Evolutionary dynamics and stability in discrete and continuous games

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ABSTRACT

We investigate the correspondence between discrete-trait games (for example, matrix games) and continuous-trait games, paying particular attention to the standard criteria for evolutionary stability. We show that the standard evolutionarily stable strategy conditions for discrete-trait games can be seen as a special case of the conditions employed in continuous-trait games.

Keywords: adaptive and replicator dynamics, discrete and continuous games, evolutionary stability.

INTRODUCTION

When constructing a mathematical model of some evolutionary phenomenon, there are several different possible approaches. For example, when modelling the evolution of a population's sex ratio (i.e. the proportion of individuals in the population that are male), it is possible to use a single-locus genetic model, an inclusive fitness model, any of a few different types of game-theoretic models, among other approaches (Crow and Kimura, 1970; Charnov, 1982; Bulmer, 1994). Each approach embodies a slightly different set of assumptions, and each has different strengths and weaknesses. Clearly, it is desirable that the biological conclusions that are drawn are, in large part, independent of the type of model used. Whether this is the case can be checked for any given model simply by constructing different types of models and comparing their predictions. It would be more useful, however, to have general theoretical results that specify when different approaches give similar results irrespective of the biological phenomenon being modelled.

Over the last few years, such results have been obtained for some different modelling approaches. In particular, several authors have detailed the general correspondence between phenotypic quantitative genetic models and game-theoretic models for continuous traits (Charlesworth, 1990; Iwasa *et al.*, 1991; Taper and Case, 1992; Abrams *et al.*, 1993a; Taylor, 1996; Taylor and Day, 1997). This has clarified the interrelationships between these modelling approaches, and it has also made the assumptions embodied by each more transparent. Moreover, connecting these two techniques has shed some light on the various stability conditions that are sometimes employed in evolutionary game theory (see, for example,

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Taylor and Day, 1997). The fact that such game-theoretic models are now known to give the same predictions as phenotypic quantitative genetic models under certain assumptions is extremely useful because game-theoretic models are typically far easier to analyse.

Within the context of game-theoretic modelling itself, however, a dichotomy has developed between discrete-trait game theory (which often involves matrix games) and continuous-trait game theory (Bulmer, 1994); these two game-theoretic approaches each have their own sets of conditions for characterizing evolutionary outcomes. Our purpose here is to illustrate a simple correspondence between these two types of game-theoretic models. By doing so, the methods used for continuous-trait games shed some light on those used in discrete-trait games (and vice versa). In particular, discrete-trait games can be formulated as special cases of the more general continuous-trait approach. As a result, the well-known conditions for characterizing evolutionary outcomes in discrete-trait games can be seen as special cases of the conditions employed in continuous-trait games. We focus here on symmetric games, although similar results can be obtained for asymmetric games.

We begin with a brief but systematic account of evolutionary stability for continuous-trait games, and then we consider discrete-trait games and relate the two types of models.

CONTINUOUS TRAITS

We work here with a one- or multi-dimensional quantitative trait $\mathbf{z}$, determined by a large number of loci. For simplicity, we suppose that gene action is additive in all respects, so that $\mathbf{z}$ is also the additive genetic value of the trait. The population will be described by the distribution of $\mathbf{z}$.

We suppose that selection acts on $\mathbf{z}$ and we are interested in the way in which it causes the population distribution to change. We are particularly interested to identify equilibrium distributions that are stable under the action of selection, in the sense that if the distribution is perturbed it will tend to return to the equilibrium. To get hold of the action of selection, we need to know how the fitness of an individual is determined and it is often assumed that this depends upon: (i) the individual's own trait; (ii) the trait distribution in the population (frequency dependence); and (iii) the population size (density dependence).

