

Recurrence of the Unfit

ETHAN AKIN

*Mathematics Department, The City College,
137th Street and Convent Avenue, New York, New York 10031*

AND

JOSEF HOFBAUER

Institut für Mathematik, Universität Wien, Strudlhofgasse 4, A-1080 Wien, Austria

Received 11 January 1982; revised 1 March 1982

ABSTRACT

Domination among strategies in an evolutionary game implies that the geometric mean of the frequencies of certain strategies—the unfit—approaches zero. However, as we show by example no one strategy need be eliminated in the limit.

1. INTRODUCTION

Following Taylor and Jonker [6], the differential-equation model of an evolutionary game is given by

$$\begin{aligned} \frac{dp_i}{dt} &= p_i(a_{ip} - a_{pp}), \\ a_{ip} &= \sum_j p_j a_{ij}, \quad a_{pp} = \sum_{i,j} p_i p_j a_{ij}. \end{aligned} \tag{1.1}$$

Here i varies over $\{1, \dots, n\}$, indexing the possible strategies of the game. When two players use strategies i and j , the payoffs are a_{ij} and a_{ji} to the i -player and j -player respectively. p_i is the ratio of i -players to the total population. So the vector p , thought of as a probability distribution on the set of strategies, lies in the simplex $\Delta = \{x \in R^n : x_i \geq 0 \text{ and } \sum_i x_i = 1\}$.

Equation (1.1) says that the relative rate of increase of ratio p_i is just the net advantage in payoff that an i -player has over a randomly chosen player in a population with distribution vector p .

A distribution p is called *interior* if $p_i > 0$ for all i . The set of interior distributions is denoted $\hat{\Delta}$. The remaining distributions constitute the boundary of Δ .

In general, the *support* of p , denoted $\text{supp}(p)$, is the set of i such that $p_i > 0$. So $p \in \hat{\Delta}$ if and only if $\text{supp}(p) = \{1, \dots, n\}$.

In [3] it was shown that an interior equilibrium for Equation (1.1) fails to exist only when strategy domination occurs. With $a_{qj} \equiv \sum_i q_i a_{ij}$, q_1 *dominates* q_2 ($q_1, q_2 \in \Delta$) if

$$a_{q_1 j} \geq a_{q_2 j} \quad \text{for all } j \quad (1.2)$$

with strict inequality for some j . If all of the inequalities are strict, we say q_1 *strictly dominates* q_2 .

When there exist mixed strategies q_1 and q_2 with q_1 dominating q_2 , then for any solution path of (1.1) with interior initial point $p(0)$, $p(t)$ approaches the boundary of Δ as $t \rightarrow \infty$. In fact, along the path we have $dZ/dt > 0$, where

$$Z(p) \equiv \prod_i p_i^{q_{1i}} / \prod_i p_i^{q_{2i}} \quad (p \in \hat{\Delta}).$$

Furthermore, when q_1 strictly dominates q_2 , $Z(p(t)) \rightarrow \infty$ as $t \rightarrow \infty$. Without loss of generality q_1 and q_2 can be chosen with disjoint supports, and so if $I^- \equiv \text{supp}(q_2)$ we have in the strict-domination case

$$\prod_{i \in I^-} p_i(t) \rightarrow 0 \quad \text{as } t \rightarrow \infty. \quad (1.3)$$

These results are in [3].

In particular, suppose p^* is any limit point of $p(t)$, i.e., $p(t_n) \rightarrow p^*$ with $\{t_n\}$ a sequence approaching ∞ . Equation (1.3) implies that $p_i^* = 0$ for some i in I^- . When a_{ij} is symmetric, i.e. $a_{ij} = a_{ji}$, as in the single-locus, multiallele population-genetic model, then Equation (1.1) is a gradient equation and the limit-point set is a single point (see Appendix). So in that case (1.3) implies

$$p_i(t) \rightarrow 0 \quad \text{as } t \rightarrow \infty \quad \text{for some } i \in I^-. \quad (1.4)$$

Equation (1.4) gives substance to the intuition that the strategies in I^- are unfit. It says that at least one of the I^- -strategies is eliminated in the limit. However, despite an erroneous suggestion to the contrary in [3, p. 242], it is not true that (1.3) implies (1.4) in general. The purpose of this note is to give an example where despite strict domination (1.4) fails. In fact, for most interior initial points $p(0)$, $p_i(t)$ repeatedly approaches arbitrarily close to 1 for all i . The “unfit” strategies as well as the others recur at near-fixation levels.

