point is not always SDS. **a** F_1; **b** F_2

propose two candidates of ESS in evolutionary games. One candidate of ESS, $(x_1^*, \ldots, x_n^*)$, satisfies the Nash conditions [17, 18]:

$$F_i(x_1^*, \ldots, x_i^*, \ldots, x_n^*) > F_i(x_1^*, \ldots, x_i, \ldots, x_n^*) \quad \text{for all } x_i \neq x_i^* \quad (i = 1, \ldots, n).$$

At an interior Nash equilibrium point, the above condition can be rewritten as

$$\frac{\partial F_i}{\partial x_i}(x_1^*, \ldots, x_n^*) = 0, \qquad \frac{\partial^2 F_i}{\partial x_i^2}(x_1^*, \ldots, x_n^*) < 0 \quad (i = 1, \ldots, n). \tag{2}$$

If a mutant of the ith species with strategy $x_i \neq x_i^*$ invades the population adopting a Nash ESS, x_i^*, then the mutant will be driven out because the mutant's fitness is less than that of the Nash ESS.

Example 1. This example has a Nash ESS in the 2-species game. When F_i has a quadratic form:

$$F_i = -2x_1^2 - 5x_1x_2 - 2x_2^2 \quad (i = 1, 2),$$

the contour map of the fitness for each species can be drawn as Fig. 2. Since at the origin $\partial F_i/\partial x_i = 0$ and $\partial^2 F_i/\partial x_i^2 = -4 < 0$ $(i = 1, 2)$, the origin is a Nash ESS.

Another candidate, named "strict ESS", satisfies the following condition:

$$F_i(x_1^*, \ldots, x_i^*, \ldots, x_n^*) > F_i(x_1, \ldots, x_i, \ldots, x_n) \quad \text{for all } (x_1, \ldots, x_i, \ldots, x_n) \neq (x_1^*, \ldots, x_i^*, \ldots, x_n^*).$$

This is a stricter condition than a Nash ESS. As a consequence of this definition, the fitness at a "strict ESS" point is maximum for each species. Thus, just as with the Nash ESS, a mutant will also be driven out.

Example 2.

$$F_1 = -x_1^2 + 3x_1x_2 - 3x_2^2$$
$$F_2 = -3x_1^2 + 3x_1x_2 - x_2^2.$$

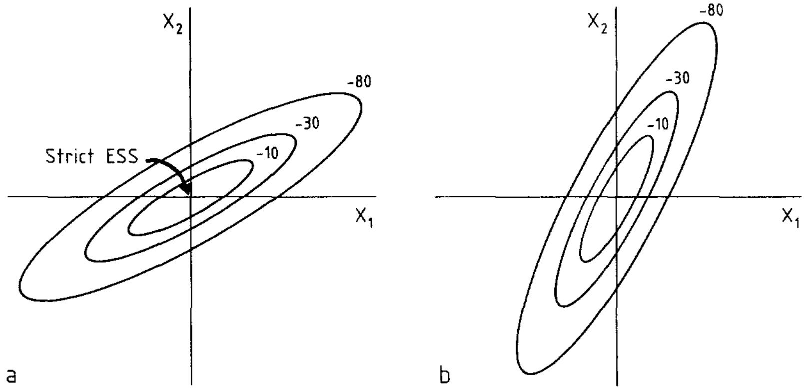

Fig. 3. The contour maps of F_i in Example 2. The numerics attached to the contour lines in the figure represent the values of F_i. Although the origin is the maximum point of the fitness of both species 1 and 2, it is a saddle point of the dynamics of Eq. (4) for any k_i's. The maximum point is not always SDS. **a** F_1; **b** F_2

As in the previous example, Fig. 3 are the contour maps of species 1 and 2, respectively. Since at the origin,

$$\frac{\partial F_i}{\partial x_1}=\frac{\partial F_i}{\partial x_2}=0, \qquad \frac{\partial^2 F_i}{\partial x_1^2}, \frac{\partial^2 F_i}{\partial x_2^2}<0 \tag{3.1}$$

and

$$\frac{\partial^2 F_i}{\partial x_1^2}\frac{\partial^2 F_i}{\partial x_2^2}-\left(\frac{\partial^2 F_i}{\partial x_1\,\partial x_2}\right)^2>0 \quad (i=1,2), \tag{3.2}$$

the origin is a maximum-fitness point for both species. It is a "strict ESS".

Now we introduce a dynamical model of evolutionary games to examine the evolutionary trajectory of a set of strategies. We make two assumptions: (a) a strategy of each species changes gradually in the course of evolution and (b) the change of the ith species' strategy always occurs in the direction of the increase of the ith species' fitness because of mutation and natural selection. Therefore, when $\partial F_i/\partial x_i>0$, the increment Δx_i, is positive and when $\partial F_i/\partial x_i<0$, Δx_i is negative. Namely we have

$$\frac{\partial F_i}{\partial x_i}\Delta x_i>0.$$

Thus we assume that the change rate of x_i can be expressed as

$$\frac{dx_i}{dt}=k_i(x_1,\ldots,x_n)\frac{\partial F_i}{\partial x_i} \quad (i=1,2,\ldots,n), \tag{4}$$

where the coefficients are positive-valued functions of $x_1, x_2, \ldots, x_n$:

$$k_i(x_1,x_2,\ldots)>0 \quad \text{for all } \boldsymbol{x}.$$

Since the first derivatives are equal to zero at both a Nash ESS and a strict ESS (Eqs. (2) and (3)), ESS points in both cases are also equilibrium points of evolutionary dynamics.

