



# Hopf Bifurcations in Two-Strategy Delayed Replicator Dynamics

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We investigate the dynamics of two-strategy replicator equations in which the fitness of each strategy is a function of the population frequencies delayed by a time interval  $T$ . We analyze two models: in the first, all terms in the fitness are delayed, while in the second, only opposite-strategy terms are delayed. We compare the two models via a linear homotopy. Taking the delay  $T$  as a bifurcation parameter, we demonstrate the existence of (nondegenerate) Hopf bifurcations in both models, and present an analysis of the resulting limit cycles using Lindstedt's method.

*Keywords:* Replicator; delay; Hopf bifurcation; limit cycle; Lindstedt.

## 1. Introduction

Evolutionary game theory models the evolution of competing strategies within a population by combining the classical economic tools of game theory with differential equations [Hofbauer & Sigmund, 1998]. The most common approach focuses on the relative frequencies of different strategies in a population using the replicator equation,

$$\dot{x}_i = x_i(f_i - \phi), \quad i = 1, \dots, n \quad (1)$$

where  $x_i$  is the frequency of (fraction of the population using) strategy  $i$ ,  $f_i(x_1, \dots, x_n)$  is the fitness

of strategy  $i$ , and  $\phi = \sum f_i x_i$  is the average fitness across the population.

Hofbauer and Sigmund [1998] have shown that the replicator equation can be derived from the Lotka–Volterra equation, the classic predator–prey model of species abundances (rather than frequencies). The  $n$ -strategy replicator equation is equivalent to the Lotka–Volterra system with  $n-1$  species. The derivation, however, requires a rescaling of time, and the correspondence between species and strategies is not one-to-one.

Furthermore, it has been shown [Taylor & Jonker, 1978; Hofbauer *et al.*, 1979; Zeeman, 1981;

Weibull, 1995] that the replicator equation can be derived from the exponential growth model

$$\dot{\xi}_i = \xi_i g_i, \quad i = 1, \dots, n \quad (2)$$

where  $\xi_i$  is the abundance of strategy  $i$ , and  $g_i(\xi_1, \dots, \xi_n)$  the fitness of strategy  $i$ . The equivalence simply uses the change of variables  $x_i = \xi_i/p$  where  $p$  is the total population, with the assumption that the fitness functions depend only on the frequencies, and not on the populations directly.

The game-theoretic component of the replicator equation lies in the choice of fitness functions. Take the payoff matrix  $A = (a_{ij})$ , where  $a_{ij}$  is the expected payoff for strategy  $i$  when it interacts with strategy  $j$ . Then the expected total fitness  $f_i$  is the expected payoff of strategy  $i$  when interacting with each strategy, weighted by the other strategies' frequencies:

$$f_i = (A \cdot \mathbf{x})_i, \quad (3)$$

where

$$\mathbf{x} = (x_1, \dots, x_n), \quad \sum_i x_i = 1. \quad (4)$$

In the standard replicator equation, therefore, interactions are assumed to occur instantaneously: the fitness of a given strategy depends on the frequency of each strategy at the given moment. In many real-world contexts, however, the fitness consequences of interactions are not immediate, but instead experience some amount of delay. In this work, we explore the consequences of such delay. Specifically, we consider the two-strategy replicator system, generalized to models in which the fitnesses are functions of the strategy frequencies delayed by a time interval  $T$ .

For ease of notation, write

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \quad (5)$$

and

$$\mathbf{x} = (x_1, x_2) = (x, y) \quad (6)$$

where  $x + y = 1$ .

Two-strategy games with delay have previously been investigated by Yi and Zuwang [1997]. This previous work considered cases that have an equilibrium in which the two strategies coexist, and obtained conditions for the instability of this interior equilibrium when all interactions are subject to delay. It did not, however, analyze the bifurcations and resulting limit cycles that occur at the change

of stability. A nonlinear perturbation analysis of Hopf bifurcations in three-strategy (Rock-Paper-Scissors) replicator equations with delay appears in [Wesson & Rand, 2014], but it only considers a single model in which all interactions are delayed.