We analyze the example by looking at the equilibria. An equilibrium is called *nondegenerate* if none of the eigenvalues of the linearization has real

part equal to zero. For a nondegenerate equilibrium e , the number of eigenvalues with negative real part (counting multiplicities) is called the index. The index is the dimension of the *inset*, or stable manifold, consisting of points whose orbits approach e as $t \rightarrow \infty$. The *outset*, or unstable manifold, consists of points whose orbits emanate from e , i.e. approach e as $t \rightarrow -\infty$. In particular, for a three-dimensional system, e is an attractor, i.e. is locally stable, if its index is 3. It is often assumed that only attracting equilibria are of importance in biological models because only an attracting equilibrium would be an observable rest point of a real system which is being buffeted by perturbations (noise). In our example, while all the equilibria are nondegenerate, none is attracting (in particular, there is no ESS). However, these “unobservable” equilibria organize the behavior of the example. Knowing how nearby points behave—as well as how the insets and outsets fit together—tells us how the whole system works.

2. EXAMPLE

In our example, $n = 4$ and the 4×4 payoff matrix a_{ij} is

$$\begin{pmatrix} 0 & -1 & -1 & 1 \\ 1 & 0 & -3 & -3 \\ -1 & 1 & 0 & -1 \\ -3 & -3 & 1 & 0 \end{pmatrix}. \tag{2.1}$$

The example has a symmetry of order 2. Let π be the permutation of $\{1, 2, 3, 4\}$ consisting of the disjoint two-cycles $(1, 3), (2, 4)$. Then π induces an involution of Δ map, also called π , by $\pi(p)_i \equiv p_{\pi i}$. So

$$\pi(p_1, p_2, p_3, p_4) = (p_3, p_4, p_1, p_2). \tag{2.2}$$

By inspection $a_{ij} = a_{\pi(i)\pi(j)}$, from which it easily follows that the involution of Δ maps the dynamical system to itself. So if $p(t)$ is a solution path of (1.1), so is $\pi(p(t))$.

Let v_i ($i = 1, \dots, 4$) denote the vertex with i -coordinate equal to one. In addition to the vertex equilibria, define

$$\begin{aligned} H &= \left(\frac{1}{2}, 0, \frac{1}{2}, 0\right) = \frac{1}{2}v_1 + \frac{1}{2}v_3, \\ R &= \left(0, \frac{1}{2}, 0, \frac{1}{2}\right) = \frac{1}{2}v_2 + \frac{1}{2}v_4, \\ S_2 &= 9^{-1}(3, 0, 5, 1), \\ S_4 &= 9^{-1}(5, 1, 3, 0). \end{aligned} \tag{2.3}$$

Recall that $p_0 \in \Delta$ is an equilibrium for (1.1) if and only if a_{ip_0} is independent of i as i varies in $\text{supp}(p_0)$. In particular, every vertex is an

equilibrium, and it is easy to check that the points defined by (2.3) are also. We will see below that these eight points are the only equilibria. Note that $\pi(H) = H$, $\pi(R) = R$ and $\pi(S_2) = S_4$.

We begin by studying the three-strategy subgames, i.e. the restriction of the dynamical system to the two-dimensional faces of the three-simplex Δ .

A. 1-2-4 AND 2-3-4 SUBGAMES

Eliminating strategy 3 yields the 1-2-4 subgame with 3×3 matrix

$$\begin{pmatrix} 0 & -1 & 1 \\ 1 & 0 & -3 \\ -3 & -3 & 0 \end{pmatrix}. \quad (2.4)$$

Because the first row is term by term greater than the third row, v_1 strictly dominates v_4 in the subgame. Consequently, there is no interior equilibrium, and for any solution path $p(t)$ in the interior of the face $[v_1, v_2, v_4]$ the function $p_1(t)/p_4(t)$ increases monotonically to ∞ . So $\lim_{t \rightarrow \infty} p_4(t) = 0$ as $t \rightarrow \infty$. On the edge $[v_1, v_4]$, v_1 strictly dominates v_4 . However, on the edge $[v_1, v_2]$, v_2 strictly dominates v_1 [cf. the upper left 2×2 matrix in (2.4)]. R is an interior equilibrium for the edge $[v_2, v_4]$ with each vertex locally attracting, since $0 = a_{22} = a_{44} > a_{42} = a_{24} = -3$ [cf. the lower right 2×2 matrix in (2.4)]. Consequently, R is a repeller.

