A simple system with a continuum of stable steady states

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I. Introduction

The system

$$u_t = \{(1 + \alpha v)u\}_{xx} + (R_1 - au - bv)\, u \tag{1.1}$$

$$v_t = (R_2 - bu - av)v$$

$$\{(1 + \alpha v)u\}_x = 0 \quad \text{at} \quad x = 0 \quad \text{and} \quad x = 1$$

with

$$\frac{1}{2}\left(\frac{a}{b} + \frac{b}{a}\right) < \frac{R_1}{R_2} < \frac{a}{b} \tag{1.2}$$

and

$$\alpha > \frac{a(a^2 - b^2)}{2abR_1 - (a^2 + b^2)R_2} \tag{1.3}$$

was considered by M. Mimura [2] as a model for the population densities of two competing species, one of which increases its migration rate in response to crowding by the other species. It is a special case of the model of N. Shigesada, K. Kawasaki, and E. Teramoto [3].

Numerical computation by D.G. Aronson and P.N. Brown seems to indicate that the solution converges to a steady state in which v has one or more discontinuities, and that these discoutinuities move continuously with changes in the initial conditions.

The existence of a continuum of discontinuous solutions of the system (1.1) was proved by Mimura. The purpose of this lecture is to prove that there are, indeed, whole one parameter families of discontinuous solutions which are stable in a suitable topology.

The family of piecewise continuous steady states is described in Section 2.

We shall show in Section 3 that a somewhat unusual topology is needed for this problem and prove that linearized stability implies stability in this topology.

In Section 4 we give a sufficient condition for stability and show that a continuum of the discontinuous steady states satisfies this criterion.

Section 5 discusses the evolutionary consequences of the existence of stable nonconstant steady states.

This work is a part of ongoing joint research with D.G. Aronson and A. Tesei.

I am grateful to Don Aronson for getting me interested in this problem and for a great deal of useful discussion and criticism.

2. The steady state.

M. Mimura [2] introduced the new independent variable

$$w = (1 + \alpha v)u$$

in (1.1) to obtain the system

$$\begin{aligned} v_t &= G(v,w) \\ w_t &= (1 + \alpha v)(w_{xx} + H(v,w)) \end{aligned} \tag{2.1}$$

where

$$G(v,w) = v(R_2 - av - \frac{bw}{1 + \alpha v}) ,$$

$$H(v,w) = \frac{w}{1 + \alpha v} \{R_1 - \frac{aw}{1 + \alpha v} - bv + \frac{\alpha v}{1 + \alpha v} (R_2 - av - \frac{bw}{1 + \alpha v})\} . \tag{2.2}$$

The no-flux boundary conditions are

$$w_x = 0 \quad \text{at} \quad x = 0 \quad \text{and} \quad x = 1 . \tag{2.3}$$

The corresponding steady-state equations are

$$\begin{aligned} G(v,w) &= 0 , \\ w'' + H(v,w) &= 0 , \\ w' = 0 \quad \text{at} \quad x &= 0,1 . \end{aligned} \tag{2.4}$$

When

$$R_2/b < w < w_m \equiv (\alpha R_2 + a)^2/4\alpha ab \tag{2.5}$$

the equation $G(v,w) = 0$ has the three nonnegative branches of solutions

$$v_0 \equiv 0$$
$$v_1(w) = \frac{1}{2}\left(\frac{R_2}{a} - \frac{1}{\alpha}\right) - \left(\frac{b}{a\alpha}\right)^{1/2}(w_m - w)^{1/2}, \tag{2.6}$$
$$v_2(w) = \frac{1}{2}\left(\frac{R_2}{a} - \frac{1}{\alpha}\right) + \left(\frac{b}{a\alpha}\right)^{1/2}(w_m - w)^{1/2}.$$

If we substitute these in the second equation of (2.4), we find the three ordinary differential equations

$$w'' + H(0,w) = 0$$
$$w'' + H(v_1(w),w) = 0 \tag{2.7}$$
$$w'' + H(v_2(w),w) = 0$$

when w lies in the interval $(R_2/b, w_m)$. It is easy to see from the first equation of (2.1) that v tends to move away from the branch $v = v_1(w)$ for $w \varepsilon (R_2/b, w_m)$ and from $v = 0$ for $w < R_2/b$. Thus only the first and last of these equations can yield stable steady states.