Here, we ignore (iii) and restrict ourselves to the dependence in (i) and (ii). A common assumption, which we shall adopt here, is that the frequency dependence works only through the population mean $\bar{\mathbf{z}}$; that is, individual fitness has the form:

$$W(\mathbf{z}, \bar{\mathbf{z}}) \tag{1}$$

This assumption is referred to as playing the field (Maynard Smith, 1982).

Turning now to the question of stability, a particularly simple situation occurs if the population is concentrated at a single point $\mathbf{z}^*$. In this case, we say that $\mathbf{z}^*$ is an evolutionarily stable strategy (ESS) if

$$W(\mathbf{z}, \bar{\mathbf{z}}) < W(\mathbf{z}^*, \bar{\mathbf{z}}) \tag{2}$$

for any $\mathbf{z} \neq \mathbf{z}^*$ and sufficiently small $\varepsilon > 0$, where $\bar{\mathbf{z}} = \varepsilon \mathbf{z} + (1 - \varepsilon)\,\mathbf{z}^*$ is the mean of a population with trait $\mathbf{z}$ at frequency ε and trait $\mathbf{z}^*$ at frequency $1 - \varepsilon$. Condition (2) says that when a proportion, ε, of the population plays a mutant strategy, $\mathbf{z}$, and $1 - \varepsilon$ plays the ESS strategy $\mathbf{z}^*$, then the $\mathbf{z}$ players are less fit. In the limit as $\varepsilon \to 0$, we get the *Nash equilibrium condition*

$$W(\mathbf{z}, \mathbf{z}^*) \leq W(\mathbf{z}^*, \mathbf{z}^*) \tag{3}$$

which says that the fitness of any rare mutant playing **z** in a **z***-population is maximized by using the strategy **z***. Conditions (2) and (3) can be global and hold for any **z**, or local and hold for **z** sufficiently close to **z***. Locally, the Nash condition (3) implies the first-order *equilibrium condition*

$$\nabla W |_{\mathbf{z} = \bar{\mathbf{z}} = \mathbf{z}^*} = 0 \tag{4}$$

where $\nabla = (\partial/\partial z_1, \partial/\partial z_2, \ldots, \partial/\partial z_n)$ is the gradient operator, and the second-order *evolutionary stability* (ES) *condition*, that the Hessian matrix,

$$H_{ij} = \left[\frac{\partial^2 W}{\partial z_i \partial z_j} \right]_{\mathbf{z} = \bar{\mathbf{z}} = \mathbf{z}^*} \tag{5}$$

be negative semi-definite. The one-dimensional (scalar z) versions of these are the equilibrium condition

$$\frac{\partial W}{\partial z} \bigg|_{z = \bar{z} = z^*} = 0 \tag{6}$$

and the ES condition

$$\frac{\partial^2 W}{\partial z^2} \bigg|_{z = \bar{z} = z^*} \leq 0 \tag{7}$$

The field known as 'adaptive dynamics' refers to values of **z*** that satisfy the equilibrium condition (4) or (6) as evolutionarily singular states (Dieckmann and Law, 1996; Geritz *et al.*, 1998) and it refers to those values of **z*** that satisfy (4) or (6) but that do *not* satisfy (5) or (7) as branching points (technically, branching points also must satisfy the convergence stability condition, which is outlined below as well). Interestingly, it has been shown that condition (7) is related to stability conditions for the evolution of the genetic variance in quantitative genetic models as well (Taylor and Day, 1997).

This conception of evolutionary stability is static in that it says nothing about how a population evolves. Considerable work over the past 20 years has explored ways in which a dynamic might be introduced. As a first step, Eshel and Motro (1981) and Eshel (1983) proposed a condition that should hold for a scalar equilibrium z^* to be dynamically stable: for a population mean $\bar{z}$ just below, z^*, mutants just above $\bar{z}$ should be favoured, and for a population mean $\bar{z}$ just above z^*, mutants just below $\bar{z}$ should be favoured. This is accomplished by requiring the derivative $\dfrac{\partial W}{\partial z}\bigg|_{z = \bar{z}}$ to be positive when $\bar{z} < z^*$ and negative when $\bar{z} > z^*$. This can be formulated algebraically as

