On the survival probability of a slightly advantageous mutant gene in a multitype population: A multidimensional branching process model

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Abstract. The estimated survival probability of a slightly supercritical Galton-Watson process is generalized to a multitype branching process. The result is used to estimate the probability of initial success of a mutant gene whose effect on the individual carrier depends on the carrier's sex, class, etc. The probability of initial success is also estimated in a case where the effect of the mutation is manifested in terms of the distribution of types within one's progeny, e.g. in a case of a change in the sex ratio.

Key words: branching process — Galton Watson process — mutation — advantageous mutation — extinction

Introduction

With some "smoothness assumptions" on a family $\{(Y_t^{(s)})\}_{s \geqslant 0}$ $(t = 1, 2, 3)$ of one-dimensional branching processes it is known that the extinction probability of the process $(Y_t^{(s)})$ $t = 1, 2, \ldots$ characterized by a mean $1 + s > 1$ and a variance $\sigma^2 > 0$ of the individual progeny size, can be estimated by the equality

$$u(s) = 1 - \frac{2s}{\sigma^2} + o(s) \tag{1.1}$$

where $s > 0$ is small. (Kolmogorov, 1938; Ewens, 1969. For the exact "smoothness" condition for (1.1) see also Eshel, 1981.)

The approximation (1.1) is used to estimate the extinction probability of a slightly advantageous mutant gene in a large population, asexual or, under certain conditions, sexual. Thus, if mating is at random, if the sex ratio is $1:1$ and if the effect of the mutation on both sexes is the same, the number Y_t of t-generation heterozygote mutant descendants born to a single heterozygote mutant parent is well approximated by a one-dimensional branching process as $t = 1, 2, 3, \ldots$ provided the population is large enough as to ignore the probability of random mating between two mutants. However, if one or more of these conditions does not hold, the process of initial introduction of a new mutant gene is shown to

be approximated, in the same way, by a two-dimensional branching process. Thus, if the population undergoes mixed selfing and random mating, the process is determined by the pairs $(X_t^{(s)}, Y_t^{(s)})$ of homozygote and heterozygote mutant descendants. If the mutation affects the sex-ratio or else, if it affects male and female carriers in a different way, the process is determined by the pair of male and female heterozygote carriers of the mutation (Ewens, 1968; see also examples III and IV in Section 4).

A multidimensional branching process is typical, more generally, of a case in which the population is divided into a number of types, each of which can carry the new mutant, possibly with different effect. Such types can be sexes as well as classes, geographical habitats or, maybe, different genotypes, determined by another locus (Ewens, 1968).

Analysis of a multitype branching process model generalizes (1.1), provided the concepts of "viability" and "variance of viability" are appropriately generalized into a vectorial form. This follows with a general estimation of the survival probability of a slightly advantageous mutant gene in a sexual population.

2. The model

Assume an n-type branching process with a generating function $\phi^*(\mathbf{u})$. Let

$$\frac{\partial \phi_i^*(\mathbf{1})}{\partial u_j} = m_{ij}^* \qquad \|m_{ij}^*\| = M^*$$

where M^* is an aperiodic matrix with $M^{*k} > 0$ for some integer k (i.e. all types can be represented in the process with positive probability, independently of the original parental type). Assume that the leading eigenvalue of the matrix is $1 + \varepsilon$ where $\varepsilon > 0$ is small (i.e. the process is slightly supercritical) and that the n-dimensional offspring-distributions have finite second moments of all sorts. Starting with a single parent of type i ($i = 1, 2, \ldots, n$) we know that the extinction probability of the process is given by the smallest positive solution u_i^* of the equation

$$\mathbf{u}^* = \boldsymbol{\phi}^*(\mathbf{u}^*). \tag{2.1}$$

In order to estimate the vector $\mathbf{u}^*$ we define a family $\{\boldsymbol{\phi}^{(s)}(\mathbf{u})\}_{0 \leqslant s \leqslant \varepsilon}$ by

$$\boldsymbol{\phi}^{(s)}(\mathbf{u}) = \boldsymbol{\phi}^*\left(\frac{\varepsilon - s}{1 + \varepsilon} \mathbf{1} + \frac{1 + s}{1 + \varepsilon} \mathbf{u}\right). \tag{2.2}$$

Thus, $\boldsymbol{\phi}^{(\varepsilon)}(\mathbf{u}) = \boldsymbol{\phi}^*(\mathbf{u})$, and for all $0 < s \leqslant \varepsilon$, $\boldsymbol{\phi}^{(s)}(\mathbf{u})$ is obtained from the original generating function by superimposing an additional probability $(\varepsilon - s)/(1 + \varepsilon)$ that a newborn offspring will die, independently of its type. The process determined by $\boldsymbol{\phi}^{(0)}(\mathbf{u})$ is a critical process, hence, if $\mathbf{u}(s)$ is the smallest positive solution of

$$\mathbf{u}(s) = \boldsymbol{\phi}^{(s)}(\mathbf{u}(s)), \tag{2.3}$$

we know that $\mathbf{u}(0) \equiv 1$ and $\mathbf{u}(s) < 1$ for all $s > 0$. We are interested in the asymptotic behavior of $\mathbf{u}(s)$ for small but positive s, especially (if $\varepsilon > 0$ is sufficiently small)

for $s = \varepsilon$. More specifically let Y_{ij} be the number of viable offspring of type j, born to a parent of type i in the critical process determined by $\phi^{(0)}(\mathbf{u})$. Denote $EY_{ij} = m_{ij} = m_{ij}^*/(1 + \varepsilon)$. We are interested in estimating $\mathbf{u}(s)$ as a function of the matrix $M = \|m_{ij}\|$ of expectations of the critical process, the covariances $\text{cov}(Y_{ij}, Y_{ik})$ and the deviation s of the process $\phi^{(s)}(\mathbf{u})$ from the critical process.

3. Analysis of the model

Employing the implicit function theorem to differentiate (2.3) with respect to s, we get

$$u_i' = \frac{\partial}{\partial s} \phi_i^{(s)}(\mathbf{u}) + \sum_{j=1}^{n} u_j' \frac{\partial \phi_i^{(s)}(\mathbf{u})}{\partial u_j}. \tag{3.1}$$

From (2.2) we have

$$\frac{\partial}{\partial s} \phi_i^{(s)}(\mathbf{u}) = \sum_{j=1}^{n} (u_j - 1) \frac{1}{1+\varepsilon} \frac{\partial \phi_i^*}{\partial u_j} \left(\frac{\varepsilon - s}{1+\varepsilon} 1 + \frac{1+s}{1+\varepsilon} \mathbf{u} \right)$$

$$= \sum_{j=1}^{n} (u_j - 1) \frac{\partial \phi_i^{(s)}(u)}{\partial u_j}.$$

Hence, for $i = 1, 2, \ldots, n$

$$u_i' = \sum_{j=1}^{n} (u_j' + u_j - 1) \frac{\partial \phi_i^{(s)}(\mathbf{u})}{\partial u_j}. \tag{3.2}$$

