Proceedings of the ASME 2014 International Design Engineering Technical Conferences & Computers and Information in Engineering Conference
IDETC/CIE 2014
August 17-20, 2014, Buffalo, USA

DETC2014-35404

HOPF BIFURCATIONS IN TWO-PLAYER DELAYED REPLICATOR DYNAMICS

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ABSTRACT

We investigate the dynamics of two-strategy replicator equations in which competition between strategies is delayed by a given time interval T. Taking T as a bifurcation parameter, we demonstrate the existence of (non-degenerate) Hopf bifurcations in these systems, and present an analysis of the resulting limit cycles using Lindstedt's method.

INTRODUCTION

The field of evolutionary dynamics uses both game theory and differential equations to model population shifts among competing adaptive strategies. One standard approach [1, 2] uses the replicator equation, which modifies the exponential model of population growth,

$$\dot{\xi}_i = \xi_i g_i \quad (i = 1, \dots, n) \tag{1}$$

where ξ_i is the population of strategy i and $g_i(\xi_1, \dots, \xi_n)$ is the fitness of that strategy. The replicator equation [3] results from equation (1) by changing variables from the populations ξ_i to the relative abundances, defined as $x_i \equiv \xi_i / p$ where p is the total population:

$$p(t) = \sum_i \xi_i(t). \tag{2}$$

We see that

$$\dot{p} = \sum_i \dot{\xi}_i = \sum_i \xi_i g_i \tag{3}$$

$$= p \sum_i \frac{\xi_i}{p} g_i = p \sum_i x_i g_i \tag{4}$$

$$= p\phi \tag{5}$$

where $\phi \equiv \sum_i x_i g_i$ is the average fitness of the whole population.

By the product rule,

$$\dot{x}_i = \frac{\dot{\xi}_i}{p} - \frac{\xi_i \dot{p}}{p^2} \tag{6}$$

$$= \frac{\xi_i}{p} g_i - \frac{\xi_i}{p} \frac{\dot{p}}{p} \tag{7}$$

$$= x_i (g_i - \phi). \tag{8}$$

Therefore

$$\sum_i \dot{x}_i = \sum_i x_i g_i - \phi \sum_i x_i \tag{9}$$

$$= \sum_i x_i g_i - \sum_j x_j g_j \sum_i x_i. \tag{10}$$

So, using the fact that

$$\sum_i x_i = \frac{\sum_i \xi_i}{p} = \frac{p}{p} \equiv 1 \tag{11}$$

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equation (10) reduces to the identity

$$\sum_i \dot{x}_i = 0. \tag{12}$$

The fitness of a strategy is assumed to depend only on the relative abundance of each strategy in the overall population, since the model only seeks to capture the effect of competition between strategies, not any environmental or other factors. Therefore, we assume that g_i has the form

$$g_i(\xi_1,\ldots,\xi_n) = f_i\left(\frac{\xi_1}{p},\ldots,\frac{\xi_n}{p}\right) = f_i(x_1,\ldots,x_n). \tag{13}$$

Under this assumption, equation (8) is the replicator equation,

$$\dot{x}_i = x_i(f_i - \phi), \tag{14}$$

where ϕ is now expressed entirely in terms of the x_i, as

$$\phi = \sum_i x_i f_i. \tag{15}$$

Mathematically, ϕ is a coupling term that introduces dependence on the abundance and fitness of other strategies.

The game-theoretic component of the replicator model lies in the choice of fitness functions. Take the payoff matrix $A = (a_{ij})$, where a_{ij} is the expected reward for strategy i when it competes with strategy j. Then the fitness f_i is the total expected payoff of strategy i vs. all strategies, weighted by their frequency:

$$f_i = (A\cdot\mathbf{x})_i. \tag{16}$$

where

$$\mathbf{x} = (x_1,\ldots,x_n). \tag{17}$$

In this work, we generalize the replicator model to systems in which competition with other strategies is delayed by a given time interval T, but competition between same-strategy players is not delayed. Then at time t, the available opponents for a strategy i player are $x_i(t)$ of her compatriots, and $x_j(t-T)$ time-delayed players of each strategy $j \neq i$. If we write $\bar{x}_i \equiv x_i(t-T)$ and define