$$(\bar{z} - z^*) \frac{\partial W}{\partial z} \bigg|_{z = \bar{z}} < 0 \tag{8}$$

or with a slightly stronger local second-derivative condition as

$$\frac{\mathrm{d}}{\mathrm{d}\bar{z}} \left[\frac{\partial W}{\partial z} \bigg|_{z = \bar{z}} \right]_{\bar{z} = z^*} < 0 \tag{9}$$

We term (8) or (9) the *convergence stability* (CS) condition (Christiansen, 1991). An obvious candidate for a multi-dimensional version of this condition (Leimar, in press) is to generalize (8) as

$$(\bar{\mathbf{z}} - \mathbf{z}^*)^{\mathrm{T}} \cdot \nabla W \big|_{\mathbf{z} = \bar{\mathbf{z}}} < 0 \tag{10}$$

which says that the gradient $\nabla W|_{\mathbf{z} = \bar{\mathbf{z}}}$ should point more in the direction of $\mathbf{z}^* - \bar{\mathbf{z}}$ than in the opposite direction. We will refer to (10) as the multi-dimensional CS condition and, as we will see (equation 22), it provides a useful connection to discrete-trait games.

A full dynamic requires a specification of the rate of frequency change of each $\mathbf{z}$ value and a common assumption is that this is proportional to its relative fitness. If these changes are averaged, we get a fundamental equation for the rate of change of the population mean:

$$\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}t} = \mathrm{cov}(\mathbf{z}, \, W(\mathbf{z}, \bar{\mathbf{z}})) \tag{11}$$

This classic equation, which displays the change in character mean as a covariance between the character value and fitness, is valid for both a discrete and a continuous distribution and was independently discovered by Robertson (1966), Li (1967) and Price (1970). We might have inserted a constant into equation (11) to translate fitness into rate of change, but we will assume that fitness has been scaled to accomplish this.

A simple approximation of equation (11) is obtained if we assume that the first derivative of W does not change much over the bulk of the $\mathbf{z}$-distribution. In this case $\mathrm{cov}(\mathbf{z}, W)$ can be approximated by $\mathbf{G}\nabla W|_{\mathbf{z} = \bar{\mathbf{z}}}$, where $\mathbf{G}$ is the covariance matrix of the trait $\mathbf{z}$ and ∇ is the gradient operator. This approximation is exact if W is a linear function of $\mathbf{z}$, having the form $W = a(\bar{\mathbf{z}}) + \mathbf{b}(\bar{\mathbf{z}})^{\mathrm{T}} \mathbf{z}$. With this approximation, (11) becomes

$$\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}t} = \mathbf{G}(\bar{\mathbf{z}})\nabla W \big|_{\mathbf{z} = \bar{\mathbf{z}}} \tag{12}$$

where we have allowed the additive covariance to depend on the population mean. The scalar version of equation (12) is

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = G(\bar{z}) \frac{\partial W}{\partial z} \bigg|_{z = \bar{z}} \tag{13}$$

(Iwasa *et al.*, 1991; Abrams *et al.*, 1993b; Taylor, 1996; for the derivation of a similar equation, see Roughgarden, 1983; Vincent and Brown, 1988). Additionally, an important special case of equation (12) arises when the $\mathbf{z}$-distribution is Gaussian; in this case, integration by parts yields

$$\frac{\mathrm{d}\bar{\mathbf{z}}}{\mathrm{d}t} = \mathbf{G}(\bar{\mathbf{z}})E(\nabla W \big|_{\mathbf{z} = \bar{\mathbf{z}}}) \tag{14}$$

(Lande and Arnold, 1983; Taylor and Day, 1997). Equation (14) is exact for any smooth fitness function W.