But as $s \to 0$, $\mathbf{u} \to 1$ and

$$\frac{\partial \phi_i^{(s)}(\mathbf{u}(s))}{\partial u_j} \to m_{ij}.$$

If we set $u_i'(0)$ for the right derivative of $u_i(s)$ at $s = 0$, we therefore get

$$\mathbf{u}'(0) = M\mathbf{u}'(0). \tag{3.3}$$

But $M = 1/(\varepsilon + 1)M^*$ is an aperiodic matrix with $M^k > 0$ for some integer k. From Frobenius' theorem it therefore follows that its leading eigenvalue is real and positive and we already know that this eigenvalue is 1. Thus, (3.3) asserts that $\mathbf{u}'(0)$ is a right eigenvector of M, corresponding to its leading eigenvalue. We also know from Frobenius' theorem that there are a unique positive left eigenvector $\mathbf{p}$ and a unique positive right eigenvector $\mathbf{v}$ of M (and, indeed of $M^* = (1 + \varepsilon)M$) such that

$$\sum p_i = 1 \tag{3.4}$$

$$\sum p_i v_i = 1. \tag{3.5}$$

Moreover, each left (right) eigenvector of M, corresponding to the eigenvalue 1 is proportional to $\mathbf{p}$ (resp. $\mathbf{v}$). Hence, it follows from (3.3) that a constant c exists such that

$$\mathbf{u}'(0) = c\mathbf{v}. \tag{3.6}$$

To calculate the value of c we multiply both sides of (3.2) by p_i and sum over i. This yields (for $0 < s < \varepsilon$)

$$\sum_i p_i u_i' = \sum_{ij} (u_j' + u_j - 1) p_i \frac{\partial \phi_i^{(s)}(\mathbf{u})}{\partial u_j}$$

$$= \sum_i (u_i' + u_i - 1) \sum_j p_j \frac{\partial \phi_j^{(s)}(\mathbf{u})}{\partial u_i} \tag{3.7}$$

or

$$\sum_i \left\{ p_i - \sum_j p_j \frac{\partial \phi_j^{(s)}(\mathbf{u})}{\partial u_i} \right\} u_i'(s) = \sum_i (u_i - 1) \sum_j p_j \frac{\partial \phi_j^{(s)}(\mathbf{u})}{\partial u_i}. \tag{3.8}$$

As $s \downarrow 0$ we know that

$$p_i - \sum_j p_j \frac{\partial \phi_j^{(s)}(\mathbf{u})}{\partial u_i} \to p_i - \sum_j p_j m_{ji} = 0$$

$$u_i - 1 \to 0.$$

Hence, differentiating (3.8) with respect to s at $s = 0$ one gets

$$-\sum_{ij} p_j u_i'(0) \left\{ \frac{d}{ds} \left(\frac{\partial \phi_j^{(s)}(\mathbf{u})}{\partial u_i} \right) \right\}_{s=0} = \sum_{ij} p_j u_i'(0) \frac{\partial \phi_j^{(0)}(\mathbf{u})}{\partial u_i}$$

$$= \sum_{ij} p_j m_{ji} u_i'(0). \tag{3.9}$$

Now differentiating (2.2) with respect to u_i and then with respect to s and setting $s = 0$, one obtains

$$\left\{ \frac{d}{ds} \left(\frac{\partial \phi_j^{(s)}(\mathbf{u})}{\partial u_i} \right) \right\}_{s=0} = m_{ji} + \sum_k u_k'(0) \frac{\partial^2 \phi_j^{(0)}(\mathbf{1})}{\partial u_i \, \partial u_k}$$

$$= m_{ji} + \sum_{k=0}^n u_k'(0)(E(Y_{ij} Y_{ik}) - \delta_{jk} Y_{ij})$$

where δ_{jk} is Kronecker's delta. Equation (3.9) therefore becomes

$$2 \sum_{ij} p_j m_{ji} u_i'(0) = \sum_{ijk} p_j u_i'(0) u_k'(0)(E(Y_{ij} Y_{ik}) - \delta_{jk} Y_{ij}). \tag{3.10}$$

By inserting (3.6) and then (3.4) and (3.5), (3.10) becomes

$$2c = -c^2 \sum_i p_i \sum_{jk} v_j u_k (E(Y_{ij} Y_{ik}) - \delta_{jk} Y_{ij}) \tag{3.11}$$

with two possible solutions for c, corresponding to the two solutions of (2.3). The solution $c = 0$ indeed corresponds to the constant solution $u(s) \equiv 1$. Since we are interested in the other, smallest positive solution $u(s) < 1$ we obtain

$$c = -\frac{2}{\sum_i p_i \sum v_j v_k (E(Y_{ij} Y_{ik} - \delta_{ik} Y_{ij})}. \tag{3.12}$$

By a straightforward calculation (employing (3.4) and (3.5)) this becomes

$$c = \frac{-2}{\sum_i p_i \, \mathrm{Var}(\sum_j v_j Y_{ij})} \tag{3.13}$$

and from (3.6) we obtain

$$1 - u_i(s) = \frac{2v_i s}{\sum_i p_i \, \mathrm{Var}(\sum_j v_j Y_{ij})} + o(s) \tag{3.14}$$

(see for comparison Pollak, 1972).

As a special case, if the Y_{ij} are independent Poisson random variables, then

$$\sum_i p_i \, \mathrm{Var}\left(\sum_j v_j Y_{ij}\right) = \sum_{ij} p_i v_j^2 m_{ij} = \sum_j p_j v_j^2 + O(s) \tag{3.15}$$

and (3.14) becomes

$$1 - u_i(s) = \frac{2v_i s}{\sum_j p_j v_j^2} + o(s) \tag{3.16}$$

(see Ewens, 1968).

4. Biological examples and discussion

Note that if the population does not become extinct, then its size tends to infinity in probability 1 and the vector of relative frequencies tends to the left eigenvector **p** (e.g. Harris, 1963).

This is true for the original branching process (with the generating function ϕ^*) as well as for the assigned critical process (with the g.f. ϕ). Note that both share the same right and left eigenvectors **p** and **v**.

The expected number of n-generation descendents of a parent of type i in the critical process (or that value, multiplied by $(1 + \varepsilon)^n$ in the supercritical process) tends, on the other hand, to the component v_i of the right eigenvector **v** as $n \to \infty$. This value has therefore been interpreted as the "evolutionary value" of the type i in an infinite population (e.g. Oster et al., 1977). As it is shown here, (3.14), the survival probability of a slightly advantageous mutant gene, occurring in a given type (male, female, high or low class individual etc.), is proportional to the "evolutionary value" of the type in question. Moreover, denote

$$Y_i = \sum_{j=1}^n Y_{ij} v_j. \tag{4.1}$$

This is the total "evolutionary value" of offspring born to an individual of type i. Indeed $EY_i = \sum_{j=1}^n m_{ij} v_j = v_i$ and equality (3.14) becomes

$$1 - u_i(s) = \frac{2sEY_i}{\sum_{j=1}^n p_j \, \mathrm{Var} \, Y_j} + o(s). \tag{4.2}$$

The denominator is the average variance of the $Y_j - s$, weighed according to the limit relative frequencies of a non extinct population.