$$\bar{\mathbf{x}}^i \equiv (\bar{x}_1,\ldots,\bar{x}_{i-1},x_i,\bar{x}_{i+1},\ldots,\bar{x}_n) \tag{18}$$

then the total expected payoff – i.e. the fitness – for strategy i is given by

$$f_i = (A\cdot\bar{\mathbf{x}}^i)_i. \tag{19}$$

The use of delayed fitness functions makes the replicator equation into the delay differential equation (DDE)

$$\dot{x}_i = x_i(f_i - \phi) \tag{20}$$

where

$$\phi = \sum_i x_i f_i = \sum_i x_i (A\cdot\bar{\mathbf{x}}^i)_i. \tag{21}$$

As a system of ODEs, the standard replicator equation is an $(n-1)$ - dimensional problem, since $n-1$ of the x_i are required to specify a point in phase space. The delayed replicator equation, by contrast, is an infinite-dimensional problem [4] whose solution is a flow on the space of functions on the interval $[-T,0)$.

For a concrete interpretation of this system, imagine a situation in which the different strategies are geographically separated, so each group has a delayed estimate of the other groups' populations. Each group sets its rate of reproduction based on the most current population data available: up-to-date for its own population and delayed by a fixed time T for all the others.

This system may also be considered as a model for playing games by mail, with asynchronous score-updating for each group; or of competition between species with a fixed gestation time.

1 DERIVATION

We analyze delayed evolutionary games with two strategies. For ease of notation, write $(x_1,x_2) = (x,y)$, and let

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}. \tag{22}$$

Then

$$\dot{x} = x(f_1 - \phi) \quad \text{and} \quad \dot{y} = y(f_2 - \phi) \tag{23}$$

where

$$f_1 = ax + b\bar{y} \quad \text{and} \quad f_2 = c\bar{x} + dy, \tag{24}$$

which means

$$\phi = xf_1 + yf_2 = x(ax + b\bar{x}) + y(c\bar{x} + dy). \tag{25}$$

Substituting in these values, and writing $y = 1 - x$, the system is reduced to the single delay differential equation

$$\dot{x} = x(1-x)\left((a+d)x - (b+c)\bar{x} + b - d\right). \tag{26}$$

At this point, we note that the four payoff parameters appear in only three independent groupings. So, we replace the four parameters a, b, c, d with q, r, s, defined by

$$q \equiv a + d \tag{27}$$
$$r \equiv -b - c \tag{28}$$
$$s \equiv b - d \tag{29}$$

Then equation (26) becomes

$$\dot{x} = x(1-x)\left(qx + r\bar{x} + s\right). \tag{30}$$

2 ANALYSIS

The equilibrium points of equation (30) satisfy $\dot{x} = 0$ and $\bar{x} = x$. There are three equilibria:

$$x = 0, \quad x = 1, \quad x = \frac{-s}{q+r}. \tag{31}$$

The first two are the endpoints of the interval of physical relevance, since we require that $x \in [0,1]$. The third lies in the interval $(0,1)$ if and only if

$$|s| < |q+r| \quad \text{and} \quad s(q+r) < 0. \tag{32}$$

We examine the stability of the three points.

Taylor expanding about $x = 0$ and $x = 1$, respectively, we obtain the linearized systems

$$\dot{x} = sx \qquad \text{about } x = 0 \tag{33}$$
$$(x-1)^{\cdot} = -(q+r+s)(x-1) \qquad \text{about } x = 1 \tag{34}$$

These two linearizations do not depend on $\bar{x}$, so the stability of the endpoints depends only on the payoff coefficients and not on the delay. If the inequalities (32) hold, then the coefficients s and $-(q+r+s)$ have the same sign, so the two endpoints have the same stability. If $s > 0$ and the inequalities (32) hold, we find that both endpoints are unstable; if $s < 0$ and the inequalities hold, then both endpoints are stable.