With this information one has the qualitative information needed to construct Figure 1. Notice that v_2 is an attracting equilibrium. Every interior orbit emanates from the repeller R (i.e. approaches R as $t \rightarrow -\infty$) and is attracted to v_2 (approaches v_2 as $t \rightarrow +\infty$).

Finally, the 1-2-4 subgame is mapped to the 2-3-4 subgame by π . In particular, every interior orbit approaches R as $t \rightarrow -\infty$ and v_4 as $t \rightarrow +\infty$. When the two faces are flattened out along the common edge as in Figure 1, the two sides are origin-symmetric about R .

B. 1-2-3 AND 1-3-4 SUBGAMES

Eliminating strategy 4 yields the 1-2-3 subgame with 3×3 matrix

$$\begin{pmatrix} 0 & -1 & -1 \\ 1 & 0 & -3 \\ -1 & 1 & 0 \end{pmatrix}. \quad (2.5)$$

The only new edge is $[v_1, v_3]$, in which each vertex is locally attracting because $0 = a_{11} = a_{33} > a_{13} = a_{31} = -1$. Thus, the equilibrium H is repelling in the edge game. However, $-\frac{1}{2} = a_{HH} > a_{2H} = -1$, and so in the two-dimensional dynamic H is hyperbolic.

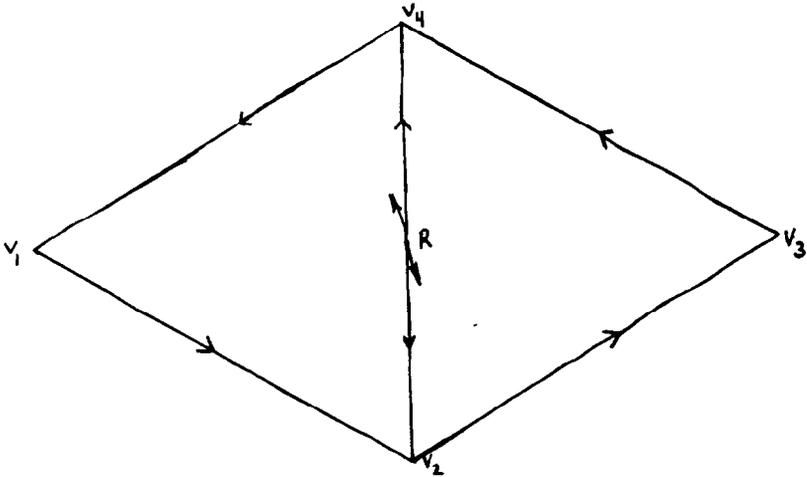


FIG. 1. Each subgame is type S_2 (minus) in classification of Zeeman [7].

In the full subgame there is no domination, as S_4 is an interior equilibrium. Linearizing at S_4 , one can check that it is a repelling spiral equilibrium as the eigenvalues are a complex conjugate pair with positive real part. One orbit, labeled σ_4 in Figure 2, emanates from S_4 and approaches H . This is the stable manifold for H . The remaining interior orbits emanate from S_4 and approach the attractor v_3 .

Again, the symmetry π maps the 1-2-3 subgame to the 1-3-4 subgame so that the flattened-out portrait in Figure 2 is origin-symmetric about H . Except for the orbit σ_2 , every interior orbit of the 1-3-4 subgame originates from S_2 and approaches v_1 .

In summary, each vertex is an attractor for one of the two-dimensional subgames, as summarized in Table 1.

C. FOUR-STRATEGY GAME

The characteristics of each vertex and edge equilibrium are determined by the subgames. For example, the directions of approach to H along σ_2 and σ_4 are independent in the simplex, and so H is an equilibrium of index 2, with a two-dimensional stable manifold (inset) and one-dimensional unstable manifold (outset). For the face equilibria S_j ($j = 2, 4$) we note that $-\frac{15}{9} = a_{jS_j} < a_{S_j S_j} = -\frac{4}{9}$; so S_2 and S_4 have index 1, each attracting a single orbit from the interior of Δ . The properties of the equilibria are summarized in Table 2. Thus, v_1 , for example, has index 2, attracting orbits in the open two-simplex $(v_1 v_3 v_4)$, except for σ_2 and the rest point S_2 , as well as orbits in the open segments (Hv_1) and $(v_1 v_4)$.