Example I. The effect of the mutation on the viability depends on the carrier's type

Assume that the viability of a mutant heterozygote, if belonging to type i is $1 + \varepsilon_i$ times that of a wild type individual of the same type. ε_i is either positive or negative, but small in absolute value. The mutation has no other effect on the individual. Assume, for simplicity, two alternative types (classes, sexes, habitats, etc.). The matrix of expected number of viable heterozygote mutants of types $j = 1, 2$, born to a heterozygote parent of type $i = 1, 2$ is given by

$$M(\varepsilon_1, \varepsilon_2) = \left\| \begin{matrix} (1 + \varepsilon_1)m_{11} & (1 + \varepsilon_2)m_{12} \\ (1 + \varepsilon_1)m_{21} & (1 + \varepsilon_2)m_{22} \end{matrix} \right\|$$

where $M = \|m_{ij}\|$ is the matrix of (absolute) fitness corresponding to the (infinite) wild type population and we know $|M - I| = 0$, (i.e. the population size is fixed).

By a direct calculation one can verify that the largest eigenvalue of $M(\varepsilon_1, \varepsilon_2)$ is

$$\lambda = 1 + \frac{(1 - m_{22})\varepsilon_1 + (1 - m_{11})\varepsilon_2}{2 - m_{11} - m_{22}} + o(\varepsilon_1, \varepsilon_2).$$

A straightforward calculation also yields

$$v_1 = \frac{m_{12} + 1 - m_{22}}{2 - m_{11} - m_{22}}, \qquad p_1 = \frac{1 - m_{22}}{m_{12} + 1 - m_{22}}$$
$$\tag{4.3}$$
$$v_2 = \frac{m_{21} + 1 - m_{11}}{2 - m_{11} - m_{22}}, \qquad p_2 = \frac{1 - m_{11}}{m_{21} + 1 - m_{11}}.$$

Hence

$$\lambda = 1 + p_1 v_1 \varepsilon_1 + p_2 v_2 \varepsilon_2. \tag{4.4}$$

The process of establishment of the new mutant is, therefore supercritical if and only if

$$p_1 v_1 \varepsilon_1 + p_2 v_2 \varepsilon_2 > 0. \tag{4.5}$$

(Note that the left side of (4.5) measures the average increase in expected "evolutionary value" of viable offsprings due to the effect of the mutation).

If (4.5) holds, then, using (4.2) we know that the progeny-survival probability of a single mutant heterozygote occurring in type i ($i = 1, 2$) is

$$1 - u_i = 2 \frac{p_1 v_1 \varepsilon_1 + p_2 v_2 \varepsilon_2}{p_1 \operatorname{Var} Y_1 + p_2 \operatorname{Var} Y_2} v_i + o(\varepsilon_1 \varepsilon_2). \tag{4.6}$$

Example II. (A special case of example I): The effect of the mutation on the viability of the two sexes is different

Assume an infinite sexual population with a sex-ratio $m : 1 - m$. Mating is not necessarily random. If the viabilities of the (heterozygote) mutant male and female are $1 + \varepsilon_1$ and $1 + \varepsilon_2$ times those of the wild-type male and female respectively,

then the matrix of expected progeny-sizes will be

$$M(\varepsilon_1, \varepsilon_2) = \left\| \begin{matrix} \dfrac{(1+\varepsilon_1)}{2} & \dfrac{(1+\varepsilon_2)(1-m)}{2m} \\ \dfrac{(1+\varepsilon_1)m}{2(1-m)} & \dfrac{1+\varepsilon_2}{2} \end{matrix} \right\|. \tag{4.7}$$

From (4.3) we get

$$v_1 = \frac{1}{2m}, \qquad p_1 = m$$

$$v_2 = \frac{1}{2(1-m)}, \qquad p_2 = (1-m).$$

Thus, the process is supercritical if and only if $\varepsilon_1 + \varepsilon_2 > 0$. In this case

$$\left. \begin{aligned} 1 - u_1 &= \frac{\varepsilon_1 + \varepsilon_2}{m \operatorname{Var} Y_1 + (1-m) \operatorname{Var} Y_2} \cdot \frac{1}{m} + o(\varepsilon_1, \varepsilon_2) \\ 1 - u_2 &= \frac{\varepsilon_1 + \varepsilon_2}{m \operatorname{Var} Y_1 + (1-m) \operatorname{Var} Y_2} \frac{1}{(1-m)} + o(\varepsilon_1, \varepsilon_2) \end{aligned} \right\}. \tag{4.8}$$

If the progeny size of a female is a two-dimensional Poisson distribution and if mating is random (so that the male progeny size is also a two-dimensional Poisson), then we have:

$$\left. \begin{aligned} 1 - u_1 &= \frac{\varepsilon_1 + \varepsilon_2}{m} + o(\varepsilon_1, \varepsilon_2) \\ 1 - u_2 &= \frac{\varepsilon_1 + \varepsilon_2}{(1-m)} + o(\varepsilon_1, \varepsilon_2) \end{aligned} \right\}. \tag{4.9}$$

However, if few males make most of the matings, then $\operatorname{Var} Y_1$ indeed becomes much larger and the right sides of (4.8) are much smaller.

Example III. A mutation affecting the sex ratio

Let the (infinite) wild-type population be the same as in the previous example. The mutation changes the sex ratio within the progeny of its (either male or female carrier) to $m + \varepsilon : 1 - m - \varepsilon$. The corresponding matrix of expected progeny sizes is

$$M(\varepsilon) = \left\| \begin{matrix} \dfrac{m+\varepsilon}{2m} & \dfrac{1-m-\varepsilon}{2m} \\ \dfrac{m+\varepsilon}{2(1-m)} & \dfrac{1-m-\varepsilon}{2(1-m)} \end{matrix} \right\|. \tag{4.10}$$

This matrix can be obtained from (4.7) by setting

$$\varepsilon_1 = \frac{\varepsilon}{m}, \qquad \varepsilon_2 = \frac{-\varepsilon}{1-m}.$$

The process is supercritical if and only if

$$(1 - 2m)\varepsilon < 0 \tag{4.11}$$

i.e. if the mutation initially renders the sex ratio closer to half. In this case, assuming a two-dimensional Poisson distribution of offspring, (4.9) becomes

$$\left. \begin{aligned} 1 - u_i &= \frac{(1 - 2m)\varepsilon}{m^2(1 - m)} + o(\varepsilon) \\ 1 - u_2 &= \frac{(1 - 2m)\varepsilon}{m(1 - m)^2} + o(\varepsilon) \end{aligned} \right\}. \tag{4.12}$$

With sexual selection operating on males, the progeny survival probability of the new mutants (as it appears from (4.8)) is smaller.