Easy computations show that $H(0,w) < 0$ for $w > R_2/b$ while $H(v_2(w),w) > 0$ for $w \varepsilon (0,w_m)$. If we integrate the first and third equations of (2.7) and use the boundary conditions $w_x = 0$, we see that neither one can have a solution with $w \varepsilon (R_2/b, w_m)$.

One can, however, obtain solutions by letting v jump from the branch v_0 to the branch v_2 and back again while keeping w and w_x continuous. This can be seen from the method of first integrals (see [2]) or from phase plane diagrams. The points of discontinuity are rather arbitrary, so that one obtains a large continuum of steady-state solutions with $w \in (R_2/b, w_m)$ and discontinuous v. In particular, by introducing sufficiently many discontinuities one can keep w arbitrarily close to any constant in $(R_2/b, w_m)$.

These solutions with discontinuous v are the only candidates for stable solutions.

3. The stability of discontinuous solutions.

We shall investigate the stability of a steady-state solution $(\tilde{v}(x), \tilde{w}(x))$ with piecewise continuous $\tilde{v}$, as discussed in the preceding Section. It is not difficult to prove the asymptotic stability of such a solution in the norm $\|v\|_{L_\infty} + \|w\|_{H^1}$ when the linearized operator is stable. (See Remark 2 after Theorem 1.)

This fact seems surprising because the points of discontinuity of v can be chosen rather freely. However, in the L_∞ norm the distance between a function with a jump at x_0 and one without a jump at x_0 is at least half the magnitude of the jump. Therefore in this norm solutions with discontinuities at different points are isolated from each other.

For the same reason a sufficiently small neighborhood of a discontinuous function contains no continuous functions. Since a solution of the system (2.1), (2.3) with smooth initial data remains smooth, it cannot converge to a discontinuous solution in the L_∞ norm. Thus the L_∞ topology on the v-component of the solution is not appropriate for this problem.

We shall, instead, use the weaker topology with the neighborhood base

$$N_\varepsilon(\tilde{v}) = \{r \in L_\infty : \text{meas}\{x : |r(x) - \tilde{v}(x)| > \varepsilon\} < \varepsilon^4\}$$

for the v-component. The closure of the set of continuous functions in this topology is the set of functions which are almost everywhere continuous.

It is usual to relate the stability of the steady-state solution of the system (2.1) to the spectrum of the linearized operator

$$L \begin{pmatrix} \eta \\ \zeta \end{pmatrix} \equiv \begin{pmatrix} G_v(\tilde{v},\tilde{w})\eta + G_w(\tilde{v},\tilde{w})\zeta \\ [1 + \alpha\tilde{v}][\zeta'' + H_v(\tilde{v},\tilde{w})\eta + H_w(\tilde{v},\tilde{w})\zeta] \end{pmatrix} . \tag{3.1}$$

with the boundary conditions $\zeta' = 0$ at 0 and 1. We shall show that this can also be done in our topology by proving the following result.

THEOREM 1 Let $(\tilde{v},\tilde{w})$ be a steady-state solution of (2.1), (2.3) with $\tilde{v}$ piecewise continuous, $\tilde{w}$ continuously differentiable, $0 \leq \tilde{v} < R_2/a$, and $R_2/b < \tilde{w} < w_m$. Suppose that the spectrum of the operator L in (3.1) lies uniformly in the left half-plane

$$\mathrm{Re}\,\lambda \leq -2k < 0 . \tag{3.2}$$

Then there exist positive constants ε_0 and A with the property that if (v,w) is a solution of (2.1), (2.3) such that $0 \leq v(x,0) \leq R_2/a$,

$$\| v(x,0) - \tilde{v}(x) \|^2_{L_\infty(S)} + \| w(x,0) - \tilde{w}(x) \|^2_{H^1} \leq \varepsilon^2 \tag{3.3}$$

where the measure $|S'|$ of the complement of the subset S of $[0,1]$ satisfies

$$|S'| \leq \varepsilon^4 , \tag{3.4}$$

and if $\varepsilon < \varepsilon_0$, the inequality

$$\|v(x,t) - \tilde{v}(x)\|^2_{L_\infty(S)} + \|w(x,t) - \tilde{w}(x)\|^2_{H^1} < A\varepsilon^2 . \tag{3.5}$$

is valid for all $t > 0$.