In the present paper, we extend the previous work in two ways. First, we go beyond the linear stability analysis, which predicts the existence of a Hopf bifurcation, and include the nonlinear terms of the replicator equation. This allows us to approximate the resulting limit cycles using Lindstedt's method. Second, we consider models in which not all interactions are equally subject to delay: interactions between agents with different strategies may be more likely to be delayed than interactions between agents with the same strategy. Specifically, we consider a range of models indexed by a homotopy parameter  $\gamma$  that determines the relative weights of delayed and nondelayed terms in the fitness functions.

At one extreme is the case considered previously [Yi & Zuwang, 1997; Alboszta & Miekisz, 2004; Wesson & Rand, 2014], in which all interactions are delayed by  $T$  time units. We refer to this as the *full* delay model: If we write  $\bar{x}_i \equiv x_i(t - T)$  and define

$$\bar{\mathbf{x}} \equiv (\bar{x}, \bar{y}) \quad (7)$$

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

$$f_i = (A \cdot \bar{\mathbf{x}})_i. \quad (8)$$

That is,

$$f_1 = a\bar{x} + b\bar{y}, \quad f_2 = c\bar{x} + d\bar{y}. \quad (9)$$

Thus each agent's payoff at the current moment depends on the frequencies of each strategy  $T$  time units ago (i.e. the expected payoff of that agent's strategy  $T$  time units ago). This could represent a situation in which human learners preferentially imitate those with higher payoffs, but information about the payoff of each strategy is delayed by  $T$ ; or a situation in which organisms evolving in a well-mixed population consume resources produced by other organisms to determine their fitness, and resources take  $T$  time use to diffuse between one organism and the next.

At the other end of the spectrum, only interactions between agents with different strategies are delayed, while interactions between agents with the same strategy are instantaneous. We refer to this

as the *off-diagonal* delay model. In this case, if we define

$$\bar{\mathbf{x}}^1 \equiv (x, \bar{y}), \quad \bar{\mathbf{x}}^2 \equiv (\bar{x}, y) \quad (10)$$

then the fitness for strategy  $i$  is given by

$$f_i = (A \cdot \bar{\mathbf{x}}^i)_i. \quad (11)$$

That is,

$$f_1 = ax + b\bar{y}, \quad f_2 = c\bar{x} + dy. \quad (12)$$

Note that in this model, the fitness cannot be considered an expected payoff, as  $\bar{\mathbf{x}}^i$  is not a unit vector. This model may be interpreted as the result of a certain form of assortment. For example, human learners have immediate information about the payoff consequences of interactions with those having their own strategy, but information about the outcome of interactions with people using the other strategy is delayed by  $T$ . Alternatively, nonhuman organisms might interact (e.g. affect each other's fitnesses) by exchanging resources such as nutrients or toxins; and the resources produced by organisms of one's own type may be immediately available (perhaps because of spatial colocalization of agents of the same type) while it takes  $T$  time units for the resources produced by the other type of organism to reach one via diffusion.

In general, we can bridge the two extreme models by introducing a linear homotopy (i.e. a convex combination) between them: we define

$$\bar{\mathbf{x}}_\gamma^i \equiv \gamma \bar{\mathbf{x}}^i + (1 - \gamma) \bar{\mathbf{x}} \quad (13)$$

and consider the fitness functions

$$f_i = (A \cdot \bar{\mathbf{x}}_\gamma^i)_i. \quad (14)$$

That is,

$$\begin{aligned} f_1 &= a(\gamma x + (1 - \gamma)\bar{x}) + b\bar{y}, \\ f_2 &= c\bar{x} + d(\gamma y + (1 - \gamma)\bar{y}). \end{aligned} \quad (15)$$

When  $\gamma = 0$ , we are in the full-delay case; when  $\gamma = 1$ , we are in the off-diagonal delay case. For values of  $\gamma$  between 0 and 1, the system may be considered as a stochastic combination of the two: interactions with agents using the other strategy are always delayed by  $T$ , but interactions with agents using one's own strategy are instantaneous with probability  $\gamma$  and delayed with probability  $1 - \gamma$ .