Example IV. A slightly advantageous mutant gene in a mixed selfing and random mating population

Let the viability of a homozygote and a heterozygote mutant in such a population be $1 + \delta$ and $1 + \varepsilon$ respectively (ε and δ are small in absolute values but not necessarily positive). Assume that the probability of selfing is α, independently of type $0 < \alpha < 1$. The expectation matrix of the two-type branching process, corresponding to the first appearance of the mutant in a large (infinite) population is

$$M(\varepsilon, \delta) = \left\| \begin{matrix} (1 + \delta)\alpha & 2(1 + \varepsilon)(1 - \alpha) \\ \dfrac{(1 + \delta)\alpha}{4} & (1 + \varepsilon)\left(1 - \dfrac{\alpha}{2}\right) \end{matrix} \right\|$$

with the largest eigenvalue being

$$\lambda = 1 + \frac{(1 - \alpha)\varepsilon + \dfrac{\alpha}{2}\delta}{1 - \dfrac{\alpha}{2}} + o(\delta, \varepsilon).$$

The corresponding eigenvectors are

$$\mathbf{p} = \left(\frac{\alpha}{4 - 3\alpha}; \frac{4(1 - \alpha)}{4 - 3\alpha} \right) + O(\delta, \varepsilon)$$

$$\mathbf{v} = \left(\frac{4 - 3\alpha}{2 - \alpha}; \frac{4 - 3\alpha}{2(2 - \alpha)} \right) + O(\delta, \varepsilon)$$

(not surprisingly, the "value" v_1 of a homozygote mutant is twice that of a heterozygote mutant v_2). Hence, with a Poisson distribution of offspring, the survival probability of a process, starting with a single heterozygote is

$$1 - u_2 = 2(\lambda - 1)v_2 + o(\delta, \varepsilon)$$

$$= \frac{2[(1 - \alpha)\varepsilon + (\alpha/2)\delta](4 - 3\alpha)}{(2 - \alpha)^2} + o(\delta, \varepsilon).$$

If the mutant gene is dominant ($\delta = \varepsilon$) we get

$$1 - u_2 = \left(2 - \frac{\alpha}{2 - \alpha}\right)\varepsilon + o(\varepsilon).$$

The survival probability of the mutant gene is, then, decreasing with the rate of selfing α.

References

Eshel, I.: On the survival probability of a slightly advantageous mutant gene with a general distribution of progeny size—a branching process model. Journal of Mathematical Biology **12**, 355–362 (1981).

Ewens, W. J.: Some applications of multiple-type branching process in population genetics. Journal of Royal Stat. Soc. B **30**, 164–175 (1968).

Ewens, W. J.: Population Genetics. London: Methuen (1969).

Harris, T. E.: The Theory of Branching Processes. Berlin: Springer (1963).

Kolmogorov, A.: Zur lösung einer biologischen aufgabe. Izvestiya Nauchno-Issledovatelskogo Instituta Matematiki pri Tomskom Gosudarstvennom Universitete **2**, 1–6 (1938).

Oster, G., Eshel, I., Cohen, D.: Worker-queen conflict and the evolution of social insects. Theor. Pop. Biol. **12**, 49–85 (1977).

Pollak, E.: Some effects of two types of migration on the survival of a gene. Biometrics **28**, 385–400 (1972).

Coevolutionary instability of mixed Nash solutions

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1. Introduction

In 1973, Maynard Smith and Price introduced game theory to the study of intraspecific conflicts. The resulting marriage has proved very fruitful of biological models (see Krebs and Davies (1978) for examples). Even simple, biologically intuitive games with a small number of strategies yield evolutionary stable equilibria with an unexpectedly rich mixture of strategy types. Furthermore, in the dynamics of these evolutionary games mathematicians have discovered interestingly complex behavior (see e.g. Bishop and Cannings, 1976; Taylor and Jonker, 1978; Zeeman, 1979).

Here we consider the analogous applications of game theory to conflicts between species (see also Hines (1981)) and examine the dynamics of the resulting coevolutionary games. Our main result, illustrated in detail for 2×2 games, is that no equilibrium of mixed strategies is locally stable. This means that a "coevolutionarily stable situation" is either a vertex equilibrium where each species relies on a single pure strategy, or else it consists of a set of mixed strategies showing no tendency to equilibrium but instead more complicated recurrence, i.e. some sort of cycling of the strategic mixtures.

We would like to express our thanks to Professors Samuel Karlin and Marcus Feldman for stimulating discussions.

2. Coevolutionary processes

We regard the members of a population P as having a choice of strategies indexed by some finite set I. For each choice $i \in I$ there is a payoff A_i which is not constant but will usually depend upon the state of the environment. The state of the population is described by its current distribution of strategies which is a vector $p = \{p_i : i \in I\}$ with $1 \geqslant p_i \geqslant 0$ for all i and $\sum_i p_i = 1$. If the population is in state p then the mean, or average, payoff $A_p = \sum_i p_i A_i$.

For a distribution vector p strategy i is called *active* if $p_i > 0$. The set of active strategies is the support of p, i.e. $\mathrm{supp}(p) = \{i \in I : p_i > 0\}$. p is called *fully mixed*

or *interior* if all strategies are active. At the other extreme, we identify the pure strategy i with the vector δ_i such that $\delta_{ii} = 1$ and $\delta_{ij} = 0$ for $j \neq i$. So supp$(\delta_i) = \{i\}$.

If the current generation is in state p then we assume that the weight of strategy i in the next generation will be more or less than p_i according to whether — in the current environment — the payoff A_i is more or less than the mean payoff A_p. Formally, we assume that the transition from the current state to the next state is given by a continuous function (a discrete time dynamical system) satisfying:

$$\text{sgn}(\Delta p_i) = \text{sgn}(A_i - A_p) \qquad (1 > p_i > 0), \tag{2.1}$$

where the sign of a real number r, sgn(r), is $+$, 0, or $-$, according to whether r is positive, zero or negative.

Condition (2.1) is not assumed for extreme values of p_i. If $p_i = 0$ then Δp_i cannot be negative as p_i cannot decrease below zero. For behavior on the boundary there are two alternate assumptions. We call the dynamical system *boundary-preserving* if, in addition to (2.1),

$$\Delta p_i = 0 \quad (\text{when } p_i = 0). \tag{2.2B}$$

This condition means that the pure strategies "breed true". If i is not active in the current population then it cannot appear in subsequent generations.

Alternatively, we call the dynamical system *inward-pointing* if, in addition to (2.1),

$$\text{sgn}(\Delta p_i) = \max(0, \text{sgn}(A_i - A_p)) \quad (\text{when } p_i = 0) \tag{2.2I}$$

which means that p_i becomes positive if $A_i > A_p$ but remains at zero if $A_i \leqslant A_p$.

The latter condition should not be confused with the effect of mutation — which we are ignoring. Mutation would instead impose a perturbation on a boundary preserving system (and would override condition (2.1) when p_i is small but positive.

Proposition 1. *In order that p^* be an equilibrium relative to the current environment it is necessary that*

$$A_i = A_{p^*} \quad \text{for all } i \in \text{supp}(p^*) \tag{2.3}$$

or equivalently, that the payoff for all strategies active for p^* be the same. If the system is boundary-preserving this condition is also sufficient.

If the system is inward pointing it is necessary and sufficient for equilibrium that (2.3) hold and, in addition,

$$A_i \leqslant A_{p^*} \quad \text{for all } i \in I. \tag{2.4}$$

Proof: If $A_i = C$ for all $i \in \text{supp}(p^*)$ then $C = \sum p_i^* C = \sum p_i^* A_i = A_{p^*}$ because the sums are the same whether taken over all i or just over $i \in \text{supp}(p^*)$.

