Evolution via Strategy Dynamics*

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Consider a community of various species newly introduced into a stable environment. Evolutionary processes acting on this community will produce, over time, a community of surviving species. Methods for predicting the evolutionarily stable strategies (ESSs) used by the surviving species are now available for a large class of dynamic population models. Here we expand a previously developed evolutionary game theory, which can be used to predict ESSs in a large class of models, by introducing strategy dynamics. By so doing, a more complete description of the evolutionary process is obtained. One not only obtains a convenient way of determining evolutionarily stable strategies, but interesting features about the evolutionary process itself can be observed. Of particular interest here, we show that the number of strategies which are evolutionarily stable can change as certain environmental factors involved with the model change. The process by which the ESS is formed is examined in terms of an "adaptive landscape" formed by our fitness generating function (G-function). The G-function has properties that enhance the likelihood that the various adaptive peaks will be occupied.   © 1993 Academic Press, Inc.

INTRODUCTION

In Maynard's Smith's words (1982), "An ESS [evolutionarily stable strategy] is a strategy such that, if all members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection." The concept of an ESS is useful in providing an idealized state (which may, in turn, be changing with time) toward which individual members of a biological community may evolve. It does not imply goal oriented behavior, but rather an ESS results from the natural selection process itself (Mitchell and Valone, 1990).

There is an extensive literature on translating the ESS concept into a methematical setting (see, for example, the reviews by Riechert and Hammerstein (1983) and Hines (1987)). This includes our own work by Vincent and Brown (1984) and Brown and Vincent (1987a) on the development of an *evolutionary game theory* for determining ESS strategies. In our previous theoretical developments, strategy dynamics were not explicitly included. If an ESS exists in a population model, the theory can be used to find it. Some of the interesting consequences include the number of species which can coexist at the ESS and how the ESS depends on the parameters used in the model (Brown and Vincent, 1992). Thus while our evolutionary game theory can be used to predict ESS strategies by means of an *ESS maximum principle*, it does not explicitly take into account any mechanism for how a population attains an ESS. Indeed it was not necessary, since this theory dealt not with how an ESS evolves but rather the conditions under which it may exist. The strategies obtained using the ESS maximum principle can be tested against arbitrary "mutant" strategies by simply examining the dynamics of individual population densities as time goes on (see, for example, Brown and Vincent, 1987c; Vincent and Fisher, 1988).

Here we will include a distribution of strategies that each species transfers to its offspring. From this, we develop a strategy dynamic. By appending the strategy dynamic to the population dynamic, we gain a more detailed picture of the evolutionary process. Under the assumptions used here, the ESS maximum principle remains unchanged, but now one can examine the evolutionary process itself and gain insights into the dynamics of how strategies evolve toward an ESS.

Since the fitness of each individual organism in a biological community may be affected by the strategies of all other individuals, the essential element of a "game" exists. This game is an evolutionary game where the individual organisms (players) inherit their survival strategies (phenotypic characteristics) from a continuous play of the game from generation to generation. The evolutionary game includes both ecological and evolutionary processes. The evological process involves the interaction between

individuals and the environment that determine fitness. The evolutionary process involves dynamics which translates the fitness of an individual into changes in the number and frequency of individuals using particular strategies. Through appropriate models, the evolutionary game may be given a mathematical setting. Most commonly, the strategies are assumed to be constants associated with certain adaptive parameters in the model. The ESS is a particular strategy (or vector of strategies) which provide the stability property described by Maynard Smith.

In the development of the ESS maximum principle, it was assumed that individuals breed true. This assumption is most easily visualized in terms of asexual or clonal reproduction, where there is not variance in the strategies of the parent's offspring and there is no cross brreding between individuals of different strategies. Under this assumption, the strategies themselves could not evolve and individuals could be (and were) identified by their strategy values. In such a setting, the evolutionary process simply tests the survivability of different strategies played together and allows for the experimental determination of an ESS in a given evolutionary game by continually 'seeding" the modeled community with random strategies (Brown and Vincent, 1987a). This procedure is neither computationally efficient (when compared with using the ESS maximum principle) nor is it likely to occur in nature, except perhaps, in some situations where a constant flow of different species over a given "environment" can be expected (e.g., flow a wind born leaf fungi and molds over trees or the flow of tide driven barnacle spores over boat hulls). In such situations, an ESS strategy may arise in an evolving community.

The breed true assumption does not reduce the usefulness of the ESS maximum principle for finding ESS strategies, it simply sweeps under the evolutionary rug the issue of how an ESS might come about. Indeed, the necessary conditions provided by the principle can be used to analytically determine ESS strategies whether the model requires individuals to breed true or not.

If we relax the assumption that individuals breed true, we can no longer identify individuals by their own strategies (as was done in our previous analysis). Rather, we will, in a manner analogous to quantitative genetics, identify an individual by a characteristic strategy $\mathbf{u}^i$ which distinguishes the entire interbreeding population to which the individual belongs. The strategies $\mathbf{u}^i$ may be either scalar $\mathbf{u}^i = u^i$, or vector-valued $\mathbf{u}^i = [u_1^i, ..., u_\beta^i]$.

We will say that interbreeding individuals are of the same *species* provided that they *are evolutionary identical* (Vincent and Brown, 1988). Two individuals are said to be evolutionarily identical if they share the same strategy set and if the ecological consequences of using those strategies are the same for both individuals. Evolutionarily identical individuals will not be of the same species unless they can interbreed.

We will identify the population size of various species with the numerical label x_i. In this paper cross breeding between species is not allowed, but within each species there will be a distribution of strategies which allows for evolution to take place. The mean strategy $\bar{u}^i$ used by individuals of species x_i may, through evolution, change with time. Evolutionarily identical species may, or may not, evolve to the same mean strategy.

Consider a community of r species all of which are evolutionarily identical. For notational convince we will designate the vector of population densities for all species in the community by

$$\mathbf{x} = [x_1, ..., x_r],\tag{1}$$

and all strategies used by the r different species in the community by

$$\tilde{\mathbf{u}} = [\mathbf{u}^1, ..., \mathbf{u}^r].\tag{2}$$

Assume that the environment is fixed so that a fitness function, $H_i[\tilde{\mathbf{u}}, \mathbf{x}(t)]$ for each of the species may be defined in terms of $\mathbf{x}$ and $\tilde{\mathbf{u}}$. By definition of fitness, changes in population density for a given species is described by difference equations of the form

$$x_i(t+1) = x_i(t)\{1 + H_i[\tilde{\mathbf{u}}, \mathbf{x}(t)]\},\tag{3}$$

where t is a generation counter. Henceforth, when the meaning is clear, we will drop the t from variables (e.g., $\mathbf{x}(t)]$ which are evaluated at generation time t. Alternate difference equation models or differential equation models are also possible and will yield similar results (Vincent and Fisher, 1988).

We have previously introduced the notation of a *fitness generating function* which we call a *G-function* for short (Vincent and Brown, 1984; Brown and Vincent, 1987a; Vincent and Brown, 1988). See also Parker and Maynard Smith (1990), Iwasa *et al.* (1991), and Taper and Case (1992) for developments with similarities to the *G*-function approach used here. The *G*-function is required for the development of the *ESS Maximum Principle*, which gives necessary conditions for an ESS. A function $G(\mathbf{u}, \tilde{\mathbf{u}}, \mathbf{x})$ is said to be a *G*-function for the r species in a community of evolutionarily identical individuals if

$$G(\mathbf{u}^i, \tilde{\mathbf{u}}, \mathbf{x}) = H_i(\tilde{\mathbf{u}}, \mathbf{x})\tag{4}$$

for all of the indices i corresponding to the r species. We will assume here that the community can be described in terms of a single *G*-function. In a more general setting a given community could be composed of more than one group of evolutionarily identical individuals each with their own *G*-function. This more general setting has been discussed in detail elsewhere (Brown and Vincent, 1987b; Vincent and Brown, 1989).