Further justification for the dynamic (12) comes from the fact that it provides an approximation to phenotypic quantitative genetic models under certain assumptions (Charlesworth, 1990; Iwasa *et al.*, 1991; Taper and Case, 1992; Abrams *et al.*, 1993a; Taylor, 1996). We refer to the evolutionary dynamic (12) and (13) as the adaptive dynamic (Hofbauer and Sigmund, 1998; also see Dieckmann and Law, 1996; Geritz *et al.*, 1998).

Note that the equilibria of (12) and (13) correspond to values of $\bar{z}$ that satisfy the first-order condition (4) and (6) (neglecting equilibria that occur where the genetic variance is zero), and we can use the local stability condition for (12) and (13) near such equilibria as a stability condition guaranteeing evolution towards such equilibria. We refer to this stability condition as the 'adaptive dynamic stability' condition (the ADS condition).

Note that, in the scalar case, the ADS condition (stability of 14) is equivalent to the CS condition (9), but this is not so in the multivariate case; that is, the stability of (12) is not equivalent to the multi-dimensional CS condition (10). Similar findings have been discussed by Takada and Kigami (1991).

DISCRETE TRAITS

We now see how discrete-trait games correspond to the general theory presented above. The exposition below is presented for quite a broad class of discrete-trait games, although our primary focus will be on the special case of matrix games, as this has received most of the attention in the literature. In the typical set-up, there are a finite number of alternative discrete actions indexed by i with $i = 1, \ldots, n$. An individual that plays action i with probability p_i will have strategy vector $\mathbf{p} = (p_i)$ and the population average strategy will be denoted $\bar{\mathbf{p}}$. Here, $\mathbf{p}$ plays the role of the vector $\mathbf{z}$ in the general theory above. The population can be viewed in one of two ways. In the first (the 'mixed-strategy' interpretation), each individual randomly chooses an action on any given encounter according to the probability distribution $\mathbf{p}$. In the second interpretation (the 'pure-strategy' interpretation), each individual within the population uses only one of the n actions. An individual's strategy can still be represented by a vector of probabilities but only one entry is non-zero (and it is equal to 1). Under this interpretation, the components of $\bar{\mathbf{p}}$ give the proportion of the population using different actions i.

We now specify fitness. In the pure-strategy interpretation, we define the fitness of an i-individual in a $\bar{\mathbf{p}}$ population to be $w_i(\bar{\mathbf{p}})$. In the mixed-strategy interpretation, we assume that the fitness of a $\mathbf{p}$-strategist is the $\mathbf{p}$-average of such w_i. Fitness is then

$$W(\mathbf{p}, \bar{\mathbf{p}}) = \mathbf{p}^{\mathrm{T}} \mathbf{w}(\bar{\mathbf{p}}) \qquad (15)$$

where $\mathbf{w}(\bar{\mathbf{p}})$ is the vector with components $w_i(\bar{\mathbf{p}})$. Games with this property are called linear, because W is a linear function of $\mathbf{p}$.

In an important class of games, called *matrix games*, W is also linear in $\bar{\mathbf{p}}$ and thus $\mathbf{w}$ has the form $\mathbf{w}(\bar{\mathbf{p}}) = \mathbf{A}\bar{\mathbf{p}}$ for an $n \times n$ matrix $\mathbf{A} = (a_{ij})$. Such games can be regarded as the result of a sequence of pairwise encounters with random individuals in the population. Here we take a_{ij} to be the fitness of an i-strategist against a j-opponent, and assume that overall fitness is the average fitness over many bouts, then $w_i(\bar{\mathbf{p}}) = \Sigma_j a_{ij} \bar{p}_j$ and

$$W(\mathbf{p}, \bar{\mathbf{p}}) = \mathbf{p}^{\mathrm{T}} \mathbf{A} \bar{\mathbf{p}} \qquad (16)$$

Much of the classical work in evolutionary game theory is concerned with matrix games.