Now consider the third equilibrium. Assume that it lies in the interval $(0,1)$; that is, inequalities (32) hold. To determine its stability, we set

$$z = x + \frac{s}{q+r}. \tag{35}$$

In terms of z, equation (30) is

$$\dot{z} = -\frac{(s - z(q+r))(q+r+s-z(q+r))(qz + r\bar{z})}{(q+r)^2}. \tag{36}$$

We linearize about $z = 0$ to get

$$\dot{z} = -\frac{s(q+r+s)(qz + r\bar{z})}{(q+r)^2}. \tag{37}$$

First, note that if delay $T = 0$, the linearization reduces to

$$\dot{z} = -\frac{s(q+r+s)z}{(q+r)}. \tag{38}$$

Recall that the inequalities (32), which we are assuming are true, imply that the sign of s is opposite the sign of $(q+r)$ and $(q+r+s)$. Therefore, if $s > 0$, we find that the point $z = 0$ is stable; if $s < 0$, then it is unstable.

In general, however, the linearization (37) has a non-zero $\bar{z}$ term, so it is reasonable to expect that the stability will depend on the delay T. Given that, we analyze the system for a Hopf bifurcation, taking T as the bifurcation parameter.

Set $z(t) = e^{\lambda t}$ (and $\bar{z} = e^{\lambda(t-T)}$) in equation (37) to obtain the characteristic equation

$$\lambda = -\frac{s(q+r+s)(q + re^{-\lambda T})}{(q+r)^2}. \tag{39}$$

At the critical value of delay for a Hopf bifurcation, the eigenvalues are pure imaginary, so we take $T = T_{cr}$ and $\lambda = i\omega$. Substituting this into the characteristic equation and taking the real and imaginary parts, we obtain

$$\cos \omega T_{cr} = -\frac{q}{r} \tag{40}$$

$$\sin \omega T_{cr} = -\frac{(q+r)^2}{rs(q+r+s)}\omega. \tag{41}$$

Squaring these equations and adding them, we can solve for the critical frequency ω:

$$\omega = \sqrt{\frac{(r-q)s^2(q+r+s)^2}{(q+r)^3}}. \quad (42)$$

It can be shown that the frequency is real and non-zero if and only if (in addition to (32))

$$|q| < |r|. \quad (43)$$

Thus (43) is a necessary condition for a Hopf bifurcation to exist. We will assume that this is the case. Then, substituting the value of ω back into (40), we obtain the critical delay T_{cr}:

$$T_{cr} = \cos^{-1}(-q/r)\sqrt{\frac{(q+r)^3}{s^2(r-q)(q+r+s)^2}}. \quad (44)$$

This result agrees with the values of T_{cr} and ω given by Rand and Verdugo [5]. We also apply the results of [5] to obtain an approximation for the amplitude of the limit cycle generated by the Hopf bifurcation. (See Appendix A.) If $T = T_{cr} + \mu$, the amplitude R is given by

$$R = \sqrt{\mu P/Q} \quad (45)$$

where

$$P = \frac{4r^3s^7(r-q)(5r-4q)(q+r+s)^7}{(q+r)^{12}} \quad (46)$$

$$Q = \frac{r^3s^4(r-q)(q+r+s)^4}{(q+r)^{11}}\left[(2q-r)(q+r)^2(q+r+2s)^2 + T_{cr}s(q+r+s)\left(3r^2(q+r)^2 + s(q+r+s)(4q^2-qr+7r^2)\right)\right]. \quad (47)$$

Since R is real, μ must have the same sign as P/Q. This determines whether the Hopf bifurcation is sub- or supercritical. In particular, if the point $z = 0$ is stable for delay $T < T_{cr}$ and $\mu > 0$, then the limit cycle is stable and the bifurcation is supercritical. We will treat an example of this type in the next section.

3 EXAMPLE: HAWK-DOVE GAMES

As an example, consider the hawk-dove system described by Nowak [6]. There are two strategies competing for a resource with benefit b: "hawks," who will escalate fights against other players, and "doves," who will retreat from fights. So, if a hawk meets a dove, the hawk always wins, receiving payoff b, while the dove receives nothing. If two doves meet, each is equally likely to win the resource, so the expected payoff is $b/2$. If two hawks meet, they fight over the resource; each expects to gain benefit $b/2$ and incur a cost of injury $c/2$, for an expected payoff of $\frac{b-c}{2}$. Therefore the game is represented by the payoff matrix

$$A = \begin{pmatrix} \frac{b-c}{2} & b \\ 0 & \frac{b}{2} \end{pmatrix} \quad (48)$$

where b and c are positive numbers.