<u>Proof</u> We first observe that

$$G(0,w) = 0 \quad , \; G(R_2/a,w) < 0$$
$$H(v,0) = 0 \quad , \; H(v,w_M) < 0$$

when

$$\begin{aligned} &0 < v < R_2/a \\ &0 < w < w_M \equiv (\alpha R_1 + b)^2/4\alpha ab . \end{aligned} \tag{3.6}$$

It follows [4] that the set (3.6) is an invariant set for the system (2.1), (2.3). That is, if $(v(x,0) , w(x,0))$ satisfies these inequalities, so does $(v(x,t),w(x,t))$ for all $t > 0$.

We agree to choose ε_0 so small that for $\varepsilon < \varepsilon_0$ the inequalities (3.3) imply that the initial values, and hence also the solution, satisfy (3.6). (The inequality (1.3) implies that $w_M > w_m$.)

We now define

$$\eta(x,t) = v(x,t) - \tilde{v}(x) \quad , \quad \zeta(x,t) = w(x,t) - \dot{w}(x)$$
$$\eta_0(x) = v(x,0) - \tilde{v}(x) \quad , \quad \zeta_0(x) = w(x,0) - w(x)$$

and write the system (2.1), (2.3) in the form

$$\frac{\partial}{\partial t}\binom{\eta}{\zeta} - L\binom{\eta}{\zeta} = \binom{\rho}{\sigma} \tag{3.7}$$

$$\zeta_x(0,t) = \zeta_x(1,t) = 0$$

$$\eta(x,0) = \eta_0(x)$$

$$\zeta(x,0) = \zeta_0(x)$$

where L is defined by (3.1) and

$$\begin{aligned} \rho &= G(\tilde{v} + \eta, \tilde{w} + \zeta) - [G(\tilde{v},\tilde{w}) + G_v(\tilde{v},\tilde{w})\eta + G_w(\tilde{v},\tilde{w})\zeta] \ , \\ \sigma &= \frac{\eta\zeta_t}{1 + \alpha(\tilde{v} + \eta)} + (1 + \alpha\tilde{v})\{H(\tilde{v} + \eta, \tilde{w} + \zeta) - \\ &\qquad [H(\tilde{v},\tilde{w}) + H_v(\tilde{v},\tilde{w})\eta + H_w(\tilde{v},\tilde{w})\zeta]\} \ . \end{aligned} \tag{3.8}$$

We first treat (3.7) as a linear system. Because the spectrum of L is in the half-plane (3.2), a standard estimate (see e.g. [1, Theo. 1.3.4]) shows that

$$\begin{aligned} \|\eta(\cdot,t)\|_{L_1} + \|\zeta(\cdot,t)\|_{L_1} &< c\{[\|\eta_0\|_{L_1} + \|\zeta_0\|_{L_1}]e^{-kt} \\ &+ \int_0^t [\|\rho(\cdot,\tau)\|_{L_1} + \|\sigma(\cdot,\tau)\|_{L_1}]e^{-k(t-\tau)}d\tau\} \ . \end{aligned} \tag{3.9}$$

Here and in all that follows c stands for any constant which depends only on bounds for G and H and their partial derivatives on the set (3.6), and on k.

Because the second equation of (3.7) is parabolic, we can find a bound of the form

$$\|\zeta\|_{L_2}^2 < c\{\|\zeta_o\|_{L_2}^2 e^{-3kt} + \int_o^t[\|\sigma\|_{L_1} + \|\eta\|_{L_1} + \|\zeta\|_{L_1}]^2 e^{-3k(t-\tau)}d\tau\} . \quad (3.10)$$

The first equation of (3.7) can be solved for η by quadratures in terms of ρ and ζ. It is easily seen that the closure of the range of $G_v(v,w)$ lies in the spectrum of L so that the spectral bound (3.2) implies that $G_v < -2k$. Consequently we find that

$$|\eta(x,t)| < |\eta_o(x)|e^{-2kt} + c \int_o^t[|\zeta(x,\tau)| + |\rho(x,\tau)|]e^{-2k(t - \tau)}d\tau . \quad (3.11)$$

It follows that

$$\|\eta\|_{L_2}^2 < c\{\|\eta_o\|_{L_2}^2 e^{-3kt} + \int_o^t [\|\zeta\|_{L_2}^2 + \|\rho\|_{L_2}^2]e^{-3k(t - \tau)}d\tau\} .$$