In this equation the derivative terms represent the direction of evolution due to natural selection. k_i is a function which should be determined on some genetic bases or paleontological data. But in the present discussion we do not specify the functional form of k_i because it is generally an unknown factor. Some authors (Lande [14] and Roughgarden [18]) use the similar dynamical form: in Roughgarden's case $k_i = 1$, and in Lande's case $k_i = h^2\sigma^2/W$, where h^2 is the heritability, σ^2 is a phenotypic variance and W is the average fitness. Thus Eq. (4) is an expanded version of Lande's and Roughgarden's works.

3. Strongly determined stability and theorems

Since in the present discussion we do not know an exact functional form of k_i, we cannot directly examine both the trajectory of evolutionary games and the local stability of the equilibrium point for a given F_i and Eq. (4). Therefore we propose a stability concept: strongly determined stability (SDS). It is defined by two conditions:

(I) An equilibrium point is locally stable for any functional form of $k_i > 0$.
(II) Condition (I) remains unchanged under small perturbations for F_i.

The stability condition is similar to the D-stability proposed by Arrow and others [1–3]. The difference between the two concepts is the above condition (II). We need the structural stability of the evolutionary dynamics (Eq. (4)), which is expressed by condition (II), because fitness functions are usually perturbed in the course of evolution.

Using this notation of stability, we can examine the attainability of ESS even if we do not know an explicit functional form of k_i; i.e., if an equilibrium point is SDS, we can assure that the evolutionary trajectory of a set of strategies can attain the equilibrium point.

First we consider a relation between an n-species system and a subsystem consisting of less than n species. We fix a pair $(F, \boldsymbol{x}^*)$, where $F = (F_1, \ldots, F_n)$ is the fitness functions and $\boldsymbol{x}^* = (x_1^*, x_2^*, \ldots, x_n^*)$ is an equilibrium point of F, that is, $\boldsymbol{x}^*$ satisfies $(\partial F_i/\partial x_i)|_* = 0$ for each i. Now, we define the subsystem of $(F, \boldsymbol{x}^*)$ which consists of m-species $p_1, p_2, \ldots, p_m$ with $1 \leqslant p_1 < p_2 < \cdots < p_m \leqslant n$. Let

$$G_i(y_1, \ldots, y_m) = F_p(z_1, \ldots, z_n),$$

where

$$z_i = \begin{cases} y_j & \text{if } i = p_j \text{ for some } j, \\ x_i^* & \text{otherwise.} \end{cases}$$

Then $G = (G_1, \ldots, G_m)$ has an equilibrium point $\boldsymbol{y}^* = (y_1^*, \ldots, y_m^*) = (x_{p_1}^*, \ldots, x_{p_m}^*)$ corresponding to $\boldsymbol{x}^*$. This pair $(G, \boldsymbol{y}^*)$ is called the subsystem of $(F, \boldsymbol{x}^*)$. The number of subsystems of m species is $n!/m!(n-m)!$. And the number of all subsystems is

$$\sum_{m=1}^{n-1} \frac{n!}{m!(n-m)!} = 2^n - 2.$$

Then the following theorem about SDS holds.

Theorem 1. *If an equilibrium point of an n-species system is* SDS, *then the corresponding equilibrium point* $\boldsymbol{y}^*$ *of any subsystem is* SDS.

Proof. Here we will prove the contrapositive proposition of Theorem 1; i.e., if there exists a subsystem such that the corresponding equilibrium point is not SDS, then the equilibrium of an n-species system is not SDS.

Consider an n-species system and an equilibrium point of the system, $(x_1^*, x_2^*, \ldots, x_n^*)$. The Jacobian matrix at the equilibrium point can be written as follows:

$$J = \{a_{ij}\} : n \times n \text{ matrix},$$

where

$$a_{ij} = k_i(x_1^*, \ldots, x_n^*) \left. \frac{\partial^2 F_i}{\partial x_i \, \partial x_j} \right|_* .$$

Hereafter, $*$ means the derivative value at the equilibrium point. Next we consider an m-species subsystem consisting of $p_1, p_2, \ldots, p_m$-th species and the corresponding equilibrium point, $\boldsymbol{y}^*$, of it. The Jacobian matrix of the subsystem is a submatrix of the above matrix (J), obtained by selecting $p_1, p_2, \ldots, p_m$-th lines and $p_1, p_2, \ldots, p_m$-th columns from J. If there exists a set of k_i's ($i = p_1, p_2, \ldots, p_m$) such that the corresponding equilibrium point of the m-species subsystem is unstable (i.e., if it is not SDS), then the equilibrium point of the n-species system can be unstable when k_i's ($i = p_1, p_2, \ldots, p_m$) become very large. Thus the equilibrium point of the n-species system is not stable irrespective of k_i; i.e., it is not SDS. (Q.E.D.)