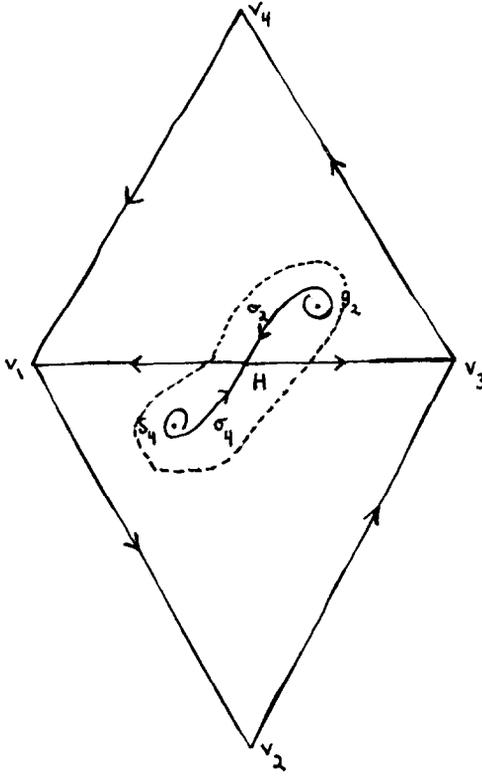


FIG. 2. Each subgame is type 5_1 (minus) in the classification of Zeeman [7]. Dotted lines show isolating block for σ .

Look back at (2.1) and observe that the sum of the first and third rows is term by term greater than the sum of the second and fourth rows. This means that H strictly dominates R . So there is no equilibrium in $\hat{\Delta}$ and along any interior solution path $p(t)$, $dZ/dt > 0$, where

$$Z(p) = p_1 p_3 / p_2 p_4.$$

TABLE 1

Subgame	Attractor
1-3-4	v_1
1-2-4	v_2
1-2-3	v_3
2-3-4	v_4

TABLE 2

Equilibrium	Index	Inset	Outset
R	0	\emptyset	$\dot{\Delta} \cup (Rv_2) \cup (Rv_4)$
S_2	1	Single orbit in $\dot{\Delta}$	$(v_1v_3v_4) - \{S_2\}$
S_4	1	Single orbit in $\dot{\Delta}$	$(v_1v_2v_3) - \{S_4\}$
H	2	Two-dimensional set in Δ intersecting the boundary in $\sigma_2 \cup \sigma_4$	$(Hv_1) \cup (Hv_3)$
v_1	2	$[(v_1v_3v_4) - (\sigma_2 \cup S_2)]$ $\cup (v_1v_4) \cup (Hv_1)$	(v_1v_2)
v_2	2	$(v_1v_2v_4) \cup (v_1v_2) \cup (Rv_2)$	(v_2v_3)
v_3	2	$[(v_1v_2v_3) - (\sigma_4 \cup S_4)]$ $\cup (v_2v_3) \cup (Hv_3)$	(v_3v_4)
v_4	2	$(v_2v_3v_4) \cup (v_3v_4) \cup (Rv_4)$	(v_1v_4)

By [3, Lemma 7], the strict domination implies

$$\lim_{t \rightarrow \infty} p_2(t)p_4(t) = 0. \tag{2.6}$$

Now define the compact invariant set Γ to be the union of four of the six edges:

$$\Gamma = [v_1v_2] \cup [v_2v_3] \cup [v_3v_4] \cup [v_4v_1].$$

THEOREM

There is an open, dense, invariant subset D of $\dot{\Delta}$ such that if $p(t)$ is a solution path with $p(0)$ in D , then the limit-point set as t approaches ∞ of $p(t)$ is exactly Γ . In particular, for $j = 1, 2, 3, 4$ there exist sequences $\{t_n^j\}$ approaching ∞ such that

$$\lim_{n \rightarrow \infty} p(t_n^j) = v_j, \quad j = 1, 2, 3, 4.$$

Proof. The limit-point set Ω of the path is defined to be

$$\Omega = \{p^* : p(t_n) \rightarrow p^* \text{ for some sequence } t_n \rightarrow \infty\}. \tag{2.7}$$

Ω is a compact connected invariant subset of Δ , and by (2.6), $p_4p_2 = 0$ on Ω , i.e. $\Omega \subset [v_1v_2v_3] \cup [v_1v_3v_4]$.

