

群淘汰のおもちゃモデルにおける安定な平衡多型

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Stable polymorphic equilibria in a toy model of group selection¹⁾

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ABSTRACT

A basic model of group selection was formulated by Eshel (1972) and corrected for an "unnatural" assumption by Roughgarden (1979). The model assumes two counteracting selective forces, i.e. group selection and individual selection, in a deme-structured population; and was proposed in relation to the evolution of altruistic behavior. In this paper, I derive further properties of this model, concentrating on the special case of two haploid individuals per deme. Specifically, I prove the existence and stability of polymorphic equilibria in the extreme case of migration rate 1. The existence and stability of other equilibria are studied systematically by defining four regions in the (m, k) -parameter space for fixed s . Here, k is a measure of group selection, s is the selection coefficient against the individually deleterious type, and m is the migration rate. One region appears to correspond to stable polymorphic equilibria. The results are discussed in relation to the critical equality $k=2Nms$ where N is the deme size (Aoki, 1982), and also in relation to polymorphic equilibria in the diffusion approximation when mutation is ignored (Kimura, 1983, 1984; Ogura and Shimakura, submitted).

1. INTRODUCTION

There is undiminished interest in group selection theory (Kimura 1983, 1984; Leigh 1983; Crow and Aoki 1984; Fix 1985; Nunney 1985), including the theory of cultural group selection (Boyd and Richerson 1985). Group selection theory deals with the action of two counteracting selective forces, i. e. group selection and individual selection, in a deme-structured population. It has been studied mainly in relation to the evolution of altruistic behavior (Wilson 1975), and that is my concern in this paper.

Given this interest, it seems worthwhile to restudy a basic model of group selection. A better understanding of the properties of this basic model should illuminate the results obtained on derived or modified models. The basic model I refer to is the one first formulated most clearly by Eshel (1972), although this formulation contained an "unnatural" assumption which was corrected by Roughgarden (1979, p. 286). Aoki (1982) obtained a simple approximate criterion for group selection to prevail, and Kimura (1983, 1984)

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made a most elegant analysis of the diffusion approximation to this model.

The present paper treats a very special case of the basic model in which the deme size is 2 haploid individuals. Borrowing a phrase from Dyson (1985), I will refer to this special case as the "toy model". Although a deme-structured population with demes of size 2 is unrealistic, interesting properties are revealed which may carry over to the general case of N individuals per deme.

I focus on stable polymorphic equilibria, i. e. stationary distributions that are stable to small perturbations. Their existence is strongly suggested by various methods (Eshel 1972; Levin and Kilmer 1974; Roughgarden 1979; Aoki 1982), but has not been proven. This problem is of particular interest in relation to the status of polymorphic equilibria in the diffusion approximation when mutation is ignored (Ogura and Shimakura submitted).

Specifically, I prove the existence of stable polymorphic equilibria in the extreme case of migration rate 1. Then, I partition a parameter space into four regions according to the stability properties of the two monomorphic equilibria. Finally, I argue by way of numerical examples that one region of this parameter space corresponds to stable polymorphic equilibria.

2. BASIC MODEL

Assume a population subdivided into an infinite number of demes each comprising N haploid individuals. Let there be two alleles at one locus, one altruistic and the other nonaltruistic, which determine whether an individual is an altruist or nonaltruist, respectively. Let f_i , $i=0, 1, \dots, N$, be the probability distribution of demes with i altruists. We assume that the life cycle consists of group selection, migration, individual selection, mutation, random genetic drift, and recolonization, in that order.

Group selection occurs by the differential survival of demes. Let z_i be the survival probability per generation of a deme with i altruists. We assume that z_i is monotone nondecreasing in i , i. e. altruists are assumed to contribute to the survival of a deme. Put

$$\bar{z} = \sum_{i=0}^N z_i f_i, \quad [1a]$$

$$\bar{y} = \sum_{i=0}^N i z_i f_i. \quad [1b]$$

Now define

$$\bar{p}^* = \bar{y} / (N\bar{z}). \quad [2]$$

This is the frequency of altruists in the population after group selection.