Theorem 2. *The necessary and sufficient conditions for an equilibrium point of* 1, 2 *and* 3-*species system to be* SDS *are as follows, respectively*:

Case n = 1

$$\left. \frac{\partial^2 F_1}{\partial x_1^2} \right|_* < 0 \tag{5.1}$$

Case n = 2

$$\left. \frac{\partial^2 F_i}{\partial x_i^2} \right|_* < 0 \quad (i = 1, 2) \tag{5.2}$$

and

$$J_*\left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}\right) = \left. \frac{\partial^2 F_1}{\partial x_1^2} \frac{\partial^2 F_2}{\partial x_2^2} - \frac{\partial^2 F_1}{\partial x_1 \partial x_2} \frac{\partial^2 F_2}{\partial x_1 \partial x_2} \right|_* > 0,$$

where $J(\, . \, , \, . \,)$ *is a Jacobian.*

Case n = 3

$$M_{12}, M_{23}, M_{31} > 0, \quad D > 0, \quad \sqrt{D} < \sqrt{M_{12}} + \sqrt{M_{23}} + \sqrt{M_{31}} \tag{5.3}$$

and

$$\left. \frac{\partial^2 F_i}{\partial x_i^2} \right|_* < 0 \quad (i = 1, 2, 3),$$

where

$$M_{ij} = \left(\frac{\partial^2 F_i}{\partial x_i^2} \frac{\partial^2 F_j}{\partial x_j^2} \right)_*^{-1} J_* \left(\frac{\partial F_i}{\partial x_i}, \frac{\partial F_j}{\partial x_j} \right),$$

$$D = \left(\frac{\partial^2 F_1}{\partial x_1^2} \frac{\partial^2 F_2}{\partial x_2^2} \frac{\partial^2 F_3}{\partial x_3^2} \right)_*^{-1} J_* \left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}, \frac{\partial F_3}{\partial x_3} \right).$$

A proof is given in Appendix 1.

Here it should be noticed that, since Eq. (5) contains only the derivatives of the fitness, whether an equilibrium is SDS or not is not altered by adding a constant to each fitness function. Although we use fitness functions with negative values in some examples in the present paper, we can change them by adding a positive constant as the result remains unchanged.

The first condition in the 2-species case is the same as the Nash condition, Eq. (2). The Nash condition, therefore, is a necessary, but not a sufficient, condition for a 2-species system to be strongly determined stable (SDS). Thus from this theorem we can examine the attainability of a Nash ESS irrespective of k_i by checking only the second condition. The Nash ESS is attainable if the determinant of the Jacobian is positive and the dynamical trajectory never attains the Nash ESS if the determinant is negative. The SDS condition of a 3-species game is slightly complicated and consists of 4 inequalities. The first two conditions are the same as the SDS condition of a 2-species system. In comparing between the SDS conditions of $n = 1$, 2 and 3 systems, the condition of a 2-species system includes the condition for a 1-species system. And the condition of a 3-species system includes the condition of 1 and 2-species system and so on (see Theorem 1).

We will go back to the previous two examples. In Example 1 the Nash solution, which satisfies Eq. (2) is $(x_1^*, x_2^*) = (0, 0)$. Since $F_i = -(2x_1 + x_2)(x_1 + 2x_2) > 0$ in the regions B and D of Fig. 2, both species can obtain higher fitness in these regions than at the Nash point. The Jacobian of Example 1 is

$$J_*\left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}\right) = \begin{vmatrix} -4 & -5 \\ -5 & -4 \end{vmatrix} = -9 < 0.$$

Using the SDS condition of a 2-species game (Eq. (5.2)) we find that the Nash point is not SDS and furthermore that it is locally unstable for any functional form of k_i. Thus the dynamics of evolution from any initial point does not attain the Nash equilibrium. Although the Nash solution is generally accepted as one of the equilibrium points in game theory, it is not always possible to attain the Nash solution. Results of our analysis also show that there is a large difference between the statical and dynamical approach to evolutionary games.

In Example 2, both species can obtain the highest fitness at the equilibrium point. However, as in the previous example, it does not satisfy the SDS condition because the determinant of the Jacobian,

$$J_*\left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}\right) = \begin{vmatrix} -2 & 3 \\ 3 & -2 \end{vmatrix},$$

is negative. As shown by the example, the maximal condition is not sufficient for SDS nor is it a necessary condition for SDS (compare Eq. (3) and (5.2)). Strictly ESS, the fittest strategies for both species, seems to be considered as the solution of evolution in evolutionary theory. However, although both species 1 and 2 improve their own strategies, they cannot obtain the highest fitness in Example 2; the dynamics of this example cannot attain the strictly ESS point.