We combine this inequality with (3.9) and (3.10) to obtain

$$\|\eta\|_{L_2}^2 + \|\zeta\|_{L_2}^2 < c\{[\|\eta_o\|_{L_2}^2 + \|\zeta_o\|_{L_2}^2]e^{-2kt} \quad (3.12)$$

$$+ \int^t[\|\rho\|_{L_2}^2 + \|\sigma\|_{L_1}^2]e^{-2k(t - \tau)}d\tau\} .$$

We see from (3.8) that

$$\|\rho\|_{L_2}^2 + \|\sigma\|_{L_1}^2 < c[\|\eta\|_{L_2}^2\|\zeta_t\|_{L_2}^2 + \|\eta\|_{L_4}^4 + \|\zeta\|_{L_4}^4] . \quad (3.13)$$

In order to use (3.12) and (3.13) we need bounds for an integral of

$\|\zeta_t\|^2_{L_2}$ and for $\|\zeta\|^4_{L_4}$. For this purpose we write the second equation of (2.1) in the form

$$\frac{1}{1 + \alpha v}\zeta_t - \zeta_{xx} + \zeta = H(v + \eta, w + \zeta) - H(v,w) + \zeta .$$

We multiply by $(\zeta_t + \frac{1}{2}k\zeta)e^{kt}$, integrate by parts, and use (3.12) and (3.13) to find that

$$\int_0^t \|\zeta_t\|^2 e^{-k(t-\tau)}d\tau + \|\zeta\|^2_{H^1} \leq c_1\{[\|\zeta_0\|^2_{H^1} + \|\eta_0\|^2_{L_2}]e^{-kt} + \int_0^t [\|\eta\|^2_{L_2}\|\zeta_t\|^2_{L_2} + \|\eta\|^4_{L_4} + \|\zeta\|^4_{L_4}]e^{-k(t-\tau)}d\tau\} . \tag{3.14}$$

Suppose that on a time interval $[0,t_1)$ we have

$$c_1\|\eta\|^2_{L_2} \leq 1 . \tag{3.15}$$

Then (3.14) shows that on this interval

$$\|\zeta\|^2_{H^1} \leq c_1\{[\|\zeta_0\|^2_{H^1} + \|\eta_0\|^2_{L_2}]e^{-kt} + \int_0^t [\|\eta\|^4_{L_4} + \|\zeta\|^4_{L_4}]e^{-k(t-\tau)}d\tau \} . \tag{3.16}$$

We now observe that because of the bound (3.6)

$$\|\eta\|^p_{L_p} \leq \|\eta\|^p_{L_\infty(S)} + (R_2/a)|S'| . \tag{3.17}$$

We find from (3.11) and Sobolev's inequality that

$$\|\eta\|_{L_\infty(S)} \leq c\{\|\eta_0\|_{L_\infty(S)}e^{-2kt} + \int_0^t [\|\zeta\|_{H^1} + \|\zeta\|_{H^1}^2 + \|\eta\|_{L_\infty(S)}^2]e^{-2k(t-\tau)}d\tau\} .$$

We combine this with (3.16) and (3.17) to obtain the inequality

$$\|\eta\|_{L_\infty(S)}^2 + \|\zeta\|_{H^1}^2 \leq c_2\{[\|\eta_0\|_{L_\infty(S)}^2 + \|\zeta_0\|_{H^1}^2 +$$

$$+ (\|\eta_0\|_{L_\infty(S)}^2 + \|\zeta_0\|_{H^1}^2)^2]e^{-kt} \tag{3.18}$$

$$+ \int^t[(\|\eta\|_{L_\infty(S)}^2 + \|\zeta\|_{H^1}^2)^2 + (\|\eta\|_{L_\infty(S)}^2 + \|\zeta\|_{H^1}^2)^4]e^{-k(t - \tau)}d\tau$$

$$+ |S'| + |S'|^2\} .$$

Choose any A such that

$$A > \max(c_2,1)$$

where c_2 is the constant in (3.18) . Let ε_0 be so small that the inequalities

$$c_1A\varepsilon_0^2 < 1 ,$$

$$1 + (2 + \frac{A^2}{k})\varepsilon_0^2 + (1 + \frac{A^4}{k})\varepsilon_0^6 < A/c_2$$

are valid. Then the inequality (3.3) implies (3.5) for sufficiently small t . Moreover, if (3.5) holds in an interval $[0,t_1)$, then (3.15) is valid there and (3.18) implies that this inequality is still valid at $t = t_1$. Thus the maximal interval where (3.5) holds is both open and closed. That is, (3.5) is valid for all positive t, which proves the Theorem.