In this case, equation (30) becomes

$$\dot{x} = \frac{1}{2}x(1-x)\left((2b-c)x - 2b\bar{x} + b\right) \quad (49)$$

so we have

$$q = \frac{2b-c}{2}, \quad r = -b, \quad s = \frac{b}{2}. \quad (50)$$

The equilibria of the system are

$$x = 0, \quad x = 1, \quad x = \frac{b}{c}. \quad (51)$$

The condition (32) for the third equilibrium to lie in the interval of relevance $0 < x < 1$ reduces to

$$0 < b < c. \quad (52)$$

If we let

$$z = x - \frac{b}{c} \quad (53)$$

then the linearization about $z = 0$ in the case of no delay ($T = 0$ and $\bar{z} = z$) is

$$\dot{z} = \frac{b(b-c)z}{2c}. \quad (54)$$

Therefore, if (52) holds – that is, if the third equilibrium lies in the interval of relevance – the point $z = 0$ is stable for $T = 0$.

If there is a Hopf bifurcation, its critical frequency (42) is

$$\omega = \sqrt{\frac{b^2(b-c)^2(4b-c)}{c^3}} \tag{55}$$

and the necessary condition (43) for ω to be real and nonzero is

$$c < 4b. \tag{56}$$

So, the condition for the point $z = 0$ to both lie in the interval of relevance and have a Hopf bifurcation is

$$0 < b < c < 4b. \tag{57}$$

It is useful to enforce condition (57) by defining a new parameter k, such that

$$c = kb, \quad 1 < k < 4. \tag{58}$$

Then in terms of b and k, the frequency ω is

$$\omega = bk^{2/3}(k-1)\sqrt{4-k} \tag{59}$$

The critical delay (44) is

$$T_{cr} = 2\cos^{-1}\left(1 - \frac{c}{2b}\right)\sqrt{\frac{c^3}{b^2(b-c)^2(4b-c)}} \tag{60}$$

$$= \frac{2\cos^{-1}\left(1-\frac{k}{2}\right)}{bk^{2/3}(k-1)\sqrt{4-k}}. \tag{61}$$

and the amplitude of the limit cycle that is born in this bifurcation is given by equations (45)-(47):

$$R = \sqrt{\mu P/Q} \tag{62}$$

where $\mu = T - T_{cr}$. The ratio P/Q can be written in terms of b and k as

$$\frac{P}{Q} = -2b\sqrt{\frac{4}{k}-1}(k-1)^3(2k-9) \Big/ \left[\sqrt{\frac{4}{k}-1}(k-3)(k-2)^2k^3 + (24-(k-3)k(2k-11))k^2\cos^{-1}\left(1-\frac{k}{2}\right)\right]. \tag{63}$$