4. Applications

4.1. Competitive cases

In this section we consider a competitive case in which two species compete with each other.

Theorem 3. *If a set of the fitness functions, F_1 and F_2, has a Nash equilibrium (x_1^*, x_2^*), and there exists a function of $h(z)$ such that*

$$F_1 = h(F_2) \quad \textit{and} \quad dh/dz < 0 \tag{6}$$

for some neighborhood of (x_1^*, x_2^*), then

(*i*)
$$\left.\frac{\partial F_1}{\partial x_2}\right|_* = \left.\frac{\partial F_2}{\partial x_1}\right|_* = 0,$$

$$\left.\frac{\partial^2 F_1}{\partial x_i \, \partial x_j}\right|_* = h'(z)|_{z=F_2(x_1^*, x_2^*)} \left.\frac{\partial^2 F_2}{\partial x_i \, \partial x_j}\right|_* \quad (i, j = 1, 2)$$

and

(*ii*) *Nash solution is* SDS.

A proof is given in Appendix 2.

Condition (6) means that the increase of the first species' fitness (F_1) for some neighborhood of a Nash equilibrium always leads to the decrease of the second species' fitness (F_2) and vice versa; i.e. the interaction between two species is competitive. In this case, the Nash solution is always SDS. Thus we can adopt the Nash solution as a goal of the evolutionary game.

Collorary of Theorem 3. (zero-sum games). *When a zero-sum game ($F_1 + F_2 = 0$) has a Nash solution, the Nash solution is always* SDS.

Proof. We consider a function of $h(z) \equiv -z$. This function satisfies the condition (6) of Theorem 3 because $F_1 = -F_2$ and $dh/dz = -1$. According to Theorem 3, the Nash solution is always SDS. (Q.D.E.)

Thus zero-sum games, already treated in the game theory, represent one class of example for the competitive case. In this case the Nash solution is always SDS. Here we show two examples included in the competitive case with Nash solution.

Example (*a*)

$$F_1 = -x_1^2 + 3x_1x_2 + 2x_2^2$$
$$F_2 = x_1^2 - 3x_1x_2 - 2x_2^2.$$

Since $F_1 + F_2 = 0$, the Nash solution of the example (0, 0) is SDS from the collorary of Theorem 3.

Example (*b*)

$$F_1 = -x_1^2 + 3x_1x_2 + 2x_2^2$$
$$F_2 = \exp(x_1^2 - 3x_1x_2 - 2x_2^2).$$

Since F_1 and F_2 satisfy the condition (6) (i.e. $h(z) = -\ln z$ and $dh/dz = -1/z < 0$ because of $F_2 > 0$), the Nash solution (0, 0) is SDS.

4.2. Biological examples

(*a*) *Wasps game.* In order to explain the greatly different sex ratios among gregarious parasitoids, Suzuki and Iwasa [21] constructed a model for the non-cooperative game among two haplo-diploidy female wasps. They especially focused on the difference in strategies of two females that oviposit on the same host. The first female attacks an unparasitized host and the second an already parasitized host. They denote the inclusive fitness of the ith wasp with F_i $(i = 1, 2)$:

$$F_1 = (1-p)(r_d + r_s)(1-x_1)N_1 h(N_1) + pN_1 h(N_1+N_2) \times \left\{ r_d(1-x_1) + r_s x_1 \left(\frac{N_1+N_2}{N_1x_1+N_2x_2} - 1 \right) \right\},$$

$$F_2 = N_2 h(N_1+N_2) \left\{ r_d(1-x_2) + r_s x_2 \left(\frac{N_1+N_2}{N_1x_1+N_2x_2} - 1 \right) \right\},$$

where x_i is the progeny sex ratio of the ith player, r_d, r_s is the relatedness of daughters and sons respectively, N_i is the number of eggs by the ith wasp, p is the proportion of doubly parasitized hosts among parasitized hosts and $h(N)$ is a decreasing function describing the density effect on the reproductive success. They analyzed the model and obtained a Nash equilibrium (x_1^*, x_2^*) as a goal of the evolutionary game among the first and second females. The Nash solution is

$$x_1^* = \frac{\frac{J}{2}(1+N)}{\left(\frac{1-p}{pf} + 2\right)^2}, \qquad x_2^* = \frac{\frac{J}{2}(1+N)\left(\frac{1-p}{pf} + 1\right)}{\left(\frac{1-p}{pf} + 2\right)^2 N},$$

where $J = 2r_s/(r_d + r_s)$, $N = N_2/N_1$ and $f = h(N_1+N_2)/h(N_1)$.