The G-function has the property that the fitness of an individual, H_i, using one of the strategies of $\tilde{u}$ is obtained when u is replaced by that individual's strategy. Thinking of the variables $\tilde{u}$ and x as defining the current environment, it follows that the fitness of an individual then depends on its "choice" for u.

We will need to distinguish between strategies which make up the ESS and those strategies which do not. Let the composite of the first σ strategies of $\tilde{u}$ be called the coalition vector $u^c = [u^1, ..., u^\sigma]$ where $\sigma \geqslant 1$. Let the composite of the remaining $r - \sigma$ strategies be called the remnant vector designated by $u^m = [u^{\sigma + 1}, ..., u^r]$. The total number of all individuals in the community is given by

$$N = \sum_{i=1}^{r} x_i. \tag{5}$$

We will assume that the population dynamics are such that N remains finite for all time t. An ESS may now be defined in terms of the coalition vector:

A coalition vector u^c is said to be an ESS if for all remnant strategies u^m, and all initial frequencies $x_i(0)/N$ satisfying the conditions

   (i) $x_i(0) > 0$ for $i = 1, ..., \sigma$

   (ii) $x_i(0) \geqslant 0$ for $i = \sigma + 1, ..., r$

   (iii) $1 - \varepsilon < \{\sum x_i(0)/N, i = 1 ... \sigma\} < 1$, for some ε in the interval $0 < \varepsilon < 1$,

the dynamics given by (3) yields

$$\lim_{t \to \infty} \sum_{i=1}^{\sigma} \frac{x_i(t)}{N} = 1 \tag{6}$$

with

$$\lim_{t \to \infty} \frac{x_i(t)}{N} > 0, \qquad i = 1 ... \sigma. \tag{7}$$

Under this definition any number of non-ESS remnant strategies are allowed by simply specifying a remnant vector with non-zero initial density. Also the ESS may be a coalition of any number of strategies with non-zero initial densities. The definition is global with respect to strategies, but it is local with respect to frequency since $\{\sum x_i(0)/N, i = 1 ... \sigma\}$ is allowed to be arbitrarily close to 1. If the definition holds for ε close to one then the ESS would be a global attractor in frequency space as well. Since

$$\sum_{i=1}^{\sigma} x_i + \sum_{i=\sigma+1}^{r} x_i = N, \tag{8}$$

the dynamics of the non-ESS remnant individuals must obey

$$\lim_{t \to \infty} \sum_{i=\sigma+1}^{r} \frac{x_i(t)}{N} = 0. \tag{9}$$

This definition is consistent with Maynard Smith's word definition given earlier. Species identified by the strategies in the coalition vector $\mathbf{u}^c$ will persist through time not matter how many remnant strategies are introduced. Moreover, the number of individuals using non-ESS stategies will become vanishingly small with time.

We have previously shown (Vincent, 1985; Brown and Vincent, 1987b; Vincent and Fisher, 1988) that this definition, along with the definition of the G-function, leads to the following *ESS Maximum Principle*:

> Let $G(\mathbf{u}, \tilde{\mathbf{u}}, \mathbf{x})$ be a fitness generating function for a community of r species. If $\mathbf{u}^c$ is an ESS such that $\{\sum x_i(t)/N, i = 1 \ldots \sigma\}$ is a monotone increasing sequence for all $t \geqslant t_m \geqslant 0$ such that $\mathbf{x}^*$ is an asymptotically stable equilibrium point for (3), then in the limit as $t \to \infty$, $G(\mathbf{u}, \tilde{\mathbf{u}}, \mathbf{x}^*)$ must take on a maximum with respect to $\mathbf{u}$ at $\mathbf{u}^1 \ldots \mathbf{u}^\sigma$.

Other, more general theorem, may be given which do not resuire asymptotic stability on $\mathbf{x}^*$ and which are not restricted to a single G-functions [Vincent and Brown, 1987; Brown and Vincent, 1987b].

In applying the ESS maximum principle, it is useful to work in terms of a G^*-function defined as follows:

$$G^*(\mathbf{u}) \triangleq G(\mathbf{u}, \tilde{\mathbf{u}}, \mathbf{x}^*), \tag{10}$$

where $\tilde{\mathbf{u}}$ and $\mathbf{x}^*$ are fixed. Assuming that the strategies are unbounded, the above theorem is equivalent to requiring that for $i = 1 \ldots \sigma$,

$$\left(\frac{\partial G^*}{\partial \mathbf{u}} \right)_{\mathbf{u} = \mathbf{u}^i} = 0, \tag{11}$$

and for scalar u

$$\left(\frac{\partial^2 G^*}{\partial u^2} \right)_{u = u^i} < 0, \tag{12}$$

and the following equilibrium condition on population density:

$$G^*(\mathbf{u}^i) = 0. \tag{13}$$

STRATEGY DYNAMICS

Without specifying a particular genetic mechanism, Roughgarden (1976, 1983) developed a strategy dynamic that is applicable for density-dependent models of evolution, but not all forms of frequency dependence, The mean strategy of the population changes in proportion to the gradient of the fitness function and the population variance. This dynamic can be used to find combinations of strategies among different species that result in what he calls a *coevolutionary stable community* (CSC).

Here, we derive a strategy dynamic using the G-function in conjunction with the basic condition that variation in strategies exists within each species. In what follows, we obtain a general form for a strategy dynamic which will produce ESSs. Under certain assumptions, our strategy dynamic will give equivalent results to those obtained using Roughgarden's method. However, in general, the two methods will produce different results (Brown and Vincent, 1987c; Taper and Case, 1992).

We will obtain dynamics for both the mean strategy and the variance from the basic assumption that within each species, some variation in strategy values exists around the characteristic value $\mathbf{u}^i$. Assuming a symmetric distribution in strategies with a small variance we will show that the mean strategy dynamic is proportional to the variance times the gradient of the G-function. In addition, the variance is shown to remain constant.

Assume that individuals of species i, as identified by x_i, are actually using a distribution of strategies about $\mathbf{u}^i$. Assume that all the strategies used by species i is given by

$$\mathbf{v}^{ij} = \mathbf{u}^i + j\,\delta\mathbf{u}^i \qquad \text{where} \quad j = -m \ldots 0 \ldots m, \tag{14}$$

where $\delta\mathbf{u}^i$ is a small fixed incremental change in strategy. Let y_{ij} be the number of individuals of species i using strategy $\mathbf{v}^{ij}$. Clearly

$$x_i = \sum_{j=-m}^{m} y_{ij}. \tag{15}$$

Under this arrangement, y_{i0} is actually "playing" the strategy $\mathbf{u}^i$, which in turn characterizes all individuals of the species x_i. According to our definition of a species, an individual y_{ij} can only mate with an individual identified by y_{ik}, $j, k \in [-m \ldots 0 \ldots m]$. Assume that this breeding process results in a new strategy distribution which is of the same form. That is,

$$\mathbf{v}^{ij}(t+1) = \mathbf{u}^i(t+1) + j\,\delta\mathbf{u}^i \qquad j = -m \ldots 0 \ldots m. \tag{16}$$

It follows from (15) that at $t + 1$ the population x_i is given by

$$x_i(t+1) = \sum_{j=-m}^{m} y_{ij}(t+1). \tag{17}$$

If we denote the fitness of individuals y_{ij} by $H_{ij}(\tilde{\mathbf{u}}, \mathbf{x})$ it then follows from the definition of fitness (as per (3)) that

$$y_{ij}(t+1) = y_{ij}(t)[1 + H_{ij}(\tilde{\mathbf{u}}, \mathbf{x})], \tag{18}$$

and from (4)

$$y_{ij}(t+1) = y_{ij}(t)[1 + G(\mathbf{v}^{ij}, \tilde{\mathbf{u}}, \mathbf{x})]. \tag{19}$$