REMARKS: 1. The first equation of (2.1) and (3.5) imply that there is a constant C such that if the inequality $v < v_2(w) + C\varepsilon$ is valid on the whole interval $[0,1]$ for one value of t, it is valid for all larger t, and that this inequality holds for all sufficiently large t.

2. If $|S'| = 0$, that is, if one works in the norm $\|\eta\|_{L_\infty} + \|\zeta\|_{H^1}$, the bounds

$$\|\eta\|_{L_\infty} e^{1/4kt} < A\varepsilon\ , \qquad \|\zeta\|_{H^1} e^{1/4kt} < B\varepsilon$$

follow from (3.18), so that $(\tilde{v},\tilde{w})$ is asymptotically stable in this topology.

4. A sufficient condition for stability.

We wish to derive a sufficient condition for the spectrum of the operator L defined by (3.1) to be bounded away from the right half-plane, so that the conclusion of Theorem 1 is valid.

We consider the system

$$\begin{aligned} &G_v(\tilde{v},\tilde{w})\eta + G_w\zeta - \lambda\eta = \rho \\ &(1 + \alpha\tilde{v})[\zeta'' + H_v\eta + H_w\zeta] - \lambda\zeta = \sigma \\ &\zeta'(0) = \zeta'(1) = 0 \end{aligned} \qquad (4.1)$$

whose solution gives the inverse of $L - \lambda I$ at points of its resolvent set. As we have already mentioned, the closure of the range of G_v can be shown to lie in the spectrum. Consequently, a necessary condition for (3.2) is

$$G_v(\tilde{v},\tilde{w}) < -2k < 0 . \tag{4.2}$$

Our criterion will involve the solution of the initial value problem

$$\begin{aligned} & r'' + \left\{H_w(\tilde{v},\tilde{w}) + \left[\frac{G_w(\tilde{v},\tilde{w})H_v(\tilde{v},\tilde{w})}{-G_v(\tilde{v},\tilde{w})}\right]_+\right\} r = 0 \\ & r(0) = 0 \\ & r'(0) = 1 \end{aligned} \tag{4.3}$$

As usual,

$$[s]_+ = \begin{cases} 0 & \text{if } s < 0 \\ s & \text{if } s > 0 . \end{cases}$$

<u>THEOREM</u> 2. Suppose that G_v satisfies an inequality of the form (4.2) and that the solution of (4.3) has the properties

$$\begin{aligned} & r > 0 \qquad \text{on } [0,1] \\ & r'(1) > 0 \end{aligned} \tag{4.4}$$

Then the steady-state solution v, w is stable in the sense of Theorem 1.

<u>PROOF</u>. If λ is outside the closure of the range of G_v, we can solve the first equation for v and substitute in the second to obtain the problem

$$\zeta'' + [H_w - \frac{\lambda}{1+\alpha\bar{V}} + \frac{G_w H_v}{\lambda - G_v}]\zeta = \frac{\sigma}{1+\alpha\bar{V}} - \frac{H_v \rho}{\lambda - G_v} \tag{4.5}$$

$$\zeta'(0) = \zeta'(1) = 0$$

This equation can always be solved unless there is a nontrivial solution of the equation with $\rho = \sigma = 0$. Therefore the spectrum outside the closure of the range of G_v is discrete. To locate this part of the spectrum we set $\rho = \sigma = 0$ in (4.5), multiply by the complex conjugate $\bar{\zeta}$, and integrate by parts to find an equation on whose real and imaginary parts are

$$\int\{-|\zeta'|^2 + [H_w - \frac{Re(\lambda)}{1+\alpha\bar{V}} + \frac{(Re(\lambda) - G_v)G_w H_v}{|\lambda - G_v|^2}]\}|\zeta|^2 dx = 0 \tag{4.6}$$

and

$$Im(\lambda) \int_0^1 [\frac{1}{1+\alpha V} + \frac{G_w H_v}{|\lambda - G_v|^2}]|\zeta|^2 dx = 0 \quad . \tag{4.7}$$

The second equation shows that any complex spectrum is confined to the union as x goes from 0 to 1 of the discs

$$|\lambda - G_v|^2 < -(1+\alpha v)G_w H_v ,$$

which is a bounded set. Therefore it is sufficient to show that there are no eigenvalues with $Re\ \lambda > 0$.