For any value of  $\gamma$ , the use of delayed frequencies in the fitness functions makes the replicator

equation into the delay differential equation (DDE)

$$\dot{x}_i = x_i(f_i - \phi) \quad (16)$$

where  $f_i$  is given in Eq. (15), and

$$\phi = \sum_i x_i f_i = x f_1 + y f_2. \quad (17)$$

As a system of ODEs, the standard replicator equation is an  $(n - 1)$ -dimensional problem, because  $\sum x_i = 1$ . This means  $n - 1$  of the  $x_i$  are required to specify a point in phase space. In particular, the nondelayed two-strategy replicator system reduces to a single autonomous ODE. The delayed two-strategy replicator equation reduces to a single autonomous DDE which, by contrast, is an infinite-dimensional system [Erneux, 2009] whose solution is a flow on the space of functions on the interval  $[-T, 0)$ .

## 2. Derivation

We will analyze the replicator equation Eq. (16) without specifying the homotopy parameter  $\gamma$  — that is, the fitness is given by Eq. (15). The full delay and off-diagonal delay models correspond to the special cases  $\gamma = 0$  and  $\gamma = 1$ , respectively. Then

$$\dot{x} = x(f_1 - \phi) \quad \text{and} \quad \dot{y} = y(f_2 - \phi) \quad (18)$$

where

$$\begin{aligned} f_1 &= a(\gamma x + (1 - \gamma)\bar{x}) + b\bar{y} \quad \text{and} \\ f_2 &= c\bar{x} + d(\gamma y + (1 - \gamma)\bar{y}), \end{aligned} \quad (19)$$

which means

$$\begin{aligned} \phi &= x f_1 + y f_2 \\ &= x[a(\gamma x + (1 - \gamma)\bar{x}) + b\bar{y}] \\ &\quad + y[c\bar{x} + d(\gamma y + (1 - \gamma)\bar{y})]. \end{aligned} \quad (20)$$

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

$$\begin{aligned} \dot{x} &= x(1 - x)[b - d + (a - b - c + d)\bar{x} \\ &\quad + (a + d)(x - \bar{x})\gamma]. \end{aligned} \quad (21)$$

At this point, we note that the number of parameters may be reduced by defining  $p, q, r$  as

follows:

$$p \equiv a - c \quad (22)$$

$$q \equiv d - b \quad (23)$$

$$r \equiv a + d = \text{tr } A. \quad (24)$$

Then Eq. (21) becomes

$$\dot{x} = x(1-x)(p\bar{x} + q(\bar{x} - 1) + \gamma r(x - \bar{x})). \quad (25)$$

### 3. Analysis

The equilibrium points of Eq. (25) satisfy  $\dot{x} = 0$  and  $\bar{x} = x$ . There are three equilibria:

$$x = 0, \quad x = 1, \quad x = \frac{q}{p+q}. \quad (26)$$

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  $p$  and  $q$  have the same sign. We will assume that this is the case. Notice that the equilibria do not

depend on the homotopy parameter  $\gamma$ . We examine the stability of the three points.

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

$$\frac{dx}{dt} = -qx \quad \text{about } x = 0 \quad (27)$$

$$\frac{d}{dt}(x - 1) = -p(x - 1) \quad \text{about } x = 1. \quad (28)$$

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. The two endpoints have the same stability, since by assumption  $p$  and  $q$  have the same sign. If  $p, q > 0$ , we find that both endpoints are stable; if  $p, q < 0$ , then both endpoints are unstable.