Thus (17) may be written as

$$x_i(t+1) = \sum_{j=-m}^{m} y_{ij}[1 + G(\mathbf{v}^{ij})], \tag{20}$$

where, for notational simplicity, we no longer include the functional dependance of $\tilde{\mathbf{u}}$ and $\mathbf{x}$ when writing G. If we denote the frequency of individuals of species i using strategy $\mathbf{v}^{ij}$ by

$$q_{ij} = y_{ij}/x_i, \tag{21}$$

it then follows that (20) may be written as

$$x_i(t+1) = x_i(t)[1 + \bar{G}_i], \tag{22}$$

where $\bar{G}_i$ is a mean G-function defined by

$$\bar{G}_i = \sum_{j=-m}^{m} q_{ij} G(\mathbf{v}^{ij}). \tag{23}$$

Dynamics for the Mean Strategy

The distribution of strategies within a species will result in a dynamic for the mean strategy used by a given species. The mean strategy, $\bar{\mathbf{u}}^i$ at time t is defined by

$$\bar{\mathbf{u}}^i = \sum_{j=-m}^{m} \frac{y_{ij}}{x_i} \mathbf{v}^{ij}. \tag{24}$$

Individuals y_{ij} have strategy $\mathbf{v}^{ij}$ and we wish to track how the mean $\bar{\mathbf{u}}^i$ changes as y_{ij} changes with time. The time sequence $t, t+1, \dots$ represents a series of generations in which the strategies of the various species:

1. experimence the ecological consequence of interacting with one another and the environment (we have referred to this as the inner game).

2. breed and produce offsprings (we have referred to this as the outer game).

Between t and $t+1$, while natural selection and breeding takes place, v^{ij} is constant. Therefore from (24) it follows that the mean strategy at $t+1$ is given by

$$\bar{u}^i(t+1) = \sum_{j=-m}^{m} \frac{y_{ij}(t+1)}{x_i(t+1)} v^{ij}. \tag{25}$$

Using (19) to evaluate $y_{ij}(t+1)$ and (22) to evaluate $x_i(t+1)$, it follows that

$$\bar{u}^i(t+1) = \sum_{j=-m}^{m} \frac{y_{ij}[1+G(v^{ij})]}{x_i(1+\bar{G}_i)} v^{ij}. \tag{26}$$

From the definition of q_{ij} we obtain

$$\bar{u}^i(t+1) = (1+\bar{G}_i)^{-1} \sum_{j=-m}^{m} q_{ij}[1+G(v^{ij})] v^{ij}. \tag{27}$$

It follows that

$$\bar{u}^i(t+1) = (1+\bar{G}_i)^{-1} \left[\bar{u}^i + \sum_{j=-m}^{m} q_{ij}G(v^{ij})(u^i + j\,\delta u^i) \right]. \tag{28}$$

Equation (28) is a general expression for mean strategy dynamics which is valid for non-symmetric frequency distributions and for arbitrary $j\,\delta u^i$.

If we assume that q_{ij} is symmetrically distributed about y_{i0} it then follows from (24) that

$$u^i = \bar{u}^i. \tag{29}$$

That is, the strategy which characterizes a species is also the mean strategy. Replacing $\bar{u}^i$ with u^i in (28) and rearranging with the use of (23) yields

$$u^i(t+1) = u^i + (1+\bar{G}_i)^{-1} \sum_{j=-m}^{m} q_{ij}G(v^{ij})\, j\,\delta u^i. \tag{30}$$

Equation (30) expresses the dynamics for the strategy which characterizes a species which is valid for symmetric frequency distribution and for arbitrary $j\,\delta u^i$.

In order to obtain a simpler expression for the strategy dynamics, we will now assume scalar strategies and that $j\,\delta u^i$ is small. In this case a two term Taylor series expansion of $G(v^{ij})$ yields

$$G(v^{ij}) = G(u^i) + \left(\frac{\partial G}{\partial u}\right)_{u=u^i} j\,\delta u^i. \tag{31}$$

Substituting (31) into (23) yields

$$\bar{G}_i = \sum_{j=-m}^{m} q_{ij} G(u^i) + \sum_{j=-m}^{m} q_{ij} \left(\frac{\partial G}{\partial u}\right)_{u=u^i} j\,\delta u^i. \tag{32}$$

Substituting (31) into the summation term of (30) yields

$$\sum_{j=-m}^{m} q_{ij} G(v^{ij})\, j\,\delta u^i = \sum_{j=-m}^{m} q_{ij} G(u^i)\, j\,\delta u^i + \sum_{j=-m}^{m} q_{ij} \left(\frac{\partial G}{\partial u}\right)_{u=u^i} (j\,\delta u^i)^2. \tag{33}$$

Note that since we have assumed q_{ij} to be symmetric the second term on the right side of (32) and the first term on the right side of (33) are zero. Furthermore the first term on the right side of (32) is equal to $G(u^i)$ (since the sum of the q's is one) and that the second term on the right side of (33) is simply the variance times the gradient (since $j\,\delta u^i = v^{ij} - u^i$). These expressions reduce to

$$\bar{G}_i = G(u^i) \tag{34}$$

$$\sum_{j=-m}^{m} q_{ij} G(v^{ij})\, j\,\delta u^i = \sigma_i^2 \left(\frac{\partial G}{\partial u}\right)_{u=u^i}, \tag{35}$$

where

$$\sigma_i^2 = \sum_{j=-m}^{m} q_{ij} (j\,\delta u^i)^2 \tag{36}$$

is the variance of the strategy used by species i about the mean strategy u^i. Substituting (34) and (35) into (22) and (30), we obtain

$$x_i(t+1) = x_i [1 + G(u^i)] \tag{37}$$

$$u^i(t+1) = u^i + \frac{\sigma_i^2}{[1 + G(u^i)]} \left(\frac{\partial G}{\partial u}\right)_{u=u^i} \tag{38}$$

as the population dynamic and as the strategy dynamic when $j\,\delta u^i$ is small and when q_{ij} is symmetric. The strategy dynamic as given by (38) is similar in form to Roughgarden's result, but it differs conceptually from his result through the use of the G-function. It can also lead to fundamentally different results.

The coefficient of $\partial G/\partial u$ in (38) scales the rate of evolutionary change. It plays the same role as the speed term in Rummel and Roughgarden (1985) and Vincent (1990). This coefficient has much in common with the way heritability and genetic and phenotypic variance scale evolutionary rates in quantitative genetic models (see Taper and Case, 1985). The variance in strategy u^i represents additive genetic variance, and the assumptions implicit in (25) imply that the trait has a heritability of one.

The strategy and population dynamics as given by (37)–(38) converges on the results of quantitative genetics models that rely on "statistical rather than population genetics analyses" (Turelli and Barton, 1990). They categorize this approach as the Fisher–Bulmer model, in which the phenotypic distribution and the distribution of breeding values remains approximately Gaussian in response to selection (Fisher, 1918; Bulmer, 1980). This assumption is analogous to our assumptions that the distribution of strategies following selection is symmetrical, and that strategy variance is small. Turelli and Barton (1990) and Barton and Turelli (1991) discuss the validity of these assumptions in the context of multi-loci population genetics models.