We now interpret the stability results of the continuous-trait theory in the discrete-trait game set-up. The Nash equilibrium condition (3) is

$$\mathbf{p}^{\mathrm{T}} \mathbf{w}(\mathbf{p}*) \leq \mathbf{p}*^{\mathrm{T}} \mathbf{w}(\mathbf{p}*) \qquad (17)$$

and the ESS condition (2) is

$$\mathbf{p}^{\mathrm{T}} \mathbf{w}(\bar{\mathbf{p}}) < \mathbf{p}*^{\mathrm{T}} \mathbf{w}(\bar{\mathbf{p}}) \qquad (18)$$

for any $\mathbf{p} \neq \mathbf{p}^*$ and sufficiently small $\varepsilon > 0$, where $\bar{\mathbf{p}} = \varepsilon\mathbf{p} + (1 - \varepsilon)\,\mathbf{p}^*$ (Hofbauer and Sigmund, 1998). For matrix games, this condition becomes

$$\mathbf{p}^{\mathrm{T}}\mathbf{A}\bar{\mathbf{p}} < \mathbf{p}^{*\mathrm{T}}\mathbf{A}\bar{\mathbf{p}} \tag{19}$$

In this case, if we take the limit as $\varepsilon \to 0$, we get

$$\mathbf{p}^{\mathrm{T}}\mathbf{A}\mathbf{p}^* \leq \mathbf{p}^{*\,\mathrm{T}}\mathbf{A}\mathbf{p}^* \tag{20}$$

and, if equality holds in (20), then for (19) to hold, we must have

$$\mathbf{p}^{\mathrm{T}}\mathbf{A}\mathbf{p} < \mathbf{p}^{*\mathrm{T}}\mathbf{A}\mathbf{p} \tag{21}$$

Conditions (20) and (21) are the classic matrix ESS conditions on $\mathbf{p}^*$ (Maynard Smith, 1974; Hofbauer and Sigmund, 1998, ch. 6). In the mixed-strategy interpretation we call $\mathbf{p}^*$ an *evolutionarily stable strategy*, and in the pure-strategy interpretation it is called an *evolutionarily stable state*. Thus, for linear games, the continuous and discrete formulations of the ESS are equivalent.

Now we look at dynamic stability. The CS condition (10) becomes

$$(\bar{\mathbf{p}} - \mathbf{p}^*)^{\mathrm{T}}\mathbf{w}(\bar{\mathbf{p}}) < 0 \tag{22}$$

If we write $\bar{\mathbf{p}} = \varepsilon\mathbf{p} + (1 - \varepsilon)\,\mathbf{p}^*$, this becomes

$$\mathbf{p}^{\mathrm{T}}\mathbf{w}(\bar{\mathbf{p}}) < \mathbf{p}^{*\mathrm{T}}\mathbf{w}(\bar{\mathbf{p}}) \tag{23}$$

which is the ESS condition (18). In other words, for linear games, the CSS and ESS conditions are equivalent. Incidentally, this implies that so-called branching points (Dieckmann and Law, 1996; Geritz *et al.*, 1998) cannot occur in linear games.

We turn now to the adaptive dynamics equation (12), which becomes:

$$\frac{\mathrm{d}\bar{\mathbf{p}}}{\mathrm{d}t} = \mathrm{cov}(\mathbf{p}, \mathbf{p}^{\mathrm{T}}\mathbf{w}(\bar{\mathbf{p}})) = \mathrm{cov}(\mathbf{p}, \mathbf{p})\mathbf{w}(\bar{\mathbf{p}}) = \mathbf{G}(\bar{\mathbf{p}})\mathbf{w}(\bar{\mathbf{p}}) \tag{24}$$