Now define the compact sets

$$\begin{aligned} \sigma &= \sigma_2 \cup \sigma_4 \cup \{H, S_2, S_4\}, \\ \Sigma &= \text{Inset}(H) \cup \text{Inset}(S_2) \cup \text{Inset}(S_4) \cup \{H, S_2, S_4, R\}. \end{aligned}$$

σ is the union of the two distinguished spirals together with their limiting equilibria. Σ is a two-dimensional set whose intersection with the faces defined by $p_4 p_2 = 0$ is σ . In fact, since every interior orbit emanates from R , Σ looks topologically like the cone on σ obtained by joining σ to R by line segments.

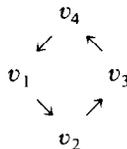
Finally, define the open dense set

$$D = \mathring{\Delta} - \Sigma.$$

Step (1): If $p(0) \in D$ then $\Omega \cap \sigma = \emptyset$. The idea is that the set Σ itself is repelling, so that if $p(t)$ does not remain in Σ for all t , then it must leave some neighborhood of Σ never to return. Then the limit-point set will be disjoint from a neighborhood of Σ . The idea is turned into a proof by using Easton and Conley's idea of an *isolating block* (see [4]). To construct an isolating block for σ , begin by drawing a closed curve around σ as in Figure 2, along which the vector field (1.1) points outward. The curve is thickened to get a squat cylinder extending into the interior of $\mathring{\Delta}$, along which the vector field points outward. By choosing K sufficiently large the cylinder can be capped off in the interior with a piece of the manifold $\{Z = K\}$. Thus inside the cylinder $Z > K$. Now there are two possibilities. $p(t)$ may enter the cylinder through the top and never leave. In that case, $\Omega \subset \sigma$. This requires that $p(0)$ lie in Σ . Otherwise, $p(t)$ never enters the cylinder or enters and leaves. If it leaves, it can never return, since Z is monotone on solution paths. So in these cases $p(t)$ is eventually bounded away from σ and $\Omega \cap \sigma = \emptyset$.

Step (2): If $p(0) \in D$ then $\Omega = \Gamma$. From Figure 2 it is clear that a closed invariant subset of the two faces which is disjoint from σ must be a subset of Γ . If $p \in \Omega$ and $p^* \notin \Gamma$, then the solution path for p^* would approach $\{H, S_2, S_4\}$ as $t \rightarrow -\infty$, and so $\sigma \cap \Omega \neq \emptyset$.

Γ is a degenerate cycle with the four rest points ordered cyclically:



Notice that Ω can't consist of a vertex alone, because the insets of the vertices lie in the boundary of Δ . In fact, if $p(t)$ is in the interior near v_i , it is

swept around to move “parallel” to the edge $[v_i, v_{i+1}]$, so that it is eventually near v_{i+1} (addition modulo 4). Thus, Ω contains all of Γ . ■

3. DISCUSSION

If the initial point $p(0)$ lies in the open dense set D , then the solution path $p(t)$ eventually approximates motion around the degenerate cycle Γ . Since the speed approaches zero as p approaches any vertex, when $p(t)$ is near v_i it moves slowly until it moves near (v_i, v_{i+1}) to slow down again near the next vertex v_{i+1} . With each turn of cycle, $p(t)$ gets closer to Γ , and so the rest times near the vertices get longer, as does the approximate period of the cycle. These times approach ∞ as $t \rightarrow \infty$.

There are two kinds of alterations of the model which change the dynamic picture.

In the systems that (1.1) purports to model, finite population size implies that p_i can't be arbitrarily small and yet positive. This leads to the phenomenon of *capture by the boundary*. As $p(t)$ approaches Γ , one of the strategy types must jump to zero and the dynamic drops into one of the four three-strategy subgames. This leads to fixation. However, which strategy is lost appears to be almost independent of the initial position. Thus if the probability that 2 or 4 is lost is k , and so the probability that 1 or 3 is lost is $1 - k$, then by Table 1 we get fixation at v_1, v_2, v_3 , or v_4 with probabilities $k/2, (1 - k)/2, k/2$, or $(1 - k)/2$ respectively. This result is quite different from the example in [3], where the terminal equilibrium depends on the initial position but is then determined.