Dynamics for the Variance

We will now examine whether the variance defined by (36) changes with time. It is assumed that $j\,\delta u^i$ does not change with time. It follows that the variance at $t + 1$ is given by

$$\sigma_i^2(t+1) = \sum_{j=-m}^{m} q_{ij}(t+1)[j\,\delta u^i]^2. \tag{39}$$

From the definition of frequency (21) we have

$$q_{ij}(t+1) = \frac{y_{ij}(t+1)}{x_i(t+1)}. \tag{40}$$

Using the G-function to evaluate $y_{ij}(t+1)$ and (22) for $x_i(t+1)$, along with (21) yields

$$q_{ij}(t+1) = q_{ij}\frac{1+G(v^{ij})}{1+\bar{G}_j}. \tag{41}$$

We now assume that $j\,\delta u^i$ is sufficiently small so that we may use the two term Taylor series expansion of $G(v^{ij})$ as given by (31) to approximate (41) as

$$q_{ij}(t+1) = q_{ij}\frac{1+G(u^i)+(\partial G/\partial u)_{u=u^i}\,j\,\delta u^i}{1+\bar{G}_i}. \tag{42}$$

If we also assume that q_{ij} is symmetric we may then use (34) to simplify (42)

$$q_{ij}(t+1) = q_{ij} \left[1 + j \, \delta u^i \, \frac{(\partial G/\partial u)_{u=u^i}}{1 + G(u^i)} \right].$$ (43)

Substituting (43) into (39) yields

$$\sigma_i^2(t+1) = \sum_{j=-m}^{m} q_{ij} [j \, \delta u^i]^2 + \frac{(\partial G/\partial u)_{u=u^i}}{1 + G(u^i)} \sum_{j=-m}^{m} q_{ij}(j \, \delta u^i)(j \, \delta u^i)^2.$$ (44)

Because of symmetry, the second term on the right side (44) sums to zero. Thus

$$\sigma_i^2(t+1) = \sigma_i^2(t).$$ (45)

We conclude that when the frequency distribution is symmetric and the variance is small, the variance does not change with time.

Evolution via Strategy Dynamics

As long as σ_i^2 is sufficiently small and q_{ij} is symmetric (37) and (38) are the appropriate equations for determining population and strategy dynamics. The magnitude of the variance will control how rapidly the strategies change (clearly if $\sigma_i^2 = 0$ then no change in strategy is possible). If a species evolves to an ESS under this system of equations, then the ESS maximum principle must be satisfied with the resultant strategy.

By solving (37) and (38) together we not only obtain the population density and strategy but, as time goes on, all surviving species may represent ESS candidates. These candidates can then be tested using the ESS maximum principle. Provided that an ESS exists, we should be able to find it using strategy dynamics, along with the ESS maximum principle. We will illustrate this procedure in the examples which follow.

We shall leave for future study, complications associated with finding ESSs when the two assumptions (σ_i^2 small and q_{ij} symmetric) are not satisfied. The properties of such systems may differ considerably, since in this case, the appropriate dynamical equations are given by (22), (23), and (28). However, since (28) determines how the mean strategy changes with time rather than u^i, they would be difficult to implement. Adding the assumption q_{ij} is symmetric would allow use of (22), (23), and (30) for a complete description of the dynamical process. Equation (39) would be useful in determining how the variance changes with time.

LOTKA–VOLTERRA COMPETITION MODEL

In this section we will examine strategy dynamics a form of the difference-equation Lotka–Volterra competition model which has been extensively studied in an evolutionary setting by Case (1982), Rummel and Roughgarden (1983, 1985), and Vincent and Brown (1987). Using the notation of Eq. (3), the H_i fitness function for a given species i, is given by

$$H_i(\tilde{\mathbf{u}}, \mathbf{x}) = R - \frac{R}{K(u^i)} \sum_{j=1}^{r} \alpha(u^i, u^j) \, x_j, \tag{46}$$

where r is the total number of species currently in the community, R is the intrinsic rate of growth common to all species, $K(u^i)$ is the carrying capacity of the species i, and $\alpha(u^i, u^j)$ is the competitive effect of species j using scalar strategy u^i on the fitness of individuals of species i. The above fitness may be expressed in terms of the following G-function,

$$G(u, \tilde{\mathbf{u}}, \mathbf{x}) = R - \frac{R}{K(u)} \sum_{j=1}^{r} \alpha(u, u^j) \, x_j. \tag{47}$$

Assuming an ESS coalition of σ strategies at equilibrium we obtain

$$G^*(u) = R - \frac{R}{K(u)} \sum_{j=1}^{\sigma} \alpha(u, u^j) \, x_j^*. \tag{48}$$

For the two models which follow, the monotone increasing property required by the ESS maximum principle may be demonstrated by simulation (Brown and Vincent, 1987c). When this property is satisfied, according to the ESS maximum principle, G^* takes on a maximum with respect to u at $u = u^1 \dots u^\sigma$ (the ESS coalition). We first apply the ESS maximum principle to determine ESS strategies. We then show how the ESS may also be obtained by solving (37) and (38).

Model 1

As a first example consider the K and α functions used by Roughgarden (1983). That is,

$$K(u) = K_m \exp[-u^2/2\sigma_k^2] \tag{49}$$

and

$$\sigma(u, u^j) = \exp[-(u - u^j)^2/2\sigma_\sigma^2]. \tag{50}$$

If we seek a coalition of 1 for this model, then

$$G^*(u) = R - \frac{R}{K(u)} \alpha(u, u^1) x_1^* \tag{51}$$

and we obtain $u^1 = 0$ from (11) and $x_1^* = K_m$ from (13) with the requirement that $\sigma_\alpha^2 \geqslant \sigma_k^2$ from (12). Provided that this condition is satisfied, and our ESS is global, we need look no further (for a coalition of two, etc.) since, by the definition of an ESS, the existence of global coalition of one precludes the possibility of any higher coalitions (composed of distinctly different strategies). This ESS may also be obtained from the dynamics. For example, using $K_m = 100$, $R = .25$, $\sigma_1^2 = 1.5$, $\sigma_\alpha^2 = 4$, $\sigma_k^2 = 1$, $x_1(0) = 10$, $u_1(0) = 2$, Figs. 1a and 1b illustrate the time history of population density and strategy as determined by (37) and (38). In this case, the population is a single species initially not at an ESS strategy. After a sufficient number of generations, the ESS strategy of $u_1 = 0$ is obtained at an equilibrium population of $x^* = 100$. Figure 1c illustrates that at these values, $G^*(u)$ is maximized, as required by the ESS maximum principle.

A number of interesting features about the process itself can be obtained using different starting conditions and species (Vincent, 1990). For example, the initial population can contain multiple species with different starting densities, strategies, and strategy variance. One or more species may arrive at the ESS, but since the ESS is a coalition of one, all species which arrive at the ESS will have the same ESS strategy of $u^1 = 0$. The equilibrium population density of all species which arrive at the ESS will sum up to 100. In this sense, we may have coexistence of more than one ESS species and as long as they do not cross breed they will maintain their identity in spite of the fact that they are indistinguishable in terms of strategy. This illustrates one process by which convergent co-evolution can be obtained.

Note that, with this model, if $\sigma_\alpha^2 < \sigma_k^2$ then G^* takes on a local minimum at $u^1 = 0$ and we conclude that a coalition of one ESS solution will not exist. However we can investigate the possibility of a coalition of 2 for this case by using the G^* given by

$$G^*(u) = R - \frac{R}{k(u)} [\alpha(u, u^1) x_1^* + \alpha(u, u^2) x_2^*]. \tag{52}$$

We obtain the same results as Roughgarden (1983, Eq. 23, p. 43). That is, using condition (11) on this G^*-function, we obtain the candidate coalition strategies