Using Theorem 2, we can analyze whether the Nash equilibrium of this wasp game is SDS or not. In Table 1, we show the second derivatives of F_1 and F_2. It should be noted that

$$\left.\frac{\partial^2 F_1}{\partial x_1\, \partial x_2}\right|_* = -p \left.\frac{\partial^2 F_2}{\partial x_1\, \partial x_2}\right|_* .$$

Thus the Nash equilibrium point is SDS for all positive parameter values $(r_d, r_s, p, h(N), N_1, N_2)$ as long as the Nash solution is an interior equilibrium point $(0 < x_1^*, x_2^* < 1)$.

(*b*) *Aphids game.* Another example we show here is a non-cooperative game model among the mother aphids subject to local mate competition [24]. Yamaguchi assumed in her paper [24],

Table 1. The second derivatives of F_i

	$\frac{\partial^2 F_i}{\partial x_1^2}$	$\frac{\partial^2 F_i}{\partial x_1\, \partial x_2}$	$\frac{\partial^2 F_i}{\partial x_2^2}$
$i = 1$	$-2pN_1x_2 g(x_1, x_2)$	$p(N_1x_1 - N_2x_2)g(x_1, x_2)$	$2pN_2x_1 g(x_1, x_2)$
$i = 2$	$2N_1x_2 g(x_1, x_2)$	$-(N_1x_1 - N_2x_2)g(x_1, x_2)$	$-2N_2x_1 g(x_1, x_2)$

where $g(x_1, x_2) = \dfrac{r_s N_1 N_2 (N_1+N_2) h(N_1+N_2)}{(N_1x_1 - N_2x_2)^3}$

(1) Females differ in their total parental investments:

$$P_1 < P_2 < \cdots < P_n,$$

where P_i is the total parental investment of the ith female.
(2) Each female can control her offspring sex ratio, x_i, which is the proportion of P_i invested in sons.
(3) Natural selection will favour offspring sex ratios that maximize each mother's inclusive fitness.

The inclusive fitness of the ith mother (F_i) in a patch founded by n mothers can be written as

$$F_i = \frac{rR_fP_i}{W_d}\{(1-x_i)+x_iB/A\},$$

where r is the relatedness of a mother to her offspring, R_f is the reproductive success of a daughter, $A = \sum P_ix_i$ and $B = \sum P_i(1-x_1)$. Yamaguchi obtained the Nash solution as the optimal sex ratios:

$$x_i^* = \frac{\sum P_i}{P_i}\frac{n-1}{2n^2}, \qquad A^* = \frac{n-1}{2n}\sum P_i. \tag{7}$$

We apply Theorem 2 to the example. The second derivatives of F_i are obtained by substituting Eq. (7):

$$\left.\frac{\partial^2 F_i}{\partial x_i^2}\right|_* = \frac{-8n}{n-1}P_iB_i \tag{8.1}$$

$$(i \neq j)\left.\frac{\partial^2 F_i}{\partial x_i\,\partial x_j}\right|_* = \frac{-4n(n-2)}{(n-1)^2}P_jB_i, \tag{8.2}$$

where

$$B_i = \frac{rR_fP_i}{W_d\sum P_i}.$$

When $n = 2$ (the game between 2 females),

$$(i \neq j)\left.\frac{\partial^2 F_i}{\partial x_i\,\partial x_j}\right|_* = 0, \qquad J_*\left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}\right) = 256P_1P_2B_1B_2 > 0$$

are obtained from Eqs. (8.1) and (8.2). Thus, according to Eq. (5.2), the equilibrium point is SDS.

When $n = 3$, substituting $n = 3$ into Eqs. (8.1) and (8.2), we can obtain

$$\left.\frac{\partial^2 F_i}{\partial x_i^2}\right|_* = -12P_iB_i < 0 \quad (i = 1, 2, 3), \qquad \left.\frac{\partial^2 F_i}{\partial x_i\,\partial x_j}\right|_* = -3P_jB_i,$$

$$J_*\left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}, \frac{\partial F_3}{\partial x_3}\right) = -1458P_1P_2P_3B_1B_2B_3,$$

$$D = -1458/(-12)^3 = 27/32 > 0,$$

$$M_{12} = M_{23} = M_{31} = 15/16 > 0,$$

$$\sqrt{13.5}/4 = \sqrt{D} < \sqrt{M_{12}} + \sqrt{M_{23}} + \sqrt{M_{31}} = 3\sqrt{15}/4.$$

Thus, according to Eq. (5.3), the equilibrium point of the 3-females game is SDS for all parameter values (r, R_f, P_i, w_d, w_s).