Notice that if $p_i^* = 1$ for some i then $p^* = \delta_i$ and $A_i = A_{p^*}$ trivially. Because of the requirement that $1 > p_i$ in (2.1), a separate argument — which we leave to the reader — is needed for these pure strategy cases.

Otherwise, $p_i^* < 1$ for all i and (2.1) says that $\Delta p_i = 0$ for $i \in \text{supp}(p^*)$ if and only if $A_i = A_{p^*}$. (2.2B) says $\Delta p_i = 0$ for all inactive i while (2.2I) says that $\Delta p_i = 0$ for inactive i if and only if $A_i \leqslant A_{p^*}$.

We need one more game theoretic concept. For $i_1, i_2 \in I$ we say that i_1 *dominates* i_2 if $A_{i_1} > A_{i_2}$ for all environmental states.

Lemma 2. *Suppose i_1 dominates i_2. If p^* is an equilibrium, then i_1 and i_2 cannot both be active for p^*, i.e. $p_{i_2} = 0$ or $p_{i_1} = 0$. If the system is inward pointing then i_2 cannot be active, i.e. $p_{i_2} = 0$.*

Proof: If $p_{i_2}^* > 0$ and $\Delta p_{i_2} = 0$ then $A_{i_1} > A_{i_2} = A_{p^*}$ by domination and (2.3). So by (2.3) again $i_1 \notin \mathrm{supp}(p^*)$. If the system is inward pointing the inequality $A_{i_1} > A_{p^*}$ violates (2.4) and so $p_{i_2}^* > 0$ contradicts the assumption that p^* is a current equilibrium.

We now apply these preliminaries to two interacting populations P and Q. The strategy choices of P and Q are indexed by finite sets I and J respectively. When an i strategist from P meets a j strategist from Q the payoffs are *constants* A_{ij} and B_{ij} to the P and Q players, respectively. So if the current state of P and Q are given by distributions p and q respectively then the average payoff to an i strategist in P is $A_{iq} \equiv \sum_J A_{ij} q_j$ and the average payoff for the population as a whole is $A_{pq} \equiv \sum_{I,J} p_i A_{ij} q_j$, with similar definitions using B_{ij} for population Q.

We define a *coevolutionary process* for P and Q to be a discrete time dynamical system as above where the state of each population determines the environment of the others. Thus

$$\mathrm{sgn}(\Delta p_i) = \mathrm{sgn}(A_{iq} - A_{pq}) \qquad (1 > p_i > 0)$$
$$\mathrm{sgn}(\Delta q_j) = \mathrm{sgn}(B_{pj} - B_{pq}) \qquad (1 > q_j > 0). \tag{2.5}$$

The process is boundary-preserving if, in addition,

$$\Delta p_i = 0 \qquad (p_i = 0)$$
$$\Delta q_j = 0 \qquad (q_j = 0). \tag{2.6B}$$

The process is inward pointing if instead

$$\mathrm{sgn}(\Delta p_i) = \max(0, \mathrm{sgn}(A_{iq} - A_{pq})) \qquad (p_i = 0)$$
$$\mathrm{sgn}(\Delta q_j) = \max(0, \mathrm{sgn}(B_{pj} - B_{pq})) \qquad (q_j = 0). \tag{2.6I}$$

Domination now becomes a finite condition: for $i_1, i_2 \in I$, i_1 dominates i_2 if $A_{i_1 j} > A_{i_2 j}$ for all $j \in J$ and similarly for domination in J. Notice that these conditions are equivalent to the apparently more general: $A_{i_1 q} > A_{i_2 q}$ for all q.

From Proposition 1 the following is immediate:

Theorem 3. *In order that the pair (p^*, q^*) be an equilibrium for the coevolutionary process it is necessary that:*

$$A_{iq^*} = A_{p^* q^*} \quad \text{for all } i \in \mathrm{supp}(p^*)$$
$$B_{p^* j} = B_{p^* q^*} \quad \text{for all } j \in \mathrm{supp}(q^*). \tag{2.7}$$

If the process is boundary preserving these conditions are sufficient as well. If the process is inward pointing it is necessary and sufficient that (2.7) hold and, in addition:

$$A_{iq^*} \leqslant A_{p^* q^*} \quad \text{for all } i$$
$$B_{p^* j} \leqslant B_{p^* q^*} \quad \text{for all } j. \tag{2.8}$$

A pair satisfying (2.7) and (2.8) is called a *Nash equilibrium*. We will call a pair satisfying (2.7) alone a *weak Nash equilibrium*. Notice that any vertex (δ_i, δ_j) is a weak Nash equilibrium but need not be Nash. On the other hand, the two concepts agree if both p^* and q^* are fully mixed.

Theorem 3 says that once the payoff matrices and boundary behavior are specified the equilibria are determined. They do not depend upon the choice of coevolutionary process.

Nash equilibria always exist. In fact, in our terminology, Nash's proof of this result consists of writing down a particular inward pointing process and applying the Brouwer fixed point theorem.

To illustrate the behavior of coevolutionary processes we specialize to the 2×2 case, i.e. we assume that each population has available two strategies labelled 0 or 1: $I = J = \{0, 1\}$. The state of P is described by the real number $p = p_1$ with $0 \le p \le 1$ and $p_0 = 1 - p$. Similarly, Q is described by $q = q_1$ with $q_0 = 1 - q$. Notice

$$A_{1q} - A_{pq} = A_{1q} - (pA_{1q} + (1-p)A_{0q}) = (1-p)(A_{1q} - A_{0q})$$

whose sign is that of $A_{1q} - A_{0q} = (A_{11} - A_{01})q + (A_{10} - A_{00})(1 - q)$ when $0 < p < 1$. Thus, (2.5) becomes:

$$\operatorname{sgn}(\Delta p) = \operatorname{sgn}(A_{1q} - A_{0q}) = \operatorname{sgn}(\alpha_1 q + \alpha_0(1 - q)) \qquad (0 < p < 1)$$
$$\operatorname{sgn}(\Delta q) = \operatorname{sgn}(B_{p1} - B_{p0}) = \operatorname{sgn}(\beta_1 p + \beta_0(1 - p)) \qquad (0 < q < 1) \tag{2.9}$$

where

$$\alpha_1 = A_{11} - A_{01}, \qquad \alpha_0 = A_{10} - A_{00}$$
$$\beta_1 = B_{11} - B_{10}, \qquad \beta_0 = B_{01} - B_{00}.$$

For the moment we restrict attention to boundary preserving processes and so assume

$$\Delta p = 0 \quad \text{when } p = 0 \text{ or } 1,$$
$$\Delta q = 0 \quad \text{when } q = 0 \text{ or } 1. \tag{2.10B}$$

Also, we assume for the moment the following nondegeneracy condition:

$$\text{None of the numbers } \alpha_0, \alpha_1, \beta_0, \beta_1 \text{ vanish.} \tag{2.11}$$

Proposition 4. (a) *If $\alpha_0, \alpha_1 < 0$ then strategy 0 dominates strategy 1 for P and for any $0 < p < 1$, $\Delta p < 0$. So p decreases monotonically over subsequent generations approaching 0 in the limit.*

If $\alpha_0, \alpha_1 > 0$ then 1 dominates 0 for P and 1 is the limit for all interior initial values.