$$u^1 = -u^2 = \sigma_\alpha \{0.5 \ln[(2\sigma_k^2/\sigma_\alpha^2) - 1]\}^{0.5}, \tag{53}$$
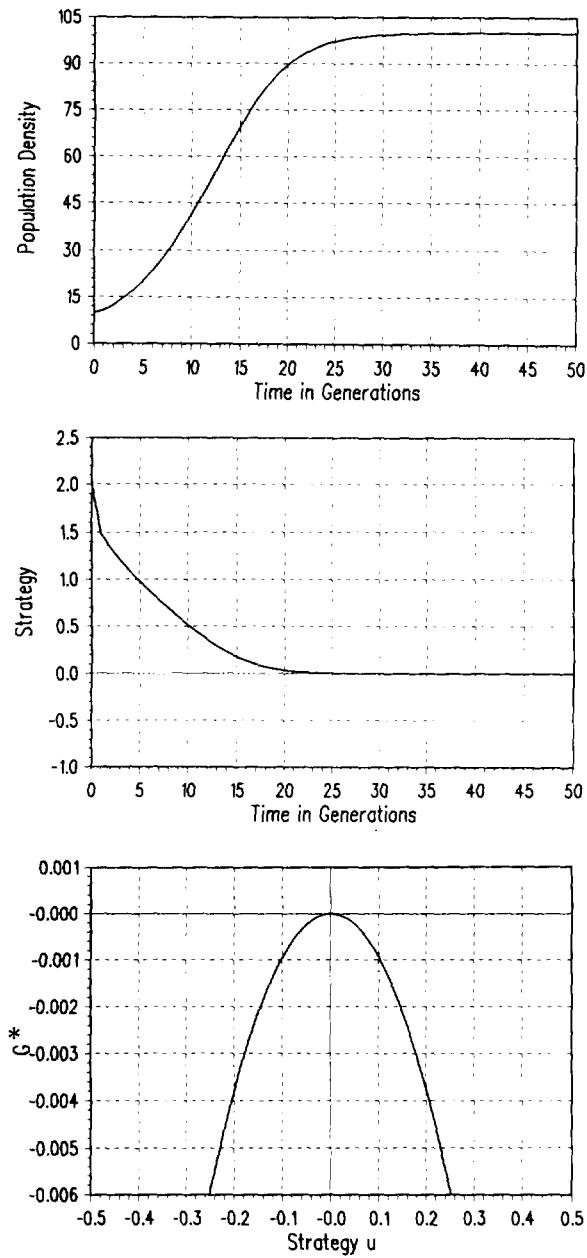
FIG. 1. (a) One species evolves to an equilibrium density under strategy dynamics. (b) Corresponding changes in strategy with time. (c) Using the ESS maximum pinciple to verify that solution obtained is an ESS.

and from (13) we obtain

$$x_1^* = x_2^* = K(u^1)/[1 + \alpha(u^1, -u^1)]. \tag{54}$$

However, (12) need not be satisfied by these solutions. In such a case, an ESS coalition of 2 does not exist. Indeed, no assumption has been made here as to the existence of an ESS, and if one does not exist, the system cannot be driven to an ESS under any given strategy dynamic. This illustrates the usefulness of the ESS maximum principle as a stand alone condition apart from attempting to obtain ESSs from a strategy dynamic. It has been previously shown that strategy dynamics may place a population on a "peak" in the G^*-function which is not global in u (Brown, 1990) or, as we will show in what follows, if the number of species is constrained, the system may evolve to strategies which have fitness minima (see also Taper and Case, 1992).

As an illustration of the above discussion consider using $K_m = 100$, $R = 0.25$, $\sigma_\alpha^2 = 4$, $\sigma_k^2 = 10$ (note $\sigma_\alpha^2 < \sigma_k^2$ as is also required by Roughgarden (1983, Eq. 23, p. 43)). In this case, Eqs. (53) and (54) yield $u^1 = -u^2 = 1.6651$, $x_1^* = x_2^* = 69.644$. These same results will also be obtained using the dynamical system (37) and (38). Figures 2a and 2b illustrate the population density and strategy obtained with K_m, R, σ_α^2, and σ_k^2 as given above an initial conditions $x_1(0) = 20$, $x_2(0) = 40$, $u^1(0) = .5$, $u^2(0) = -5$, along with the variances $\sigma_1^2 = \sigma_2^2 = 1.5$. The equilibrium solution obtained is not an ESS since it does not satisfy the ESS maximum principle as illustrated in Fig. 2c. In fact, $G^*(u)$ takes on a minimum at $u^1 = -u^2 = 1.6651$. According to Roughgarden (1983) the species using these strategies form what he calls a coevolutionary stable community (CSC).

Let us "play" the CSC strategies against a second pair $u^3 = 3$, $u^4 = 1$, under the dynamics given by (37) only. That is, without strategy dynamics or equivalently $\sigma_1^2 = \sigma_2^2 = 0$. The results are shown in Fig. 3. We start the CSC species at their equilibrium densities and with the non-CSC individuals rare. Even with these favorable starting conditions, the CSC is clearly not an ESS, in fact, it is not even a CSC (under Roughgarden's definition), since the non-CSC individuals increase in number and one of the CSC pairs is headed for extinction.

We have demonstrated here that for the above choice of parameters, and when the strategies are unbounded, that a coalition of two does not exist. By similar methods it can be shown that a coalition of 3 and 4 also do not exist. It is difficult to examine the possibility of the existence of a higher number of coalitions as the G^*-function becomes flatter as the coalition number for an ESS candidate increases. Our conjecture is that under an unbounded strategy set and with $\sigma_\alpha^2 < \sigma_k^2$, the ESS is composed of an
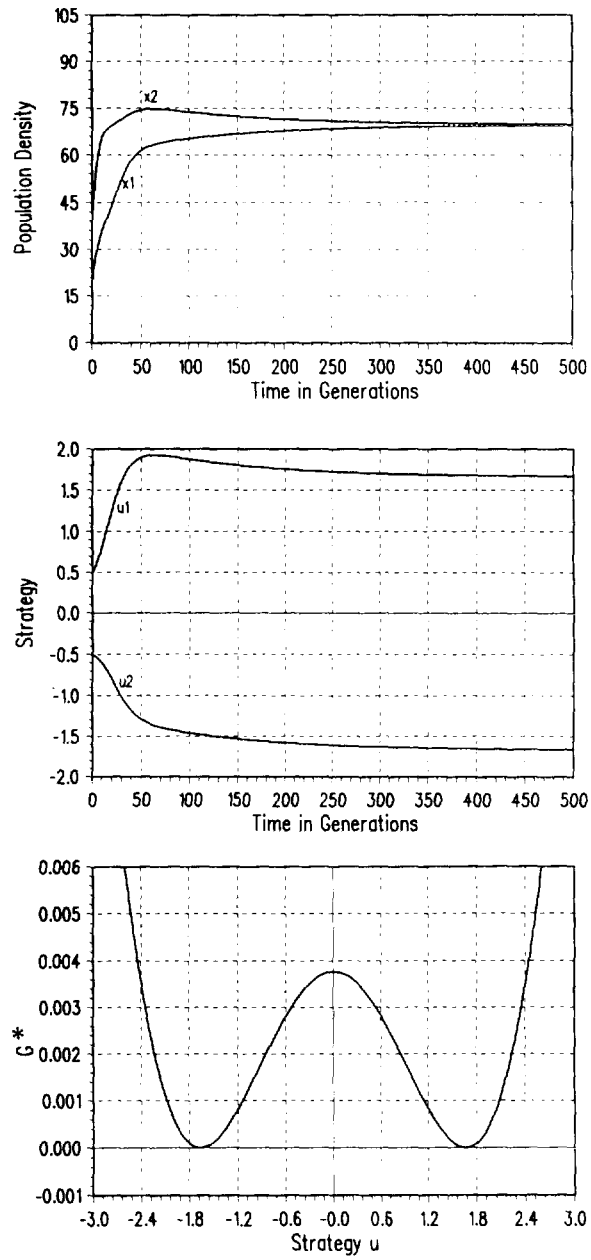
FIG. 2. (a) Two species evolve to equilibrium strategies under strategy dynamics. (b) Corresponding population densities. (c) Using the ESS maximum principle to show that the solution obtained is not an ESS.
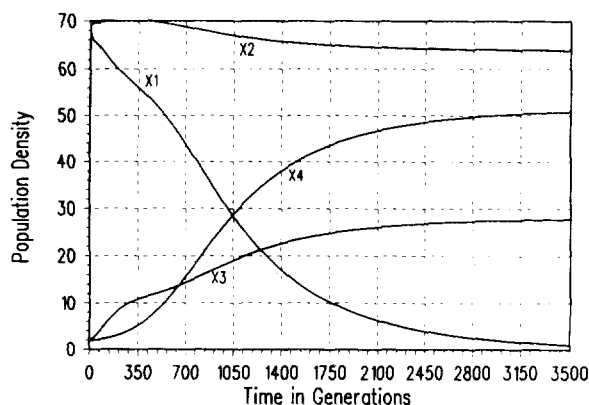
FIG. 3. Playing the CSC obtained in Fig. 2 with two other non-CSC strategies.

infinite number of strategies. It would always be possible to add new species into a community at equilibrium. It is interesting to note however, that if the strategies are bounded, then it is possible for a coalition of 2 to exist. For example, if we require $|u^i| \leqslant 1.5$, then for the same set of parameters used above we obtain the ESS coalition of two $u^1 = 1.5$, $u^2 = -1.5$, with $x_1^* = x_2^* = 67.459$. Figure 4a illustrates that this solution satisfies the ESS maximum principle. A coalition of three is also possible under a bounded strategy set. Figure 4b illustrates a coalition of three with $u^1 = 1.8$, $u^2 = -1.8$, $u^3 = 0$, $x_1^* = x_2^* = 59.53$, $x_3^* = 20.59$ under the requirement that $|u^i| \leqslant 1.8$. Clearly the last word has not been said on this interesting example. An analytical proof of the above conjecture and a more through investigation of bounds on the strategies might yield interesting insight into the question, "how many species can coexist in a given environment?" for this and other population models.