Consider now the surviving demes. Migration occurs according to the island model at rate m (Wright 1931, 1969). Within each deme, under in-

dividual selection, altruists are selected against with selection coefficient s . Mutation occurs to and from the altruistic allele at rates v' and v . Then, a deme in which the frequency of altruists is i/N before migration, individual selection, and mutation has frequency p_i afterward, where

$$p_i = (1-v)(1-s)[(1-m)(i/N) + m\bar{p}^*] / \{1-s[(1-m)(i/N) + m\bar{p}^*]\} + v'\{1-[(1-m)(i/N) + m\bar{p}^*]\} / \{1-s[(1-m)(i/N) + m\bar{p}^*]\}. \quad [3]$$

Perhaps this is the place to clarify the “unnatural” aspect of Eshel’s formulation. Eshel (1972) assumes that \bar{p}^* in Eq. [3] is the average frequency before group selection, although in other aspects his model is identical to the one described here. This implies that as the migration rate m becomes large group selection is undermined, until in the extreme case $m=1$ it becomes completely ineffective.

The deterministic processes above are followed by random genetic drift according to the Wright model (Wright 1931) within each deme. Reproduction is either asexual or sexual with random mating. Put

$$a_{ji} = {}_N C_j (p_i)^j (1-p_i)^{N-j}. \quad [4]$$

From the above, the recursion in the probability distribution f_i is

$$f'_j = \sum_{i=0}^N a_{ji} z_i f_i / \bar{z}. \quad [5]$$

Henceforth, we assume the linear group selection function

$$z_i = z_0 [1 + k(i/N)] \quad [6]$$

with $0 < z_0 < 1$ and $0 < k < z_0^{-1} - 1$. For convenience, and without loss of generality, we can put $z_0 = 1$, since z_0 cancels out of all equations. But we must remember that the upper bound on k depends on the assumed value of z_0 .

The assumptions on the other parameters are as follows: $0 \leq m \leq 1$, $0 < s < 1$, and $v = v' = 0$. We have introduced mutation in the basic model only to ignore it in all subsequent arguments.

Mathematically, the model is now complete. But from a biological standpoint we require recolonization to preserve the total number of demes. We assume that recolonization occurs in such a way that the probability distribution f_i is unaffected.

3. STABLE POLYMORPHIC EQUILIBRIA IN THE TOY MODEL

I have been able to prove the existence of stable polymorphic equilibria only in the case $m=1$. Henceforth, put $N=2$.

First, I show existence. When $m=1$, from Eqs. [3] and [2] (recalling the assumption of no mutation) we have

$$\begin{aligned} p_i &= \bar{p}^*(1-s)/(1-s\bar{p}^*) \\ &= \bar{y}(1-s)/(2\bar{z}-s\bar{y}), \end{aligned} \quad [7]$$

for $i=0, 1, 2$. For convenience, put

$$\bar{p} \equiv \bar{y}(1-s)/(2\bar{z}-s\bar{y}). \quad [8]$$

Substituting Eq. [7] in Eq. [4] and then Eq. [4] in Eq. [5], and recalling Eq. [8], we obtain the recursion

$$f'_j = {}_2C_j(\bar{p})^j(1-\bar{p})^{2-j}. \quad [9]$$

Note that \bar{p} is a function of f_i , $i=0, 1, 2$.

We denote the equilibrium values by a caret. In particular, we denote the equilibrium value of \bar{p} by ξ , i. e.

$$\hat{\bar{p}} = \xi. \quad [10]$$

Then, the stationary probability distribution $f_i^{\hat{}}$ is binomial with parameters 2 and ξ , i. e.

$$f_0^{\hat{}} = (1-\xi)^2, f_1^{\hat{}} = 2\xi(1-\xi), f_2^{\hat{}} = \xi^2. \quad [11]$$

Thus, substituting Eq. [6] in Eqs. [1a] and [1b], and noting Eq. [11], we obtain

$$\hat{z} = 1 + k\xi, \quad [12a]$$

$$\hat{y} = (k+2)\xi + k\xi^2. \quad [12b]$$

Finally, assuming equilibrium and substituting Eqs. [10], [12a], and [12b] in Eq. [8], we obtain the cubic equation in ξ

$$\xi[sk\xi^2 + (2s-k)\xi + k - s(k+2)] = 0. \quad [13]$$

From Eq. [13] it can be shown that the roots 0 and 1 always exist, and that a root between 0 and 1 also exists, i. e.

$$\xi = [k - s(k+2)]/(sk) \text{ if } 2s/(1-s) < k < 2s/(1-2s). \quad [14]$$

The upper bound on k exists only when $2s < 1$.

Thus, polymorphic equilibria exist with stationary distribution defined by Eqs. [11] and [14].