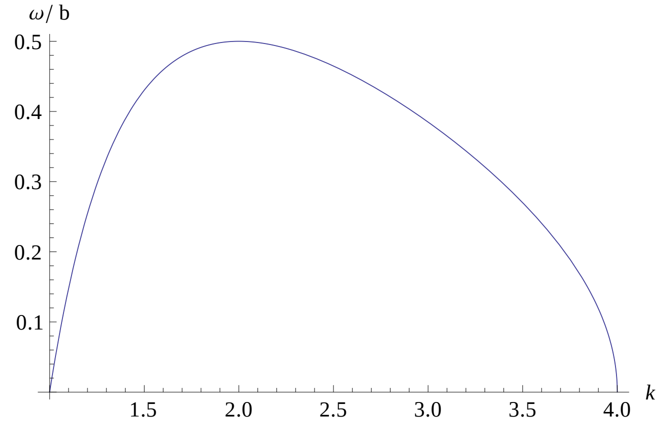

FIGURE 1. NORMALIZED FREQUENCY, ω/b, AS A FUNCTION OF $k = c/b$

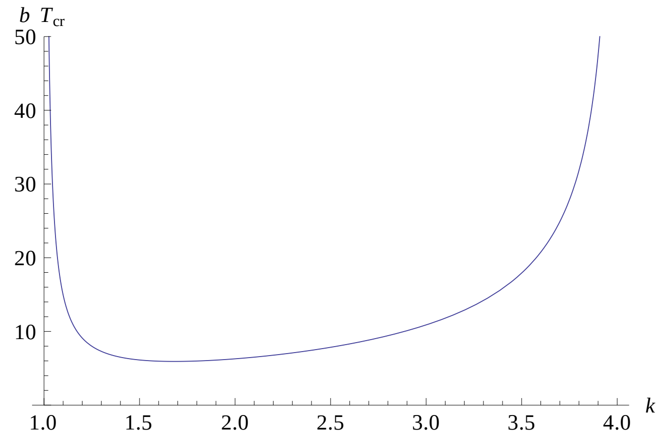

FIGURE 2. NORMALIZED CRITICAL DELAY, bT_{cr}, AS A FUNCTION OF $k = c/b$

Note that in terms of b and k,

$$\omega \propto b, \quad T_{cr} \propto \frac{1}{b}, \quad \frac{P}{Q} \propto b. \tag{64}$$

Therefore, we can divide each of these quantities by the appropriate power of b to obtain normalized versions that depend only on the parameter k.

We see by plotting these results (Fig. 3) that $P/Q > 0$, so for the amplitude R to be real, μ must also be positive. Thus the Hopf bifurcation is supercritical, and the limit cycle is stable.

Finally, we compare the results of this perturbation method to those obtained by continuation in DDE-Biftool [7] for the particular case $b = 1$ and $c = k = 3$. (The latter method is outlined by Heckman, [8].) See Fig. 4. Note that the amplitude given by DDE-Biftool is the full width of the limit cycle, twice the

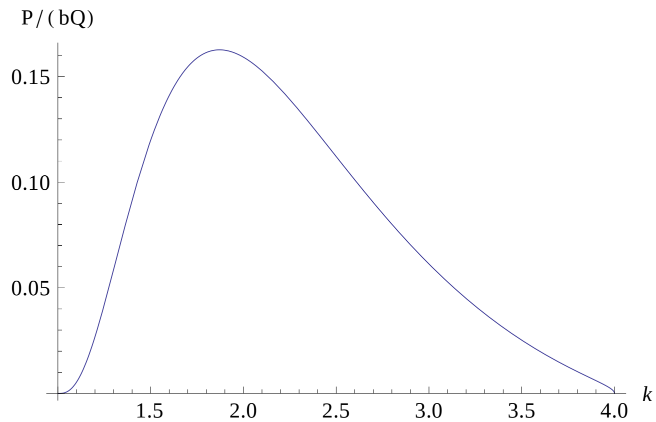

FIGURE 3. NORMALIZED GROWTH COEFFICIENT, $P/(bQ)$, AS A FUNCTION OF $k = c/b$

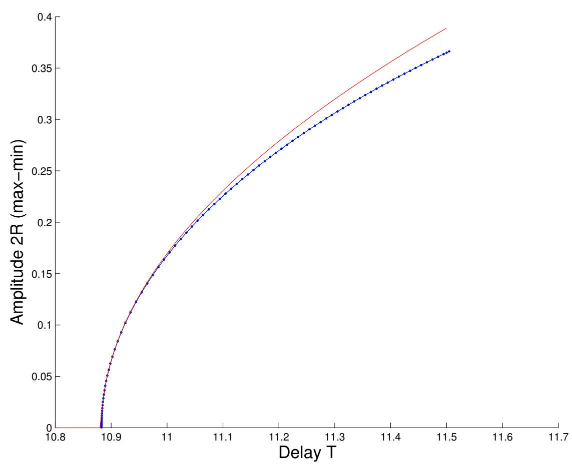

FIGURE 4. AMPLITUDE OF LIMIT CYCLE IN HAWK-DOVE SYSTEM WITH $b = 1$, $c = k = 3$ GIVEN BY LINDSTEDT (RED, SOLID) AND CONTINUATION (BLUE, DOTTED) VS. T

amplitude predicted by Lindstedt's method, which is the average displacement from the equilibrium point. We observe from Fig. 4 that the results of the two methods are in good agreement for values of T reasonably close to T_{cr}.