Furthermore, for any n, we can find a global Liapunov function of this example as follows. Let

$$F(x_1, \ldots, x_n) = \frac{P(X^2 - \sum X_i^2)}{2} - \tfrac{2}{3}X^3,$$

where $P = \sum p_i$, $X_i = p_i x_i$, $X = \sum X_i$. Then we have, for each i,

$$\frac{\partial F_i}{\partial x_i} = \frac{1}{X^2}\frac{rR_f}{w_d}\frac{\partial F}{\partial x_i}.$$

And so, for any $k_1, \ldots, k_n$, F is the Liapunov function of

$$\frac{d}{dt}\begin{pmatrix} x_1 \\ \vdots \\ x_n \end{pmatrix} = \begin{pmatrix} k_1 \dfrac{\partial F_1}{\partial x_1} \\ \vdots \\ k_n \dfrac{\partial F_n}{\partial x_n} \end{pmatrix} = \frac{1}{X^2}\frac{rR_f}{w_d}\begin{pmatrix} k_1 \dfrac{\partial F}{\partial x_1} \\ \vdots \\ k_n \dfrac{\partial F}{\partial x_n} \end{pmatrix}.$$

As a result, the equilibrium point $(x_1^*, \ldots, x_n^*)$ is asymptotically stable for any $k_1, \ldots, k_n$. It is a "dissipative system", as pointed out by Logofet [15]. Thus it is SDS (in detail, see [15]).

5. Discussion

ESS is often regarded as a goal of evolution without considering the dynamics of evolution. However, the analysis based on the present dynamical model of evolutionary games has shown that in order to confirm the attainability of ESS, it must be checked carefully. The dynamical stability of ESS has been studied by many authors [6, 9, 11, 12, 22, 25, 26] in recent years. Taylor and Jonker [22] examined the stability of ESS, using the continuous-time dynamics of mixed strategy of a single population; i.e. the time change of frequencies of individuals adopting n discrete tactics, and confirmed that ESS is locally stable. A series of studies by Hofbauer and his colleagues [11, 12] or Zeeman [25, 26] showed the same result as Taylor and Jonker's and other properties of the dynamics. Furthermore Eshel and Akin [6] proposed the coevolutionary game model describing the discrete-time dynamics of mixed strategies of multi-species. Their main result is that no equilibrium of mixed strategies is locally stable. Hines [9] also showed that a non-trivial equilibrium of mixed strategies of two species without intraspecific interaction is necessarily unstable in the discrete-time model.

In the present paper, we proposed the continuous-time model describing the evolutionary dynamics of phenotypic traits of multi-species with frequency-independent fitness, and we have examined the dynamical attainability of ESS in evolutionary games. We have obtained the conditions given by Theorems 2 and 3 as a convenient tool for checking the attainability of ESS. The main point of Theorems 2 and 3 is that we can check the attainability of ESS even if we do not know the exact form of dx_i/dt; i.e., we can check it as long as we know the set of fitness functions, F_i ($i = 1, 2, \ldots, n$).

It should be noted that there are many strange cases in evolutionary games. By using Theorem 2, we show that both the Nash solution and the solution with maximum fitness (strict ESS) are not always attainable (Examples 1 and 2). Furthermore it may happen that a species attains the point with lowest fitness in the course of evolutionary dynamics, as exemplified in the following.

Example 3

$$F_1 = -2x_1^2 + 5x_1x_2 - x_2^2$$

$$F_2 = 2x_1^2 - 2x_1x_2 + x_2^2.$$

We, furthermore, assume $k_1 = k_2 = 1$. Then the evolutionary dynamics is given by

$$\begin{aligned} dx_1/dt &= -4x_1 + 5x_2, \\ dx_2/dt &= -2x_1 + 2x_2, \end{aligned} \tag{9}$$

and the Jacobian is given by

$$J_*\left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}\right) = \begin{vmatrix} -4 & 5 \\ -2 & 2 \end{vmatrix}.$$

In this case the second species has the minimum fitness at the equilibrium point (0, 0). However, from tr $J^* < 0$ and det $J^* > 0$, the equilibrium point of Eq. (9) is locally stable (see Fig. 4). Therefore the trajectory of the dynamics attains the equilibrium point. As a result the second species finally obtains the minimum fitness although it changes its trait in the direction of fitness increasing.

Now we will try to analyze the attainability of ESS in the single-species evolution in a continuous phenotype scheme in order to clarify the difference between evolutionary games and single-species evolution. When a species has a fitness function, F, depending on n trait-values, x_i $(i = 1, \ldots, n)$, of its own, it can be written as:

$$F \equiv F(x_1, x_2, \ldots).$$

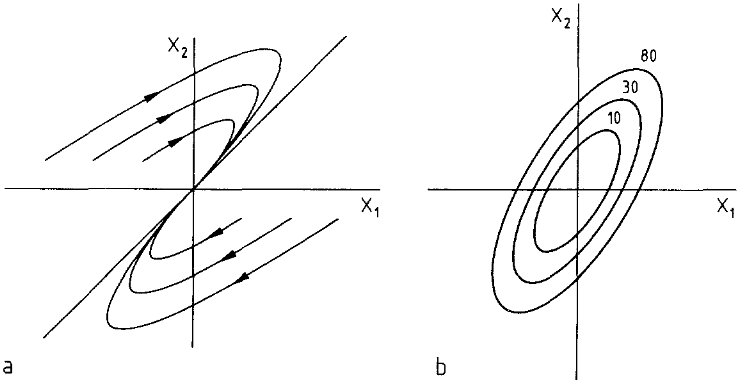

Fig. 4. a The trajectories from some arbitrary initial points in Example 3. **b** The contour map of F_2. It has the minimum value, 0, at the origin, i.e. the equilibrium point. Since the equilibrium point of Eq. (9) is stable, the trajectory attains the equilibrium point. As a result the second species finally obtains the minimum fitness although it changes its trait in the direction of fitness increasing