Next, we consider the local stability of that stationary distribution by linearizing the recursion equations [9]. Choosing f_1 and f_2 as the independent variables, the coefficient matrix of the linearized system is

$$\begin{pmatrix} a_\xi & b_\xi \\ c_\xi & d_\xi \end{pmatrix} \quad [15]$$

where

$$\begin{aligned} a_\xi &= \xi(1-\xi)(s/k)\{(k+2)/\xi + (k-2)/[(1-s)(1-\xi)] - [4(k-s) - 2sk]/(1-s)\} \\ b_\xi &= 4\xi(1-\xi)(s/k)\{(k+1)/\xi - 1/[(1-s)(1-\xi)] - 2(k-s-sk)/(1-s)\} \\ c_\xi &= \xi^2(s/k)\{(k+2)/\xi - [2(k-s) - sk]/(1-s)\} \\ d_\xi &= 4\xi^2(s/k)\{(k+1)/\xi - (k-s-sk)/(1-s)\} \end{aligned}$$

The determinant of the matrix [15] is 0, and thus one eigenvalue is 0. The other, interesting eigenvalue is

$$\lambda_\xi = 1 + [(1-s)k - 2s][(1-2s)k - 2s] / [k^2(1-s)]. \tag{16}$$

It can be shown that λ_ξ is positive (i. e. it is the maximal eigenvalue), and that it is smaller than 1 when k and s satisfy the inequality in condition [14]. That is, existence implies local stability.

4. CONDITIONS FOR STABILITY OF THE TWO MONOMORPHIC EQUILIBRIA

Eq. [5] has two monomorphic equilibria, i. e. in our toy model $(\hat{f}_0, \hat{f}_1, \hat{f}_2) = (1, 0, 0)$ and $(\hat{f}_0, \hat{f}_1, \hat{f}_2) = (0, 0, 1)$ are stationary distributions.

First consider local stability of $(1, 0, 0)$. Choosing f_1 and f_2 as independent variables and linearizing the recursion equations [5] gives the coefficient matrix

$$\begin{pmatrix} a_0 & b_0 \\ c_0 & d_0 \end{pmatrix} \tag{17}$$

where

$$\begin{aligned} a_0 &= (k+2)\{(1-s)m/2 + (1-s)(1-m)(1+m)/[2-s(1-m)]^2\} \\ b_0 &= 2(k+1)\{(1-s)m + (1-s)m(1-m)/[1-s(1-m)]^2\} \\ c_0 &= (1/2)(k+2)[(1-s)(1-m)]^2/[2-s(1-m)]^2 \\ d_0 &= (k+1)[(1-s)(1-m)]^2/[1-s(1-m)]^2 \end{aligned}$$

It is straightforward to show that the maximal eigenvalue λ_0 of the matrix [17] is real and positive. The locus of points such that $\lambda_0 = 1$ is given by

$$\begin{aligned} k &= k_0(m, s) \\ &= -1 + [a_0 + d_0 - (a_0d_0 - b_0c_0)]/[2(a_0d_0 - b_0c_0)] - \\ &\quad \{[a_0 + d_0 - (a_0d_0 - b_0c_0)]^2 - 4(a_0d_0 - b_0c_0)(1-a_0)\}^{1/2}/[2(a_0d_0 - b_0c_0)]. \end{aligned} \tag{18}$$

$k_0(m, s)$ is a continuous function of m for $0 \leq m \leq 1$.

The results of the subsequent analysis are couched in terms of the (m, k) -parameter space for fixed s . Thus, in this parameter space, $\lambda_0 > 1$ in the region above the curve $k = k_0(m, s)$, and $\lambda_0 < 1$ below.

Eq. [18] is not illuminating. For small m , retaining first order terms, we have

$$k_0(m, s) = 2ms(2-s)/(1-s). \tag{19}$$

Alternatively, if we assume m and s are both small and retain fourth order terms,

$$k_0(m, s) = 2s(2+s+s^2)m - s(2-19s/2)m^2. \tag{20}$$

Note the expansion of $(2-s)/(1-s)$ in the coefficient of m in Eq. [20]. For large m , retaining second order terms in $1-m$, we have

$$k_0(m, s) = [2s/(1-s)][1 - (2-s)(1-m)^2/2]. \tag{21}$$

Next consider local stability of $(0, 0, 1)$. Choosing f_0 and f_1 as independent variables and linearizing the recursion equations [5] gives the coefficient matrix

$$\begin{pmatrix} a_1 & b_1 \\ c_1 & d_1 \end{pmatrix} \tag{22}$$

where

$$\begin{aligned} a_1 &= [1/(k+1)](1-m)^2/(1-sm)^2 \\ b_1 &= [(k+2)/(k+1)](1-m)^2/[2[2-s(1+m)]^2] \\ c_1 &= [2/(k+1)][(1-s)m(1-m)/(1-sm)^2 + m/(1-s)] \\ d_1 &= [(k+2)/(k+1)][(1-s)(1-m)(1+m)/[2-s(1+m)]^2 + m/[2(1-s)]] \end{aligned}$$