(b) *If $\alpha_0 < 0 < \alpha_1$ then $\Delta p = 0$ when $q = q^*$ where $q^* = |\alpha_0/\alpha_1|/(1 + |\alpha_0/\alpha_1|)$ and more generally*

$$\operatorname{sgn}(\Delta p) = \operatorname{sgn}(q - q^*) \text{ for } 0 < p < 1.$$

If $\alpha_0 > 0 > \alpha_1$ then $\operatorname{sgn}(\Delta p) = -\operatorname{sgn}(q - q^*)$.

Proof: Consider the linear function of q: $\alpha_q = \alpha_1 a + \alpha_0(1 - q)$. If α_0 and α_1 have like signs then α_q shares this share for all $0 \le q \le 1$ and so Δp has this sign for all values of q $(0 < p < 1)$. Thus the successive values of p form a monotone sequence.

The limiting value must be the p coordinate of an equilibrium and so equals 0 or 1.

On the other hand, if α_0 and α_1 have opposite signs then α_q vanishes at $q = q^*$ and for $q > q^*$ ($q < q^*$) the sign of α_q is that of α_1 (resp. of α_0).

Corollary 5. *Assuming (2.11), a nonvertex equilibrium exists if and only if both α_0, α_1 and β_0, β_1 have unlike signs. There is then a unique, nonvertex equilibrium (p^*, q^*) which is fully mixed:*

$$p^* = |\beta_0/\beta_1|/(1 + |\beta_0/\beta_1|)$$
$$q^* = |\alpha_0/\alpha_1|/(1 + |\alpha_0/\alpha_1|).$$

The behavior of such a 2×2 system falls into one of four categories illustrated by the phase portraits of Figs. 1–4. In Fig. 1 both populations show domination while in Fig. 2 only one does (domination for P is illustrated). In these cases the only equilibria are the vertices. One vertex is a sink attracting every initial position in the interior of the square. The remaining vertices are locally unstable (1 source and 2 saddle points).

Figure 3, which we call the *hyperbolic case*, occurs when there is a fully mixed equilibrium and $\alpha_1 - \alpha_0, \beta_1 - \beta_0$ have like signs. Two vertices are sinks, each attracting initial values from roughly triangular regions separated by an exceptional set of initial points which tend to the saddle point (p^*, q^*). The remaining two vertices are sources.

Figure 4, which we call the *elliptic case*, occurs when there is a fully mixed equilibrium and $\alpha_1 - \alpha_0, \beta_1 - \beta_0$ have unlike signs. No vertex is locally stable as they are all saddles. The interior points orbit around (p^*, q^*). However, as we will see below this interior equilibrium is a source so that nearby orbits spiral outwards. Thus, there are no locally stable equilibria in this case.

Fig. 1. Double domination
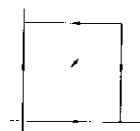
$\alpha_0, \alpha_1 < 0$

$\beta_0, \beta_1 < 0$

Fig. 2. Single domination

$\alpha_0, \alpha_1 < 0$

$\beta_0 < 0 < \beta_1$
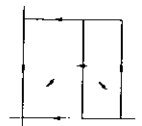
Fig. 3. Hyperbolic case

$\alpha_0 < 0 < \alpha_1$

$\beta_0 < 0 < \beta_1$
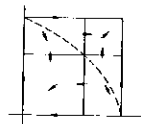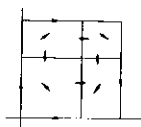

Fig. 4. Elliptic case

$\alpha_0 < 0 < \alpha_1$

$\beta_1 < 0 < \beta_0$

These four robust types are separated by degenerate cases where hypothesis (2.11) does not hold. If $\alpha_0 = \alpha_1 = 0$ then the strategies 0 and 1 are behaviorally indistinguishable for P and $\Delta p = 0$ for all points. On the other hand if only one of α_0, α_1 vanish then P exhibits a weak form of domination. For example, if $\alpha_1 < \alpha_0 = 0$ then $\Delta p < 0$ when $q > 0$ but the entire segment defined by $q = 0$ consists of equilibria.

Finally, if we replace boundary-preserving behavior by the inward pointing assumption the only vertices which are equilibria are the sinks (assuming (2.11)) because only these satisfy the Nash condition (2.8). Thus, for an inward-pointing version of the elliptic case no vertex is an equilibrium and the source (p^*, q^*) is the only equilibrium of the system.

That (p^*, q^*) is a source in the elliptic case is a special case of our main result:

Theorem 6. *A nondegenerate mixed equilibrium is never locally stable with respect to a smooth coevolutionary process.*

By a smooth coevolutionary process we intend a slight sharpening of condition (2.9). So in the 2×2 case we assume that the dynamic is defined by a function $(p, q) \to (f(p, q), g(p, q))$ with

$$
\begin{aligned}
f(p, q) &= \varphi(p, A_{0q}, A_{1q}) \\
g(p, q) &= \psi(q, B_{p0}, B_{p1})
\end{aligned}
\tag{2.12}
$$

where φ and ψ are continuously differentiable functions of three real variables satisfying

$$
\begin{aligned}
\varphi(p, a, b) &= p \\
\psi(q, a, b) &= q
\end{aligned}
\quad \text{when } a = b
\tag{2.13}
$$

and

$$
\begin{aligned}
\varphi_2 < 0, \ \varphi_3 < 0 \quad (0 < p < 1) \\
\psi_2 < 0, \ \psi_3 < 0 \quad (0 < q < 1)
\end{aligned}
\tag{2.14}
$$

where φ_2, φ_3 are the partial derivatives with respect to the second and third variables.

Equation (2.13) means that $f(p, q) = p$ when $A_{0q} = A_{1q}$. (2.14) then implies that $f(p, q) > p$ (or $< p$) if $A_{0q} < A_{1q}$ (resp. $A_{0q} > A_{1q}$). This is condition (2.9) and so explains why we regard (2.13) and (2.14) as the smooth version of (2.9).

Example: Assume that P and Q are randomly mating diploid populations with strategy choices determined by the genotype at one locus with two alleles. Suppose the two alleles for P are P_1 and P_2 and that an individual of genotype $P_\alpha P_\beta$ uses strategy 0 with probability $h_{\alpha\beta}$ ($\alpha, \beta = 1, 2$). Similarly, an individual of type $Q_\alpha Q_\beta$ uses strategy 0 with probability $k_{\alpha\beta}$ ($\alpha, \beta = 1, 2$). We assume $h_{11} \geqslant h_{12} \geqslant h_{22}$ with at least one inequality sharp and analogous ordering for the $k_{\alpha\beta}$ probabilities in population Q.

If x is the frequency of allele P_1, the gene frequency, then the strategy frequency p is given by

$$
p = h(x) \equiv x^2 h_{11} + 2x(1-x)h_{12} + (1-x)^2 h_{22}.
\tag{2.15}
$$

The strategy 0 frequency, q, in Q is the analogous function $k(y)$ of the gene frequency, y, of Q_1. Notice that the inequalities assumed about the $h_{\alpha\beta}$'s and $k_{\alpha\beta}$'s make $h(x)$ and $k(y)$ increasing functions with image the interval $[h_{22}, h_{11}]$ and $[k_{22}, k_{11}]$, respectively.