Model 2

By changing the α function it is possible to obtain ESS coalitions of one or more even with an unbounded strategy set. As our second and final example, we will use an α function which has been used by us in a number of papers (Brown and Vincent, 1987c; Vincent and Brown, 1987; Vincent, 1990). The model is given by equations (3) and (46) with $K(u)$ given by (49) and

$$\alpha(u, u^i) = 1 + \exp\left[-\frac{(u - u^i + \beta)^2}{2\sigma_\alpha^2}\right] - \exp\left[-\frac{\beta^2}{2\sigma_\alpha^2}\right]. \tag{55}$$

We start be seeking a coalition of 1 with $G^*(u)$ given by (48). From (11) we obtain

$$u^1 = \beta(\sigma_k/\sigma_\alpha)^2 \exp[-\beta^2/2\sigma_\alpha^2], \tag{56}$$
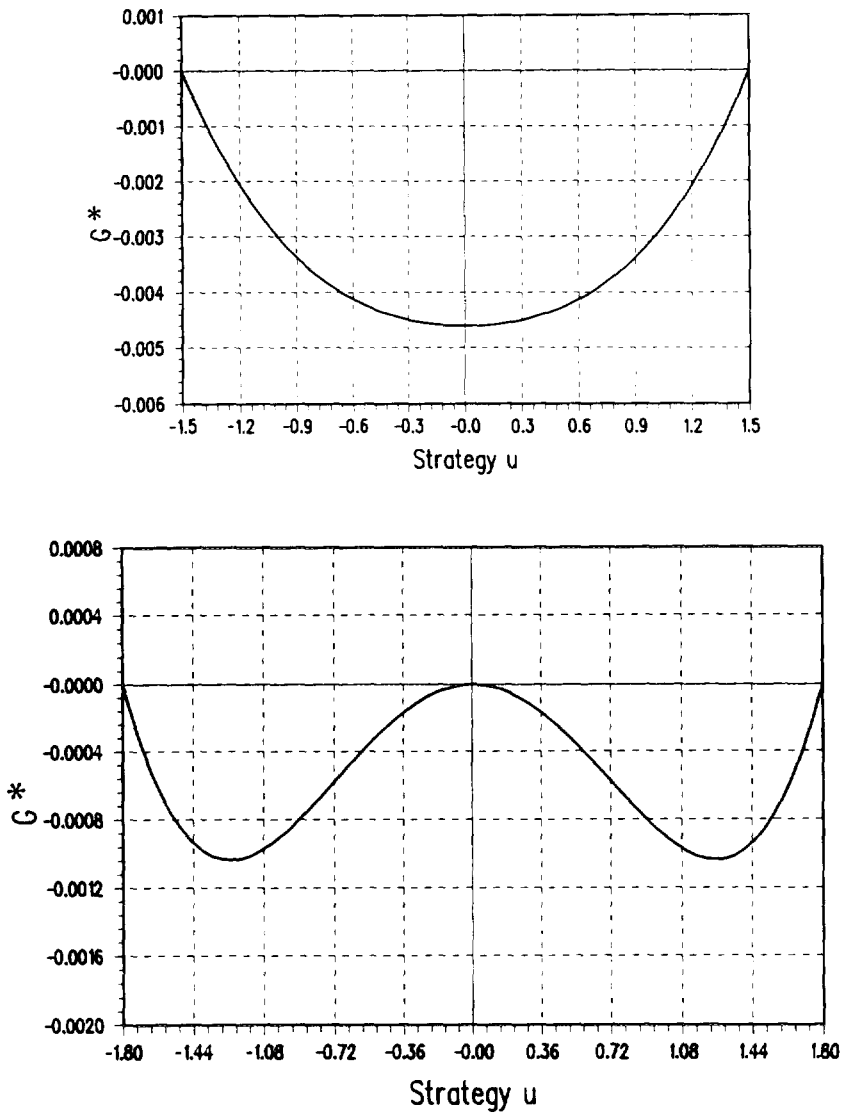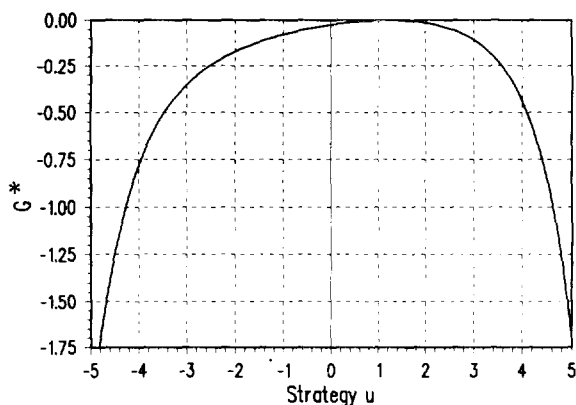
Fig. 4. (a) A coalition of two exists for Model 1 when $\sigma_k > \sigma_\alpha$ and the strategy set is bounded by $|u^i| \leq 1.5$. (b) A coalition of three exists for Model 1 when $\sigma_k > \sigma_\alpha$ and the strategy set is bounded by $|u^i| \leq 1.8$.

FIG. 5. A Colation of one exists for Model 2 when $\sigma_k = 2$.

and from (13) we obtain

$$x_1^* = K_m \exp[-(u^1)^2/2\sigma_k^2]. \tag{57}$$

Condition (12) for this problem is difficult to apply and instead we will rely on plotting the $G^*(u)$ function.

Using $K_m = 100$, $\sigma_x^2 = \sigma_k^2 = \beta^2 = 4$, we obtain from (56) and (57) that $u^1 = 1.213$, $x_1^* = 83.199$. If we substitute these values into (48) and plot G^* as a function of u, we obtain Fig. 5. This candidate satisfies the ESS maximum principle. We may test this ESS by playing it against other strategies using the dynamics given by (37) only. For example, the CSC for this model is $u^2 = 0$ with $x_2^* = 100$. When these two strategies played together the CSC species disappears, as illustrated in Fig. 6. Note that we have
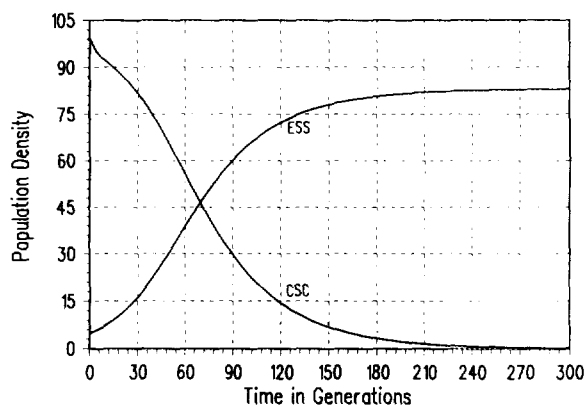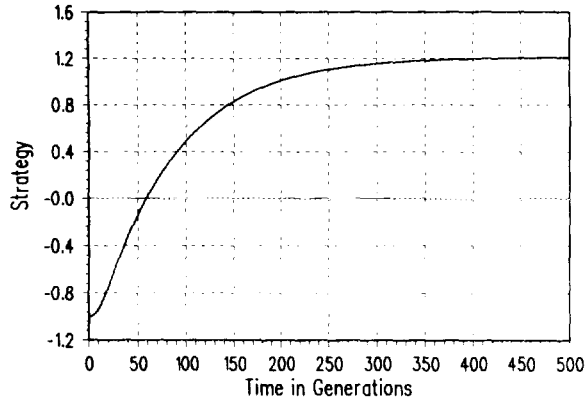

FIG. 6. Playing the ESS against a CSC.