Now suppose Equation (1.1) itself is perturbed. Because the dominations were strict and the equilibria hyperbolic, the behavior of the example is robust under slight changes of the payoff matrix (2.1) even if the changes break the π -symmetry. However, if the perturbation consists of an added mutation term, i.e. a small vector field pointing inward at every boundary point, then the attractor Γ is perturbed to a true attracting cycle $\tilde{\Gamma}$. The degenerate nature of the cycle Γ followed from the fact that the outset of v_i was contained in the inset of v_{i+1} . This was possible in a robust way because of the face-preserving nature of equations like (1.1). Once one perturbs into the interior, the Kupka-Smale theorem (see [1]) implies that in a three-dimensional system the outset of the perturbed equilibrium \tilde{v}_i will be disjoint from the inset of the perturbed equilibrium \tilde{v}_{i+1} . In fact, the outset of \tilde{v}_i will approach the new cycle $\tilde{\Gamma}$ asymptotically.

Finally, this kind of example may give an answer to the question: where does the hypercycle go? Stable limit cycles arise in these models as the matrix parameters change so that a Hopf bifurcation occurs at an interior equilibrium (see [7]). In fact, these cycles were discovered earlier when equations like (1.1) arising in the study of autocatalytic systems were studied by Eigen

and Schuster ([5] and references therein). This example suggests that as the organizing equilibrium, which is the average position over the cycle, approaches the boundary, the cycle approaches a degenerate boundary cycle like Γ .

APPENDIX

If $p(t)$ is a solution path for a vector field like (1.1), then the limit-point set Ω defined by (2.7) is a compact, connected set (because $\Omega = \bigcap_{t \geq 0} \text{Closure}[p(t, \infty)]$), which we have seen might be infinite. In this Appendix we will prove that if the matrix a_{ij} is symmetric, then Ω consists of a single point.

At first glance this result seems obvious, because when the matrix is symmetric (1.1) is a gradient system (see [2]). For a gradient system Ω consists entirely of equilibria. In particular, if the equilibria are isolated, then Ω is a singleton. However, equilibria need not be isolated in these models. Furthermore, Takens has constructed an example of a gradient system where Ω can be infinite (private communication). We show that this type of pathology does not occur among the symmetric versions of (1.1).

In the population genetic context the function $\bar{a}(p) = a_{pp}$ represents mean fitness, and Fisher's fundamental theorem of natural selection says

$$\frac{1}{2} \frac{d\bar{a}}{dt} = \sum p_i (a_{ip} - a_{pp})^2 \geq 0 \quad (a_{ij} \text{ symmetric}),$$

with equality if and only if p is an equilibrium point. Thus, $\bar{a}(p(t))$ is increasing and so approaches a limit a^* as t approaches infinity. As an invariant set upon which \bar{a} is constant, Ω consists entirely of equilibria.

THEOREM

Assume a_{ij} is a symmetric matrix. If $p(t)$ is a solution path for (1.1), then Ω consists of a single point, i. e., $\lim p(t)$ exists as $t \rightarrow \infty$.

The proof uses the following function defined with q fixed in Δ :

$$I(p) = - \sum \left\{ q_i \ln \frac{p_i}{q_i} : i \in \text{supp}(q) \right\}.$$

LEMMA

$I : \Delta \rightarrow [0, \infty]$ is a continuous, extended real-valued function which is C^∞ on the open set $\{p : I(p) < \infty\} = \{p : \text{supp}(q) \subset \text{supp}(p)\}$. Furthermore, $I(p) = 0$ if and only if $p = q$.

Proof of Lemma. $I(p) \geq -\ln \sum \{q_i (p_i/q_i) : i \in \text{supp}(q)\} \geq -\ln 1 = 0$, with equality iff all the p_i/q_i are equal for $i \in \text{supp}(q)$ and $\sum \{p_i : i \in \text{supp}(q)\} = 1$.