Given frequency q in population Q the viability of $P_\alpha P_\beta$ is:

$$w_{\alpha\beta}(q) = h_{\alpha\beta} A_{0q} + (1 - h_{\alpha\beta}) A_{1q}. \tag{2.16}$$

Hence the frequency x' of P_1 after one round of selection is given by the usual formula:

$$x' = \frac{x[w_{11}(q)x + w_{12}(q)(1-x)]}{x^2 w_{11}(q) + 2x(1-x)w_{12}(q) + (1-x)^2 w_{22}(q)}. \tag{2.17}$$

Notice that by (2.16) the denominator, the mean viability of the population, $\bar{w}(x, q)$ is just the mean payoff $A_{pq} = A_{1q} + p(A_{0q} - A_{1q})$. Substituting (2.16) into (2.17) we define a function $x' = \hat{\varphi}(x, A_{0q}, A_{1q})$. The function φ of (2.12) is obtained by conjugating with the monotone function h, i.e. $p' = h(x')$ and $p = h(x)$ or $x = h^{-1}(p)$.

$$\varphi(p, A_{0q}, A_{1q}) = h[\hat{\varphi}(h^{-1}(p), A_{0q}, A_{1q})].$$
$$\psi(q, B_{p0}, B_{p1}) = k[\hat{\psi}(k^{-1}(q), B_{p0}, B_{p1})] \tag{2.18}$$

where $\hat{\psi}(y, B_{p0}, B_{p1})$ is defined via the analogues of (2.16) and (2.17).

Conditions (2.13) and (2.14) are easily verified directly and so (2.18) defines a smooth coevolutionary process. (2.19) alone follows from Fisher's Fundamental Theorem which says, in this case, that for fixed q, $\bar{w}(x', q) \geqslant \bar{w}(x, q)$ (with equality only at equilibrium), i.e. $p'(A_{0q} - A_{1q}) \geqslant p(A_{0q} - A_{1q})$. (See for comparison Eshel 1982).

Proof of Theorem 6: Now suppose there is a fully-mixed Nash equilibrium (p^*, q^*). To discuss local stability we linearize at the equilibrium. Our result follows from the discovery that at least one eigenvalue has absolute value greater than 1.

The key fact is that $A_{0q^*} = A_{1q^*}$ and so $f(p, q^*) = p$ for all p. Consequently, $f_p = \partial f/\partial p = 1$ at (p^*, q^*). Similarly, $g_q = \partial g/\partial q = 1$ there. The matrix of the linearization is thus:

$$\begin{pmatrix} 1 & f_q \\ g_p & 1 \end{pmatrix}$$

with eigenvalues

$$\lambda_\pm = 1 \pm \sqrt{f_q g_p}.$$

If $f_p g_q > 0$: The eigenvalues are real and $\lambda_+ > 1$. Because the map preserves orientation of the square the determinant $\lambda_+ \lambda_- > 0$ and so $0 < \lambda_- < 1$. So one eigenvalue is larger than 1.

If $f_p g_q < 0$: The eigenvalues are complex conjugates and $|\lambda_+|^2 = |\lambda_-|^2 = 1 + |f_p g_q| > 1$.

With a bit more analysis we will see that these two possibilities correspond to the hyperbolic and elliptic cases respectively. Furthermore we will see that $f_p g_q = 0$ corresponds to the degenerate cases where (2.11) fails to hold.

Notice that when $a = b$, $-\varphi_2 = \varphi_3 > 0$. To see this differentiate the equation $\varphi(p, a, a) = p$ with respect to a to get $\varphi_2 + \varphi_3 = 0$ and apply (2.14).

$$f_q = \varphi_2(A_{01} - A_{00}) + \varphi_3(A_{11} - A_{10})$$
$$= -\varphi_3(A_{01} - A_{00}) + \varphi_3(A_{11} - A_{10}) = \varphi_3(\alpha_1 - \alpha_0).$$

Similarly, $g_p = \psi_3(\beta_1 - \beta_0)$ with $\psi_3 > 0$ and so the sign of $f_q g_p$ is that of $(\alpha_1 - \alpha_0)$ $(\beta_1 - \beta_0)$. In particular, $f_q g_p = 0$ is equivalent to $\alpha_1 = \alpha_0$ or $\beta_1 = \beta_0$. If $\alpha_1 = \alpha_0 \neq 0$ there is domination for P and so no fully-mixed equilibrium. If the common value is zero then as described above strategies 0 and 1 are indistinguishable for P and p does not move. Even in this case it is easy to check by looking at phase portraits with β_0, β_1 having unlike nonzero signs that there is no local stability unless $\beta_1 = \beta_0 = 0$ also. So in the 2×2 case there is local stability only in the trivial case where (p, q) never moves.

The general result — which we will just sketch — differs only in various technicalities from the 2×2 case. Now p, q are vectors and $f(p, q)$, $g(p, q)$ are vector functions of vector variables. We assume

$$f(p, q) = \varphi(p, \{A_{iq}\})$$
$$g(p, q) = \psi(q, \{B_{pj}\})$$

with

$$p = \varphi(p, \{a_i\}) \quad \text{(when all } a_i\text{'s are equal)}$$
$$q = \psi(q, \{b_j\}) \quad \text{(when all } b_j\text{'s are equal).}$$
(2.19)

The conditions analogous to (2.14) only arise in connection with degeneracy questions as we will see below.

Again, if (p^*, q^*) is a fully mixed equilibrium then differentiating $f(p, q)$ with respect to the p_i's at (p^*, q^*) yields the identity matrix and similarly for differentiating $g(p, q)$ with respect to the q_j's. Thus the matrix of the linearization at (p^*, q^*) is of the block form

$$\begin{pmatrix} 1_I & 0 \\ 0 & 1_J \end{pmatrix} + \begin{pmatrix} 0_I & U \\ V & 0_J \end{pmatrix}$$

where 1_I, 1_J are the $I \times I$ and $J \times J$ identity matrices, 0_I and 0_J are square matrices of zeros. U is the matrix of partials $(\partial f_i / \partial g_j)$ and V is the matrix of partials $(\partial g_j / \partial p_i)$.

Because the left term is the identity, the eigenvalues of the linearization consist of $\{\lambda = 1 + \mu\}$ where $\{\mu\}$ is the set of eigenvalues of the off diagonal matrix

$$M = \begin{pmatrix} 0 & U \\ V & 0 \end{pmatrix}.$$

Claim: The nonzero eigenvalues of M are exactly the square roots of the nonzero eigenvalues of UV or equivalently the square roots of the nonzero eigenvalues of VU.

To see why this is so, notice first that the square of any eigenvalue of M is an eigenvalue (with the same eigenvector) of

$$M^2 = \begin{pmatrix} UV & 0 \\ 0 & VU \end{pmatrix}.$$

Because this matrix is block diagonal its eigenvalues are those of UV and VU. (These two matrices actually have the same set of nonzero eigenvalues but we won't need that result.)