FIG. 7. Strategy dynamics of a single species when the ESS is a coalition of one.

started the CSC individuals at their equilibrium value with the ESS individuals few in number.

We may also obtain this ESS solution using dynamics. Figure 7 illustrates how the strategy changes with time when the system (37) and (38) is solved using a single species with the above parameters with $\sigma_i^2 = .04$ and initial conditions $x_1(0) = 10$ and $u^1(0) = -1$.

As in the previous model, increasing the value of σ_k^2 can change the number of strategies which make up an ESS coalition candidate. However, when we seek a coalition of 2 or more for this model, with $G^*(u)$ by (48), a simple analytical expression is no longer possible. We must either use symbolic manipulation software (e.g., *Mathematica*) for solving the ESS maximum principle directly, or use strategy dynamics to find the ESSs numerically. We have used Mathematica to show that as we increase σ_k^2 the ESS coalition changes from 1 to 2 at $\sigma_k^2 = 6.9495$ and from 2 to 3 at $\sigma_k^2 = 15.9325$. In keeping with the other examples, we will demonstrate the existence of an ESS coalition of 2 using strategy dynamics with all parameters as above except $\sigma_k^2 = 12.5$.

We start the numerical procedure with a single species using the initial conditions as in Fig. 7. From (37) and (38) we obtain the strategy dynamics illustrated in Fig. 8, yielding $u^1 = 3.79$ and $x_1^* = 56.28$. If we substitute these values into (46) and plot $G^*(u)$ illustrated in Fig. 9, we see that this result is not an ESS. The figure suggests that the ESS is a coalition of 2. Figure 10 illustrates the strategy dynamics obtained via (37) and (38) when we start with two species using the same parameters as above, but with initial conditions x_1 $(0) = x_2(0) = 10$, $u_1(0) = 0$, $u_2(0) = -1$ and $\sigma_1^2 = \sigma_2^2 = 1.5$. In due time the ESS candidate $u^1 = 3.1294$, $u^2 = -0.2397$, $x_1^* = 51.062$, and $x_2^* = 39.283$ is obtained. Figure 11 illustrates that this candidate satisfies the ESS maximum principle. As will all of the ESSs we
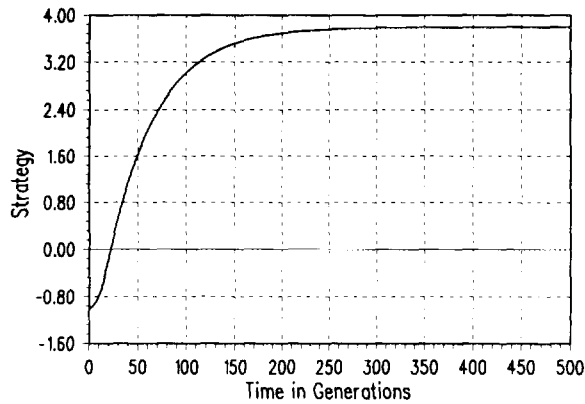
FIG. 8.   Strategy dynamics of a single species when the ESS is a coalition of two.

obtain with this model, it is a global ESS. This is illustrated in Fig. 12, where the ESS is introduced at low frequency $(x_1 = x_2 = 10)$ into a population of two other strategies $(u^3 = 4, u^4 = -4)$ coexisting at their equilibrium populations $(x_3 = 38.0368, x_4 = 37.3403)$.

It is interesting to examine the process by which the ESS solution is obtained from the numerical solution of (37) and (38). As the strategies are approaching their ESS values, the G-function itself is changing. Figure 13 illustrates a series of plots of the G-function (47) vs u at current values of x_i and u^i at various times. These represent snapshots of an "adaptive landscape" which changes shape as the species are evolving toward the ESS. At first, as illustrated in Figs. 13A and 13B, both species as identified by the large solid dots chase the $u_1 = 3.1294$ solution. When one population
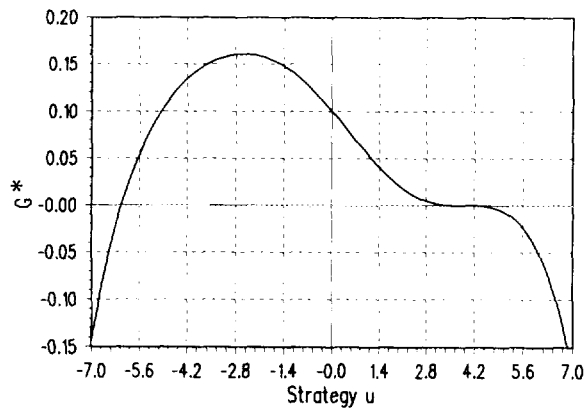

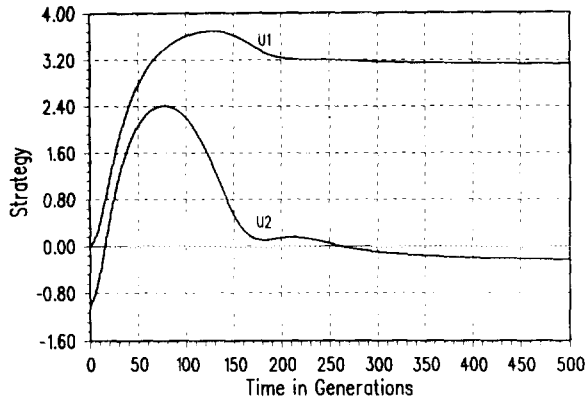FIG. 9.   The G^*-function for the equilibrium solution obtained in Fig. 8.

FIG. 10.   Strategy dynamics for two species when the ESS is a coalition of two.

comes near this solution, the valley between the peak to the left and the two species moves under one of the species, as illustrated in Fig. 13C. The species to the left then starts to climb this peak, as shown in Fig. 13D, and in the process pushes it down, as shown in Fig. 13E, until the final equilibrium solution illustrated in Fig. 13F is obtained. The second peak is at $u^2 = -0.2397$.

DISCUSSION

Our definition of an ESS is similar to Roughgarden's (1983, p. 41) definition of a CSC. However, the necessary conditions, as given by Roughgarden, under which a CSC can exist (p. 43) will, under intra-specific
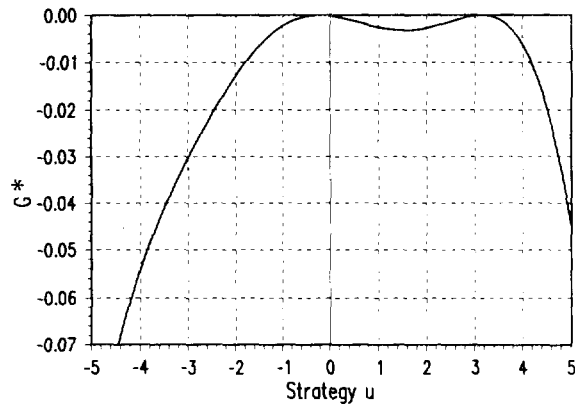

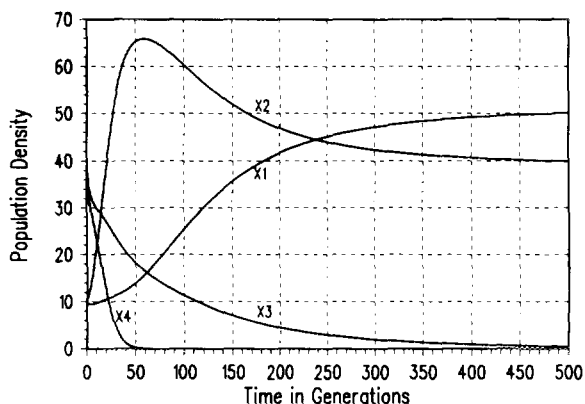FIG. 11.   The G^*-function for the equilibrium solution obtained in Fig. 10.