This equation holds for both the pure- and the mixed-strategy interpretation and any distribution on the $\mathbf{p}$-simplex. An important special case is found for the pure-strategy interpretation. In this case, the distribution is concentrated on the vertices of the simplex (with mass p_i at the pure strategy i), and

$$\mathrm{cov}(p_i, p_i) = p_i(1 - p_i)$$

$$\mathrm{cov}(p_i, p_j) = -p_i p_i \; (i \neq j)$$

With this, equation (24) can be written

$$\frac{\mathrm{d}\bar{p}_i}{\mathrm{d}t} = \bar{p}_i(w_i(\bar{\mathbf{p}}) - \Sigma_j \bar{p}_j w_j(\bar{\mathbf{p}})) = \bar{p}_i(w_i(\bar{\mathbf{p}}) - \overline{W}) \tag{25}$$

For the special case of matrix games, this is the well-known *replicator dynamic* (Taylor and Jonker, 1978; Zeeman, 1980; Hofbauer and Sigmund, 1998):

$$\frac{\mathrm{d}\bar{p}_i}{\mathrm{d}t} = \bar{p}_i((\mathbf{A}\bar{\mathbf{p}})_i - \bar{\mathbf{p}}\mathbf{A}\bar{\mathbf{p}}) \tag{26}$$

To our knowledge, this has not been noted before, that the replicator dynamics (26) is a special case of the adaptive dynamics (13) with the genetic covariance matrix resulting

from the constraint on the p_i's that they sum to unity. Consequently, anything that is true for the adaptive dynamics will also be true of the replicator dynamics. We note that a similar correspondence exists between explicit population genetic models and phenotypic quantitative genetic models (see, for example, Barton and Turelli, 1987).

CONCLUSIONS

The principal notions of evolutionary stability have evolved over the past 30 years. Often the notation and terminology have been awkward and temporary, but some clear concepts and terminology have now emerged. In the formulation of static stability, two aspects have been identified. For the population to persist in a uniform state, it must be the case that rare deviants are punished, where 'rare' signifies that the deviants have no effect on population-wide average behaviour. Secondly, if the population as a whole is shifted away from this equilibrium, a deviant behaviour which moves the average state back towards equilibrium is favoured. The first of these is now called evolutionary stability and the second of these is called convergence stability. The term evolutionarily stable state (ESS) is reserved for a condition that has aspects of both evolutionary and convergence stability. Importantly, however, as shown above, these two types of stability are equivalent for linear games.

More recently, the notion of convergence stability was sharpened through explicit dynamic equations that attempted to track the average evolutionary trajectory of a population which was disturbed from equilibrium. The two notions of replicator dynamics for discrete-trait games and adaptive dynamics for continuous-trait games shared these objectives but developed largely independently of one another.

In terms of these notions, we have here pointed to some general correspondences between discrete- and continuous-trait games. A discrete-trait game can always be recast within the framework of continuous-trait games by defining a suitable fitness function. The classic ESS condition for discrete-trait games (20–21) is seen to follow from the ESS condition (2) for continuous-trait games. Moreover, the discrete-trait replicator dynamics is seen as a special case of the more general adaptive dynamics of continuous-trait games. The main difference is that the replicator dynamics has a very special form for the genetic covariance matrix, whereas this matrix is less restricted under the general adaptive dynamics.

The results derived here demonstrate a nice correspondence between discrete- and continuous-trait games that helps to better reveal the underlying structure of both approaches. These results, combined with previous studies that demonstrate the relationship between quantitative-genetic models and continuous-trait game theoretical models (i.e. Charlesworth, 1990; Iwasa *et al.*, 1991; Taper and Case, 1992; Abrams *et al.*, 1993a; Taylor, 1996; Taylor and Day, 1997), illustrate that there are fundamental commonalities among these three seemingly disparate and widely used modelling approaches. It is interesting that all three types of model have been developed largely independently of one another, starting from very different ideas and sets of assumptions, yet all have arrived at what is essentially the same approach for characterizing evolution.

ACKNOWLEDGEMENTS

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