Just before, the evolutionary dynamics of n trait-values is given by

$$\frac{dx_i}{dt} = k_i(x_1, \ldots, x_n)\frac{\partial F}{\partial x_i} \quad (i = 1, \ldots, n). \tag{10}$$

The equilibrium point x_i^* satisfies $\partial F/\partial x_i = 0$, which is the necessary condition for maximal fitness. Equation (10) is very similar to "the gradient system", except for the multiplicity of k_i. The derivative of F by t is given by

$$\frac{dF}{dt} = \sum \frac{\partial F}{\partial x_i}\frac{dx_i}{dt} = \sum k_i \left(\frac{\partial F}{\partial x_i}\right)^2 \geqslant 0.$$

dF/dt is equal to zero if and only if it is on an equilibrium point. Thus F increases with time like a Liapunov function and approaches one of the maximal points. It may be considered as a goal of evolution. Therefore the solution obtained by the optimal strategy theory is always SDS [15].

In this paper we have presented only simple examples each of which has a single equilibrium point. When there is more than one equilibrium point, we must analyze the global properties of our dynamical model. In such cases then, we cannot discuss whether the trajectory actually attains those equilibria or not without knowing the initial condition. It should also be noticed that when the equilibrium point is located on the boundary of a possible strategy set, we cannot directly apply the present criterion. In this case, we must analyze the dynamical model by assuming $k_i = 0$ on the boundary.

Appendix 1

Proof of Theorem 2

The linear part of Eq. (4) at the equilibrium point $(x_1^*, \ldots, x_n^*)$ is given by

$$(*) \begin{pmatrix} k_1^* & \ldots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \ldots & k_n^* \end{pmatrix} J_* \left(\frac{\partial F_1}{\partial x_1}, \ldots, \frac{\partial F_n}{\partial x_n}\right),$$

where $k_i^* = k_i(x_1^*, \ldots, x_n^*)$ for each $i = 1, \ldots, n$ and x^* satisfies n equations $\partial F_i/\partial x_i = 0 \quad (i = 1, \ldots, n)$. For ease of notation, we drop "*" of k_i^*. By condition (II), the stability must persist under any small perturbation of this linear part. Hence, the degenerate cases are eliminated and all of the eigenvalues of $(*)$ have negative real parts for SDS equilibrium points.

(*i*) *Case $n = 1$.* The condition that the eigenvalue has a negative real part is calculated easily as follows:

$$k_1(x_1^*)\left.\frac{\partial^2 F_1}{\partial x_1^2}\right|_* < 0.$$

Thus the SDS condition is

$$\left.\frac{\partial^2 F_1}{\partial x_1^2}\right|_* < 0.$$

(*ii*) *Case $n = 2$.* When each eigenvalue, λ, which satisfies the following equation, has a negative real part, the system of 2-species is locally stable:

$$\lambda^2 + a_1\lambda + a_2 = 0,$$

where

$$a_1 = -k_1 \left.\frac{\partial^2 F_1}{\partial x_1^2}\right|_* - k_2 \left.\frac{\partial^2 F_2}{\partial x_2^2}\right|_*$$

$$a_2 = k_1 k_2 J_* \left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}\right).$$

The stability condition is $a_1 > 0$ and $a_2 > 0$. Thus the stability condition for arbitrary positive functions k_1, k_2 can be written as Eq. (5.2).

(*iii*) *Case $n = 3$.* When each eigenvalue, λ, which satisfies the following equation, has a negative real part, the system of 3-species is locally stable:

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0,$$

where

$$\left.\begin{aligned} a_1 &= -k_1 \left.\frac{\partial^2 F_1}{\partial x_1^2}\right|_* - k_2 \left.\frac{\partial^2 F_2}{\partial x_2^2}\right|_* - k_3 \left.\frac{\partial^2 F_3}{\partial x_3^2}\right|_* \\ a_2 &= k_1 k_2 J_* \left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}\right) + k_2 k_3 J_* \left(\frac{\partial F_2}{\partial x_2}, \frac{\partial F_3}{\partial x_3}\right) + k_3 k_1 J_* \left(\frac{\partial F_3}{\partial x_3}, \frac{\partial F_1}{\partial x_1}\right) \\ a_3 &= -k_1 k_2 k_3 J_* \left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}, \frac{\partial F_3}{\partial x_3}\right). \end{aligned}\right\} \quad \text{(A1)}$$