FIG. 12.   Playing the ESS against two non-ESS strategies.

frequency dependent selection often gives different results than will be obtained using the ESS maximum principle (Taper and Case, 1985). The ESS maximum principle is a general principle which is valid for models with both inter-specific and intra-specific frequency dependence. For those situations where a single G-function is the appropriate model to use, it is easy to show that without intra-specific frequency dependence an ESS will maximize group fitness.

While the ESS maximum principle is an effective tool for finding ESS solutions to evolutionary processes involving frequency-dependent selection, it in itself does not show how strategy frequencies change with time to obtain an ESS. The strategy dynamics developed here (without use of quantitative genetics) was intended to fill that gap. This dynamic accords well with recent advances in quantitative genetics modeling (Iwasa et al., 1991; Taper and Case, 1992) and it can provide a means for a population to achieve the ESSs characterized by the ESS maximum principle.

Of coarse, quantitative genetics is a more suitable theory for characterizing the explicit dynamics of quantitative character changes with time. However, frequency-dependent models in quantitative genetics are often computationally arduous, and some of the most important results do not apply to cases involving frequency-dependent selection (Lande, 1976; Charlesworth, 1990). Several recent papers have advanced quantitative genetic tools for characterizing the outcomes of frequency-dependent selection. Iwasa et al. (1991) derive a fitness function for the individual that has properties in common with the G-function. They then show that the direction and rate of evolution are determined by the sign and magnitude of the partial derivative of this fitness function with respect to the individuals quantitative character (see the Appendix in Iwasa et al., 1991). Taper and Case (1992) take the comparison between a quantitative genetics dynamic
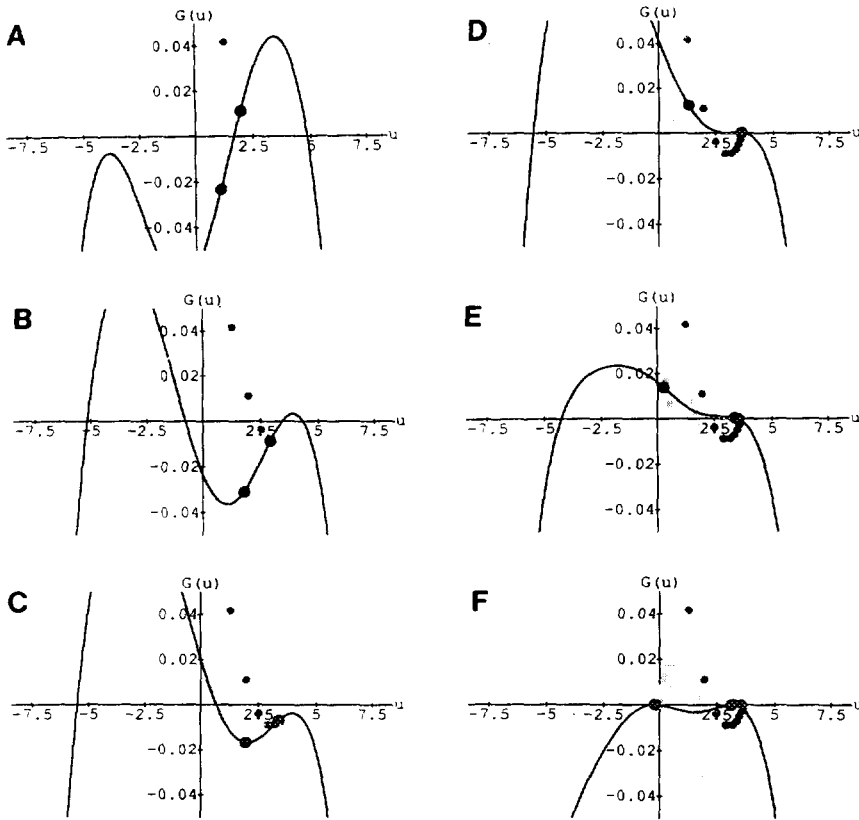
FIG. 13. The G-function, during evolution, is a flexible adaptive landscape which can mode under a strategy so that isolated peaks can be occupied. (A)–(F) Changes in the G-function as time increases.

and an ESS dynamic even further. They show that the dynamic suggested for evolutionary games (Eq. 13 of Brown and Vincent, 1987c) is the limiting case for a quantitative genetics dynamic where intraspecific phenotypic variation approaches zero (see the Appendix in Taper and Case, 1992).

We must clearly distinguish between necessary conditions which must be satisfied for an ESS to exist and questions associated with how a population might actually attain an ESS. The ESS maximum principle only addresses the question of existence. Equation (38) represents one way in which a population might attain the ESS. Certain assumptions are made in the development of (38) which may or may not apply for any given situation (e.g., symmetric distributions with little variance). Other processes may be taking place. In some situations, a strategy dynamic such as (38)

is not needed. One can attain the ESS through pure immegration of random strategies (Brown and Voncent, 1987c).

There are situations in which (38) will not drive the system to an ESS. Indeed, in the last example discussed above, there are starting conditions such that the ESS is not obtained using (38). If the simulation is started with just one species, then at equilibrium, a strategy is obtained which is not an ESS. The G-function as in Fig. 9 is obviously not maximized when equilibrium is achieved. In fact, the single species evolves via natural selection to a plateau in the adaptive landscape. Even when starting with two species, it is possible for both species to evolve to the same strategy as obtained with one species. Only when the two species evolve two different strategies is an ESS obtained. It should be noted, however, that if the community is constrained to have but one species, then the equilibrium strategy obtained by this one species is where the community will evolve in spite of the fact that an ESS coalition of two exists. Clearly restricted initial conditions or constraints placed on the number of species can interfere with the attainment on an ESS.

Our plots of G^* as a function of u are in the vein of Wright's (1977) adaptive landscape. While our landscape is pliable and readily changes shape with population density (and/or population frequency) and strategy of the various species, Wright's adaptive landscapes (which in general are not frequency dependent) are more rigid. The valleys and peaks in his landscape are relatively fixed with respect to strategy frequencies. As Wright recognized in the shifting balance theory of evolution, crossing valleys in his adaptive landscape may pose a considerable challenge to evolving populations. This challenge disappears with our landscape. As we have shown here, two population species may find themselves evolving up the same peak in the adaptive landscape. As the peak becomes occupied by one population, a valley may move under the other population in such a way that the second species is attracted to the second emerging peak. Two things are happening to make this possible: (1) as populations evolve, valleys may cross strategies rather than vice versa, and (2) as populations evolve, peaks and valleys may not become manifest until the peaks of the ESS are nearly occupied. See also Rosenzweig's (1978) example using competitive speciation.

One might question the ESS approach to modelling evolution by natural selection because of its lack of explicit genetics, equilibrium requirements, and insufficient attention to strategy dynamics. In this paper we have addressed the latter concern. We obtain a strategy dynamic which closely resembles those used in quantitative genetic models. Roughgarden (1979, p. 477) discusses some of the parallels between population genetics and the ESS concept for co-evolving species. When variation for a trait is small within a population (as assumed here), Charlesworth (1990) shows how

quantitative genetic and ESS analyses yield the same results for both scalar and vector valued strategies. Taper and Case (1992) find broad agreement between ESS and quantitative genetic analyses of co-evolving species. The results are identical when the population variance is small, but begin to diverge as the size of the environmental variation in the quantitative genetic model increases.

ACKNOWLEDGMENTS

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