$(q) = 1$, i.e., iff $p = q$. $I(p) = \infty$ iff $p_i = 0$ for some i in $\text{supp}(q)$, in which case $I(p_1)$ is large for p_1 near p . ■

Proof of Theorem. Fix q in Ω , and let $J = \{i : a_{iq} \neq a^*\}$. Define

$$Q(p) = \sum \{p_i : i \in J\},$$

$$Z(p) = \min \{(a_{ip} - a_{pp})^2 : i \in J\}.$$

If J is empty, define $Q = 0$ and $Z = 1$. Then

$$\frac{1}{2} \frac{d\bar{a}}{dt} = \sum p_i (a_{ip} - a_{pp})^2 \geq Z(p)Q(p). \quad (1)$$

By definition of J , $Z(q) = z > 0$ and so $\{p : Z(p) > z/2\}$ is an open set containing $q = \cap_{\epsilon > 0} \{p : I(p) \leq \epsilon\}$. Because the latter is a decreasing intersection of compacta, there exists ϵ^* such that

$$I(p) \leq \epsilon^* \quad \text{implies} \quad Z(p) > z/2. \quad (2)$$

On the orbit, $\text{supp}(p(t)) \supset \text{supp}(q)$, and so we can differentiate I to get

$$\begin{aligned} \frac{dI}{dt} &= - \sum q_i (a_{ip} - a_{pp}) = a_{pp} - a_{qp} \\ &= \sum (a_{pp} - a_{qj}) p_j = \sum [(a_{pp} - a_{qq}) p_j + (a_{qq} - a_{qj}) p_j] \\ &= (a_{pp} - a^*) + \sum \{(a_{jq} - a^*) p_j : j \in J\}, \end{aligned}$$

where $a^* = a_{qq}$ and $a_{jq} = a_{qj}$ by symmetry. Because $a_{pp} < a^*$ on the orbit, we have

$$\frac{dI}{dt} < KQ(p), \quad (3)$$

where $K = \max\{ |a_{jq} - a^*| : j \in J\}$.

Now choose a sequence $\{t_n\}$ approaching infinity such that $p(t_n)$ approaches q and so

$$\lim I(p(t_n)) = 0 \quad (n \rightarrow \infty).$$

For $\epsilon < \epsilon^*$ choose $N = N(\epsilon)$ such that

$$\begin{aligned} I(p(t_N)) &< \frac{\epsilon}{2}, \\ \frac{K}{z} [a^* - \bar{a}(p(t_N))] &< \frac{\epsilon}{2}. \end{aligned} \quad (4)$$

As long as $t > t_N$ and $I(p(s)) \leq \varepsilon^*$ for s in the interval $[t_N, t]$, then at $p(s)$ (1),(2), and (3) imply

$$\frac{dI}{dt} < \frac{K}{z} \frac{d\bar{a}}{dt}.$$

Integrating and applying (4), we have

$$0 \leq I(p(t)) < I(p(t_N)) + \frac{K}{z} [\bar{a}(p(t)) - \bar{a}(p(t_N))] < \varepsilon. \quad (5)$$

Because $\varepsilon < \varepsilon^*$, $p(t)$ remains in the neighborhood described by (2) for all $t \geq t_N$. So (5) holds for all such t .

Because ε was arbitrarily small, (5) implies $I(p(t))$ approaches 0 as $t \rightarrow \infty$, i.e., $p(t)$ approaches q , and so q is the unique limit point. ■

REFERENCES

- 1 R. Abraham and J. Robbin, *Transversal Mappings and Flows*, Benjamin, 1967.
- 2 E. Akin, *The Geometry of Population Genetics*, LNBM No. 31, Springer, 1979.
- 3 E. Akin, Domination of equilibrium, *Math. Biosci.* 50:239–250 (1980).
- 4 C. Conley, *Isolated Invariant Sets and the Morse Index*, CBMS Series No. 38, Amer. Math. Soc., 1978.
- 5 M. Eigen and P. Schuster, *The Hypercycle, a Principle of Natural Self-Organization*, Springer, 1979.
- 6 P. Taylor and L. Jonker, Evolutionarily stable strategies and game dynamics, *Math. Biosci.* 40:145–156 (1978).
- 7 E. C. Zeeman, Population dynamics from game theory, in *Global Theory of Dynamical Systems*, LNM No. 819, Springer, 1979.