On the other hand, suppose $UVz = \omega z$ ($\omega \neq 0$) and $\mu^2 = \omega$. It is easy to check directly that the vector

$$\begin{pmatrix} z \\ Vz/\mu \end{pmatrix}$$

is an eigenvector of M with eigenvalue μ.

Now suppose UV or VU has some nonzero eigenvalue ω.

Case 1: If ω is real and positive then $\mu = \sqrt{\omega}$ is an eigenvalue of M and so $\lambda = 1 + \sqrt{\omega}$ is an eigenvalue of the linearization, with $\lambda > 1$.

Case 2: If ω is real and negative then $\mu_{\pm} = \pm i\sqrt{|\omega|}$ is a conjugate pair of pure imaginary eigenvalues and so $\lambda_{\pm} = 1 \pm i\sqrt{|\omega|}$ is a conjugate pair for the linearization with $|\lambda_{\pm}| > 1$.

Case 3: If $\omega_{\pm}$ is a conjugate pair of complex eigenvalues then the four resulting square roots $\pm\sqrt{\omega_{\pm}}$ are symmetrically distributed about the origin and contain one conjugate pair, which we label $\mu_{\pm}$, with positive real part. Then $\lambda_{\pm} = 1 + \mu_{\pm}$ is a conjugate pair for the linearization with $|\lambda_{\pm}| > 1$.

So the only possibility remaining is that all eigenvalues of UV and VU are zero and so all of the eigenvalues of the linearization are exactly 1. This case is degenerate in the sense that given conditions analogous to (2.13) a perturbation of the payoff matrices should eliminate it as a possibility just as weak domination represented the boundary between the four robust types in the 2×2 case.

Corollary 7. *A nondegenerate, locally stable equilibrium for a smooth coevolutionary process can occur only at a vertex. i.e. pure strategies for P and Q. In particular, only a vertex can be a nondegenerate sink.*

Proof: Suppose (p^*, q^*) is an equilibrium and the supports p^* and q^* are $I_0 \subset I$ and $J_0 \subset J$ respectively. If I_0 and J_0 both contain at least two strategies then by restricting to the $I_0 \times J_0$ subgame and applying the previous theorem we see that (p^*, q^*) cannot be locally stable even with respect to perturbations having the same support. If J_0 contains only one strategy, say $J_0 = \{j_0\}$ so that $q^* = \delta_{j_0}$ then p^* is an equilibrium only if all the A_{ij_0}'s are equal. This case is degenerate if I_0 contains more than one strategy. So we are left with the vertex case.

3. Summary and discussion

For an inter population game we have shown, first, that the equilibria depend only upon the payoff matrices of the game and the boundary behavior assumptions

but are independent of the choice of coevolutionary process modelling the dynamics. Secondly, we have seen that — barring degenerate cases — only a Nash equilibrium of pure strategies can be an attracting equilibrium and so only these positions represent biologically observable stationary states. These results overlap with those of Hines (1981). Hines' models are more general in considering the use of mixed strategies by individuals. On the other hand, he restricts attention to a particular dynamical system.

Underlying the mathematics of the failure of stability for mixed equilibria is a simple idea. Suppose (p^*, q^*) is a fully-mixed equilibrium. q^* determines the environment of population P and because p^* is a fully-mixed equilibrium every strategy i for P yields the same payoff. Thus, as long as Q remains at q^* there is no selection pressure tending to hold P at p^* and it is free to drift away. Dynamically, this is the neutral stability of a cone lying on its side as opposed to balanced on its point or resting on its base. Of course, once both P and Q have drifted away from equilibrium the strategies are no longer equivalent and selection pressures begin to move both populations about. But a priori there is no reason that the dynamic behavior should tend to damp out the perturbations and return the system to (p^*, q^*). In fact, our analysis shows the opposite. Small perturbations are intensified and the populations move away from the original equilibrium.

Where then does the system go? In three of the four 2×2 cases the population comes to rest at a pure strategy Nash equilibrium. In the elliptic case there is no such equilibrium. The orbits spiral away from the center but their limiting behavior is uncertain. Do they approach the boundary or some compact set of nonequilibrium strategies in the interior (periodic points or limit cycles)? Unlike the equilibrium behavior, the answers to these questions do depend on the choice of coevolutionary process. For example, in Fig. 4 any map of the square consistent with the directions given by the arrows is a coevolutionary process and any of these outcomes can occur.

In comparing our discrete time results with a continuous time model, Maynard Smith has mentioned that mixed strategy equilibria can be locally stable in the latter case. While true we regard this result as misleading. Consider the differential equation model which generalizes the Taylor–Jonker equations:

$$\frac{dp_i}{dt} = p_i(A_{iq} - A_{pq})$$

$$\frac{dq_j}{dt} = q_j(B_{pj} - B_{pq})$$

(3.1)

At a fully mixed equilibrium the matrix of linearization is of the form

$$M = \begin{pmatrix} 0_I & U \\ V & 0_J \end{pmatrix}$$

and the proof of Theorem 6 shows that if no eigenvalues with positive real part occur then all the eigenvalues must be zero or pure imaginary. If they are not all zero then the introduction of any lag into the system at all renders the equilibrium unstable (cf. Chapter 2 of May (1973)).

More generally, using the machinery of differential forms it is possible to write down a volume form Ω on the interior $(=\{p: p_i>0 \text{ and } \sum p_i = 1\} \times \{q: q_j>0 \text{ and } \sum q_j = 1\})$ such that the flow of (3.1) preserves the associated volume or equivalently the vectorfield has zero divergence with respect to Ω. This means that the motion is like that of an incompressible fluid. Stable equilibria can occur but they are never asymptotically stable, i.e. there are no sinks. Perturbations are not intensified but neither are they damped out. In fact there can be no compact set contained in the interior which attracts all nearby orbits. For if A were such an attractor it would have a compact neighborhood U which is mapped to a smaller neighborhood in U by the flow. This is impossible because U has finite volume and this volume is preserved by the flow. Attractors can occur in the boundary — e.g. vertices which are Nash equilibria — because the volume form blows up at the boundary and so neighborhoods of vertices have infinite volume.

References

1. Bishop, R. T., Cannings, C.: Models of animal conflict. Adv. Appl. Prob. **8**, 4: 616–621 (1976)
2. Eshel, I.: Evolutionary stable strategies and natural selection in Mendelian populations. (1982). Theor. Pop. Biol. **21**, 2, 204–217
3. Hines, W. G. S.: Multi-species population models and evolutionary stable strategies. Adv. Appl. Prob. (1981)
4. Krebs, J. R., Davies, N. B.: Behavioral ecology: An evolutionary approach. Sinauer Associates, Sunderland, MA (1978)
5. May, R. M.: Stability and complexity in model ecosystems. Princeton University Press. Princeton, N.J., 1973
6. Maynard Smith, J., Price, G.: The logic of animal conflicts. Nature **246**, 15–18 (1973)
7. Taylor, P., Jonker, L.: Evolutionary stable strategies and game dynamics. Math. Biosci. 40: 145–156 (1978)
8. Zeeman, C.: Population dynamics from game theory. In: Global theory of dynamical systems. Lecture Notes in Mathematics, vol. 819. Berlin–Heidelberg–New York: Springer 1979