If $Re\ \lambda > 0$, we see from (4.2) that

$$-\frac{Re\ \lambda}{1+\alpha V} + \frac{(Re\ \lambda - G_v)G_w H_v}{|\lambda - G_v|^2} < [\frac{G_w H_v}{-G_v}]_+ \ .$$

Thus (4.6) yields the inequality

$$\int\{-|\zeta'|^2 + (H_w + [\frac{G_w H_v}{-G_v}]_+)\ |\zeta|^2\}dx > 0\ , \tag{4.8}$$

We now define

$$q = \zeta/r\ ,$$

integrate (4.8) by parts, and substitute for ζ to find that

$$-|q(1)|^2 r(1)r'(1) - \int_0^1 |q|^2 r^2\ dx > 0\ ,$$

Since the eigenfunction ζ cannot satisfy $\zeta(1) = \zeta'(1) = 0$, since $|q(1)|^2 > 0$, and since $r(1)r'(1) > 0$, this leads to a contradiction.

We conclude that if the solution of (4.3) satisfies the conditions (4.4), and if (4.2) is satisfied, then the solution (v,w) is stable, which proves our Theorem.

The conditions (4.4) are obviously satisfied when the coefficient of r in (4.3) is nonpositive. Because $H_w(0,w) < 0$ for $w > R_1/a$, $G_w(0,w) = 0$, $G_v(v_2(w),w) < 0$, and $G_w(v_2(w),w) < 0$, this is the case if $H_v > 0$ and $H_w < 0$ on the part of the range of $(\tilde{v},\tilde{w})$ where $\tilde{v} = v_2(\tilde{w})$. Computation shows that $H_v > 0$, $H_w < 0$ at $(v_2(w_m),w_m)$, so that one can construct a family of stable solutions by keeping w near a constant just below w_m .

For the limiting solutions computed by Aronson and Brown the sufficient conditions (4.4) are found to be valid in most though not all cases.

REMARK. Replacing the factor $(1+\alpha v)$ by 1 in the second equation of (2.1), yields a semilinear system with the same steady states. The above analysis shows that this system also has a continuum of stable steady states, so that quasilinearity is not needed to produce this phenomenon.

5. A biological consequence.

The system (1.1) is a model for a pair of competitors, one of which avoids the other to such an extent that the homogeneous steady state solution

$$\bar{u} = \frac{R_1 a - R_2 b}{a^2 - b^2} \qquad , \bar{v} = \frac{R_2 a - R_1 b}{a^2 - b^2}$$

is rendered unstable and inhomogeneous stable steady states $(\tilde{u},\tilde{v})$ occur instead.

It is reasonable to ask whether this mechanism is advantageous to the two species.

We integrate the steady state form of (1.1) to find that

$$\int_0^1 \tilde{u}(R_1 - a\tilde{u} - b\tilde{v})dx = 0 . \tag{5.1}$$

The second equation of (1.1) becomes $R_2 - b\tilde{u} - a\tilde{v} = 0$ when $\tilde{v} = v_2(\tilde{w})$, while $R_2 - b\tilde{u} < 0$ on the branch $\tilde{v} = 0$. Thus on both branches

$$\tilde{v} \geq \frac{R_2 - b\tilde{u}}{a} \qquad , \tag{5.2}$$

so that

$$\int_0^1 \tilde{u}(R_1 - a\tilde{u} - \frac{b}{a}(R_2 - b\tilde{u}))dx \geq 0 .$$

Since $R_1 = a\bar{u} + b\bar{v}$ and $R_2 = b\bar{u} + a\bar{v}$, we obtain the inequality

$$(a - \frac{b^2}{a}) \int_0^1 \tilde{u}(\bar{u} - \tilde{u})dx > 0$$

so that

$$\bar{u} \int(\bar{u} - \tilde{u})dx > \int(\bar{u} - \tilde{u})^2 dx .$$

Thus if $\tilde{u}(x)$ is not constant, we find that

$$\int_0^1 \tilde{u}\, dx < \bar{u} . \tag{5.3}$$

Thus the avoidance mechanism reduces the total population of the organism that possesses it.

On the other hand, (5.2) can be written in the form

$$a(\tilde{v} - \bar{v}) > b(\bar{u} - \tilde{u}) .$$

Thus, (5.3) implies that

$$\int_0^1 \tilde{v}\, dx > \bar{v} ,$$

so that the second species profits from the nervousness of the first one. The second species might thus evolve a mechanism to frighten its competitors away.

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