CONCLUSION

We have investigated the dynamics of two-strategy systems of the form

$$\dot{x}_i = x_i(f_i - \phi), \tag{65}$$

where $f_i = (A \cdot \bar{\mathbf{x}}^i)_i$ is the (delayed) fitness of strategy i.

It is well known that periodic motions cannot occur in non-delayed two-strategy replicator systems, since the phase space is one-dimensional.

In this work, we have shown that, by introducing a delay in competition between strategies, it is possible to find two-strategy replicator systems which support periodic motions. In particular, we have demonstrated a range of parameters for which Hawk-Dove systems with delayed competition exhibit stable limit cycles which are born in Hopf bifurcations.

This generalization of the replicator equation may be useful in modeling natural or social systems in which each group has a delayed estimate of the other groups' populations. This system may also be considered as a model for playing games by mail, with asynchronous score-updating for each group; or of competition between species with a fixed gestation time.

ACKNOWLEDGMENT

We wish to thank Steven Strogatz, Martin Nowak, and David Rand for helpful discussions concerning the derivation of the replicator equation, Eqs. (1)-(15).

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Appendix A: Hopf bifurcation formula for first-order DDEs

We present the formula for the radius of a limit cycle that is born in a Hopf bifurcation in a first-order constant-coefficient differential delay equation, derived by Rand and Verdugo [5].

Consider a differential delay equation (DDE)

$$\frac{dx}{dt} = \alpha x + \beta \bar{x} + a_1 x^2 + a_2 x\bar{x} + a_3 \bar{x}^2 + b_1 x^3 + b_2 x^2 \bar{x} + b_3 x \bar{x}^2 + b_4 \bar{x}^3 \tag{66}$$

where $x = x(t)$ and $\bar{x} = x(t-T)$. The associated linear DDE is

$$\frac{dx}{dt} = \alpha x + \beta \bar{x}. \tag{67}$$

Assume that equation (66) has a critical delay T_{cr} for which it has a pair of pure imaginary eigenvalues $\pm\omega i$ corresponding to the solution

$$x = c_1 \cos \omega t + c_2 \sin \omega t. \tag{68}$$

Then for values of delay T close to T_{cr},

$$T = T_{cr} + \mu \tag{69}$$

the nonlinear equation (66) will in general exhibit a periodic solution that can be approximated by