Once again the maximal eigenvalue which we denote by λ_1 is real and positive. The locus of points such that $\lambda_1=1$ is

$$\begin{aligned} k &= k_1(m, s) \\ &= -1 + [a_1 + d_1 - (a_1d_1 - b_1c_1)]/[2(1-d_1)] + \\ &\quad \{[a_1 + d_1 - (a_1d_1 - b_1c_1)]^2 - 4(a_1d_1 - b_1c_1)(1-d_1)\}^{1/2}/[2(1-d_1)]. \end{aligned} \tag{23}$$

If $2s < 1, 1-d_1 > 0$ for $0 \leq m \leq 1$. If $2s \geq 1$, there is one zero of $1-d_1$ in $0 < m \leq 1$, which we denote by m_0 . In particular, if $2s=1, m_0=1$. Thus, if $2s < 1, k_1(m, s)$ is continuous in $0 \leq m \leq 1$, and if $2s \geq 1$, it is continuous in $0 \leq m < m_0$.

For small m , expanding Eq. [23] and retaining first order terms, we have

$$k_1(m, s) = 2ms(2-s)/(1-s), \tag{24}$$

which is identical to Eq. [19]. If we assume m and s are both small and retain fourth order terms,

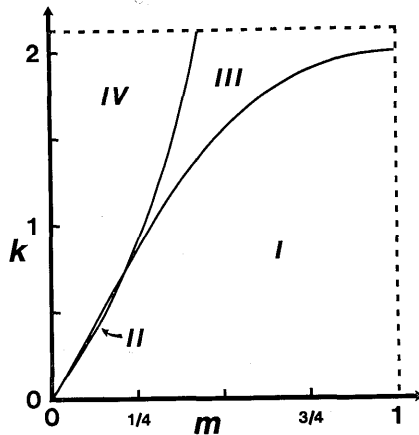


Fig. 1. (m, k) -parameter space for fixed s ; $s=1/2$, $z_0=0.32$. See text for details.

$$k_1(m, s) = 2s(2 + s + s^2)m - s(2 - 9s/2)m^2. \quad [25]$$

Note the small but important difference between Eqs. [20] and [25]. For large m , retaining second order terms in $1-m$, we have

$$k_1(m, s) = [2s/(1-2s)]\{1 - (2-s)(1-m)^2/[2(1-s)(1-2s)]\}, \quad [26]$$

provided $2s < 1$.

In the (m, k) -parameter space for fixed s , $\lambda_1 < 1$ in the region above the curve $k = k_1(m, s)$, and $\lambda_1 > 1$ below.

5. THE (m, k) -PARAMETER SPACE

The existence and stability of equilibria can be studied systematically by the use of an (m, k) -parameter space for fixed s . Fig. 1 is drawn for $s=1/2$ and $z_0=0.32$. In general, the parameter space is bounded on the left by the k -axis, on the right by $m=1$, below by the m -axis, and above by $k=z_0^{-1}-1$. With the exception of the m -axis, the boundaries are included in the parameter space.

If $2s < 1$, recall that $k_0(m, s)$ and $k_1(m, s)$ are both continuous functions of m for $0 \leq m \leq 1$. For large m , comparison of Eqs. [21] and [26] shows that $k_0(m, s)$ is smaller than $k_1(m, s)$. On the other hand, for small m , if s is also small, comparison of Eqs. [20] and [25] shows the opposite to be true. This suggests that the curves $k = k_0(m, s)$ and $k = k_1(m, s)$ must intersect an odd number of times in $0 < m < 1$. I have plotted the two curves numerically using Eqs. [18] and [23] for various values of s , and they always intersect just once, creating four regions in the parameter space. This is also true when $2s \geq 1$ (e.g. Fig. 1). However, I cannot prove this claim of four regions rigorously.