From Theorem 1 and Eq. (5.1),

$$\frac{\partial^2 F_i}{\partial x_i^2} < 0 \quad (i = 1, 2, 3). \tag{A2}$$

In addition, the 2×2 minors should be strictly positive according to Theorem 1 and Eq. (5.2). Thus, M_{12}, M_{23} and M_{31} are all positive. The Routh–Hurwitz conditions of local stability are [8, 13]

$$a_1 > 0, \tag{A3.1}$$

$$a_3 > 0, \tag{A3.2}$$

$$a_1 a_2 > a_3. \tag{A3.3}$$

Equation (A3.1) is already satisfied by Eq. (A2). Substituting Eq. (A1) into Eqs. (A3.2, 3) and dividing Eqs. (A3.2, 3) by

$$-k_1 k_2 k_3 \left(\frac{\partial^2 F_1}{\partial x_1^2}\frac{\partial^2 F_2}{\partial x_2^2}\frac{\partial^2 F_3}{\partial x_3^2}\right)_* > 0$$

(the left-hand side is positive from Eq. (A2)), we obtain

$$D = \left(\frac{\partial^2 F_1}{\partial x_1^2}\frac{\partial^2 F_2}{\partial x_2^2}\frac{\partial^2 F_3}{\partial x_3^2}\right)_*^{-1} J_* \left(\frac{\partial F_1}{\partial x_1}, \frac{\partial F_2}{\partial x_2}, \frac{\partial F_3}{\partial x_3}\right) > 0 \tag{A4}$$

and

$$\left(\frac{k_1'}{k_3'}M_{12}+\frac{k_3'}{k_1'}M_{23}\right)+\left(\frac{k_2'}{k_1'}M_{23}+\frac{k_1'}{k_2'}M_{31}\right)$$

$$+\left(\frac{k_3'}{k_2'}M_{31}+\frac{k_2'}{k_3'}M_{12}\right)+M_{12}+M_{23}+M_{31}>D, \qquad (\mathrm{A5})$$

where

$$k_i'=k_i\frac{\partial^2 F_i}{\partial x_i^2}, \qquad M_{ij}=\left(\frac{\partial^2 F_i}{\partial x_i^2}\frac{\partial^2 F_j}{\partial x_j^2}\right)^{-1} J_*\left(\frac{\partial F_i}{\partial x_i},\frac{\partial F_j}{\partial x_j}\right).$$

The left-hand side of Eq. (A5) is larger than or equal to

$$2\sqrt{M_{12}M_{23}}+2\sqrt{M_{23}M_{31}}+2\sqrt{M_{31}M_{12}}+M_{12}+M_{23}+M_{31}$$
$$=(\sqrt{M_{12}}+\sqrt{M_{23}}+\sqrt{M_{31}})^2.$$

(When the equality holds for $k_1':k_2':k_3'=\sqrt{M_{23}}:\sqrt{M_{31}}:\sqrt{M_{12}}$.) Thus

$$\sqrt{D}<\sqrt{M_{12}}+\sqrt{M_{23}}+\sqrt{M_{31}}.$$

Appendix 2

If a set of the fitness functions, F_1 and F_2, has a Nash equilibrium, then

$$\left.\frac{\partial F_1}{\partial x_1}\right|_*=\left.\frac{\partial F_2}{\partial x_2}\right|_*=0, \qquad \left.\frac{\partial^2 F_i}{\partial x_i^2}\right|_*<0 \quad (i=1,2), \qquad (\mathrm{A6.1})$$

where $*$ means the derivative coefficient at an equilibrium. If there exists a function of $h(z)$ such that $F_1=h(F_2)$ and $dh/dz<0$,

$$\frac{\partial F_1}{\partial x_1}=h'(z)\frac{\partial F_2}{\partial x_1}, \qquad \frac{\partial F_1}{\partial x_2}=h'(z)\frac{\partial F_2}{\partial x_2}.$$

From (A6.1) and $h'(z)<0$,

$$\left.\frac{\partial F_1}{\partial x_2}\right|_*=\left.\frac{\partial F_2}{\partial x_1}\right|_*=0. \qquad (\mathrm{A6.2})$$

The second derivatives at the Nash equilibrium are easily obtained in terms of Eqs. (A6.1, 2) as follows

$$\left.\frac{\partial^2 F_1}{\partial x_i\,\partial x_j}\right|_*=h'(z)\big|_{z=F_2(x_1^*,x_2^*)}\left.\frac{\partial^2 F_2}{\partial x_i\,\partial x_j}\right|_* \quad (i,j=1,2) \qquad (\mathrm{A6.3})$$

Thus the former part of Theorem 3 holds. If Eq. (A6.3) is satisfied, the Nash equilibrium point is SDS because

$$J_*\left(\frac{\partial F_1}{\partial x_1},\frac{\partial F_2}{\partial x_2}\right)=\frac{\partial^2 F_1}{\partial x_1^2}\frac{\partial^2 F_2}{\partial x_2^2}-\frac{\partial^2 F_2}{\partial x_1\,\partial x_2}\left(h'(z)\frac{\partial^2 F_2}{\partial x_1\,\partial x_2}\right)>0$$

from Theorem 2. Thus the latter part of Theorem 3 holds. (Q.E.D.)

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