$$x = R \cos \omega t \tag{70}$$

where the amplitude R satisfies

$$R^2 = \mu P/Q \tag{71}$$

where

$$P = 4\beta^3(4\alpha - 5\beta)(\beta - \alpha)(\alpha + \beta)^2 \tag{72}$$

$$\begin{aligned}
Q =& 5b_2 T_{cr}\beta^6 + 15b_4 T_{cr}\beta^6 + 15b_1\beta^5 + 5b_3\beta^5 - 4a_1^2 T_{cr}\beta^5 \\
&- 3a_2^2 T_{cr}\beta^5 - 22a_3^2 T_{cr}\beta^5 - 7a_1a_2 T_{cr}\beta^5 - 14a_1a_3 T_{cr}\beta^5 \\
&- 7a_2a_3 T_{cr}\beta^5 - 15\alpha b_1 T_{cr}\beta^5 + \alpha b_2 T_{cr}\beta^5 - 15\alpha b_3 T_{cr}\beta^5 \\
&+ 3\alpha b_4 T_{cr}\beta^5 - 18a_1^2\beta^4 - a_2^2\beta^4 - 4a_3^2\beta^4 - 9a_1a_2\beta^4 \\
&- 18a_1a_3\beta^4 - 9a_2a_3\beta^4 + 3\alpha b_1\beta^4 - 15\alpha b_2\beta^4 + \alpha b_3\beta^4 \\
&- 15\alpha b_4\beta^4 + 18\alpha a_1^2 T_{cr}\beta^4 + 7\alpha a_2^2 T_{cr}\beta^4 + 12\alpha a_3^2 T_{cr}\beta^4 \\
&+ 19\alpha a_1a_2 T_{cr}\beta^4 + 30\alpha a_1a_3 T_{cr}\beta^4 + 37\alpha a_2a_3 T_{cr}\beta^4 \\
&- 3\alpha^2 b_1 T_{cr}\beta^4 + 6\alpha^2 b_2 T_{cr}\beta^4 - 3\alpha^2 b_3 T_{cr}\beta^4 - 12\alpha^2 b_4 T_{cr}\beta^4 \\
&+ 12\alpha a_1^2\beta^3 + 11\alpha a_2^2\beta^3 + 26\alpha a_3^2\beta^3 + 33\alpha a_1a_2\beta^3 \\
&+ 30\alpha a_1a_3\beta^3 + 19\alpha a_2a_3\beta^3 - 12\alpha^2 b_1\beta^3 - 3\alpha^2 b_2\beta^3 \\
&+ 6\alpha^2 b_3\beta^3 - 3\alpha^2 b_4\beta^3 - 8\alpha^2 a_1^2 T_{cr}\beta^3 - 12\alpha^2 a_2^2 T_{cr}\beta^3 \\
&+ 4\alpha^2 a_3^2 T_{cr}\beta^3 - 26\alpha^2 a_1a_2 T_{cr}\beta^3 - 16\alpha^2 a_1a_3 T_{cr}\beta^3 \\
&- 20\alpha^2 a_2a_3 T_{cr}\beta^3 + 12\alpha^3 b_1 T_{cr}\beta^3 + 2\alpha^3 b_2 T_{cr}\beta^3 \\
&+ 12\alpha^3 b_3 T_{cr}\beta^3 - 14\alpha^2 a_2^2\beta^2 - 8\alpha^2 a_3^2\beta^2 - 18\alpha^2 a_1a_2\beta^2 \\
&- 12\alpha^2 a_1a_3\beta^2 - 32\alpha^2 a_2a_3\beta^2 + 12\alpha^3 b_2\beta^2 + 2\alpha^3 b_3\beta^2 \\
&+ 12\alpha^3 b_4\beta^2 + 8\alpha^3 a_2^2 T_{cr}\beta^2 + 8\alpha^3 a_1a_2 T_{cr}\beta^2 \\
&- 4\alpha^3 a_2a_3 T_{cr}\beta^2 - 8\alpha^4 b_2 T_{cr}\beta^2 + 4\alpha^3 a_2^2\beta \\
&- 8\alpha^3 a_3^2\beta + 8\alpha^3 a_2a_3\beta - 8\alpha^4 b_3\beta + 8\alpha^4 a_2a_3
\end{aligned} \tag{73}$$

In the two-strategy replicator equation with delayed fitness functions (30), the coefficients in (66) are given by

$$\alpha = -\frac{qs(q+r+s)}{(q+r)^2}, \quad \beta = -\frac{rs(q+r+s)}{(q+r)^2} \tag{74}$$

$$a_1 = q + \frac{2qs}{q+r}, \quad a_2 = r + \frac{2rs}{q+r} \tag{75}$$

$$b_1 = -q, \quad b_2 = -r \tag{76}$$

$$a_3 = b_3 = b_4 = 0. \tag{77}$$

The critical delay T_{cr} and frequency ω may be expressed in terms of α and β by considering the linear equation (67). Substituting equation (70) into (67) and setting the coefficients of $\sin\omega t$ and $\cos\omega t$ equal to zero gives

$$\beta \sin \omega T_{cr} = -\omega, \quad \beta \cos \omega T_{cr} = -\alpha. \tag{78}$$

Squaring and adding these, and substituting the result back in, yields

$$\omega = \sqrt{\beta^2 - \alpha^2} \tag{79}$$

and

$$T_{cr} = \frac{\cos^{-1}(-\alpha/\beta)}{\sqrt{\beta^2 - \alpha^2}}. \tag{80}$$