Table 1

	(1, 0, 0) stable	(1, 0, 0) unstable
(0, 0, 1) stable	Region II	Region IV
(0, 0, 1) unstable	Region I	Region III

Let this intersection of the two curves be m^* . Then, the four regions are defined by the following boundaries in addition to the bounds on the entire (m, k) -parameter space noted above. Region *I* is bounded on the left and above by $k=k_1(m, s)$ for $0 \leq m \leq m^*$ and $k=k_0(m, s)$ for $m^* \leq m \leq 1$. Region *II* lies between the two curves to the left of m^* , and region *III* can be described as the region between the two curves to the right of m^* . Finally, region *IV* is the remaining region bounded below and to the right by $k=k_0(m, s)$ for $0 \leq m \leq m^*$ and $k=k_1(m, s)$ for $m^* \leq m < m_0$ (or $m^* \leq m \leq 1$). The two curves do not form a part of any of the regions. (The area of region *II* has been exaggerated in the figure. The two curves are actually closer together if accurately drawn.)

From the results of the previous section, it can be seen that the four regions are characterized by the local stability properties of the two monomorphic equilibria (1, 0, 0) and (0, 0, 1). This is summarized in Table 1. For each set of parameter values, corresponding to a point in the (m, k) -parameter space for fixed s , Eq. [5] can be iterated numerically to determine equilibrium behavior. The results of many such numerical examples strongly suggest the following. In region *I*, (1, 0, 0) is globally stable. In region *II*, (1, 0, 0) and (0, 0, 1) are locally stable, and polymorphic equilibria do not exist. Each point of region *III* corresponds to a globally stable polymorphic equilibrium. In region *IV*, (0, 0, 1) is globally stable. Note that each point of the right boundary of region *III* has been proven to correspond to a locally stable equilibrium.

Let me illustrate these numerical results by examples drawn from Roughgarden (1979, pp. 288–292). The correspondence between his notation and mine where they differ is as follows: $s=1-w$, $z_0=L_0$, $k=(1-L_0)/L_0$. The parameter values for his Figs. 14.7, 14.8, and 14.11 correspond to points in my regions *IV*, *I*, and the extension above of *III*, respectively. None of Roughgarden's examples falls in my region *II*. Even a trivial analysis such as the one presented in this paper can lead to the discovery of properties missed by a numerical survey.

6. DISCUSSION

I briefly consider the case of larger deme size and the relation to the diffusion approximation.

First, it can be shown that when $m=1$ a polymorphic equilibrium exists for general N . The stationary distribution is binomial with parameters N and $[k-s(N+k)]/[(N-1)sk]$. The condition for existence is $Ns/(1-s) < k < Ns/(1-Ns)$ if $Ns < 1$. The upper bound disappears if $Ns \geq 1$. Although I have not been able to prove stability, numerical results suggest that the condition for stability is the same as that for existence.

Second, I iterated Eq. [5] numerically for $N=10$ to determine equilibrium behavior. The (m, k) -parameter space (not shown) is quite similar to Fig. 1 for $N=2$, with the exception that region *II* may not exist. Perhaps the relative area of region *II* decreases as N increases.

If we retain second order terms in Eqs. [20] and [25], we can see that the critical value of k is simply $4ms$. This value is critical in the sense that, roughly speaking and ignoring region *II*, group selection prevails for greater values and individual selection prevails for smaller values. This is a special case of Eq. [9b] of Aoki (1982). For general N ,

$$k = 2Nms. \tag{27}$$

(Note that Eq. [27] can hold when k, m, s , and $1/N$ are of the same order.)

The critical value in Eq. [27] plays an important role in the diffusion approximation (Kimura 1983, 1984). Kimura defines an index

$$D = k/m - 4Ns. \tag{28}$$

I have modified his notation to be consistent with that of the present paper. His model is diploid with additive gene action, which accounts for the coefficient 4 rather than 2. Kimura shows that this index serves as a good indicator for predicting which of the two forces, i. e. group or individual selection, prevails. Note that Eq. [27] is equivalent to $D=0$ if the difference in ploidy is accounted for.

Although Kimura's treatment was biologically realistic in that it included reversible mutation, Ogura and Shimakura (submitted) asked what would happen if this were ignored. Then, if $D > 0$, the altruistic allele is fixed. If $D < 0$, the nonaltruistic allele is fixed. If $D = 0$, what might be called a line of neutral equilibria exist. That is, for each $x (0 < x < 1)$, there exists a stationary distribution that is Beta with parameters $4Nm x$ and $4Nm(1-x)$. Each such stationary distribution is "stable" for a certain subset of initial conditions.

More work is necessary before the results of the discrete model (i. e. the one presented here) can be properly related to those of the diffusion approximation, but the toy model suggests that there may be interesting differences.

I thank Prof. Y. Ogura for the preprint to his paper, and for kindly answering my questions with regard to that paper.

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