Now consider the third equilibrium. To determine its stability, we set

$$z = x - \frac{q}{p+q}. \quad (29)$$

In terms of  $z$ , Eq. (25) is

$$\dot{z} = -\frac{(p(z-1) + qz)(z(p+q) + q)(\bar{z}(p+q - \gamma r) + \gamma rz)}{(p+q)^2}. \quad (30)$$

We linearize about  $z = 0$  to get

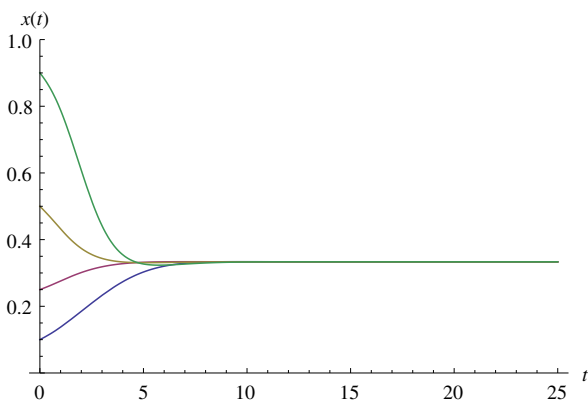
$$\dot{z} = \frac{pq(\bar{z}(p+q - \gamma r) + \gamma rz)}{(p+q)^2}. \quad (31)$$

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

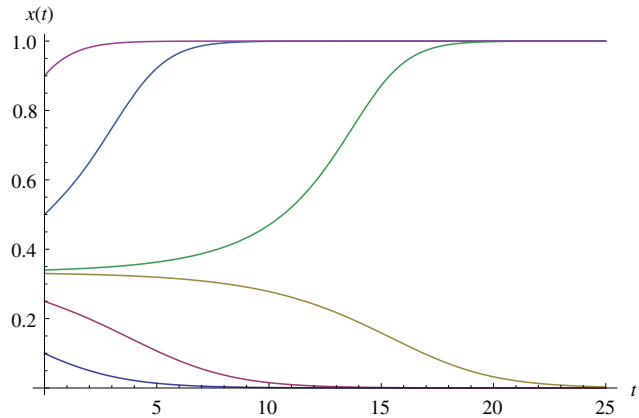
$$\dot{z} = \frac{pqz}{p+q}. \quad (32)$$

Under the assumption that  $p$  and  $q$  have the same sign, we see that the stability of the point  $z = 0$  is opposite to that of the endpoints. If  $p, q > 0$ , we find that the point  $z = 0$  is unstable when  $T = 0$ ; if  $p, q < 0$ , then it is stable. See Fig. 1.

In general, however, the linearization of Eq. (31) has a nonzero  $\bar{z}$  term, so it is reasonable to



(a)  $p = -1, q = -1/2, r = 2$



(b)  $p = 1, q = 1/2, r = 2$

Fig. 1. The stability of the endpoints depends on the sign of  $p$  and  $q$ . For  $T < T_c$ , including  $T = 0$ , the stability of the interior equilibrium is opposite to that of the endpoints. Shown: plots of  $x(t)$  versus  $t$  where  $T = 1$ ,  $\gamma = 1/3$ . Numerical solutions generated by NDSOLVE in Mathematica.

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  $z = e^{\lambda t}$  (and  $\bar{z} = e^{\lambda(t-T)}$ ) in Eq. (31) to obtain the characteristic equation

$$\lambda = \frac{pq e^{-\lambda T}(p+q + \gamma r(e^{\lambda T} - 1))}{(p+q)^2}. \quad (33)$$

At the critical value of delay for a Hopf bifurcation, the eigenvalues corresponding to the subspace in which the Hopf occurs are pure imaginary, so we take  $T = T_c$  and  $\lambda = i\omega$ . Substituting this into the characteristic equation and taking the real and imaginary parts, we obtain

$$\cos \omega T_c = -\frac{\gamma p^2 q^2 r(p+q - \gamma r)}{(\gamma p q r)^2 + \omega^2(p+q)^4} \quad (34)$$

$$\sin \omega T_c = -\frac{pq\omega(p+q)^2(p+q - \gamma r)}{(\gamma p q r)^2 + \omega^2(p+q)^4}. \quad (35)$$

Squaring these equations and adding them, we can solve for the critical frequency  $\omega$ :

$$\omega = pq \sqrt{\frac{p+q - 2\gamma r}{(p+q)^3}}. \quad (36)$$

It can be shown that the frequency is real and nonzero if and only if (in addition to  $p$  and  $q$  having the same sign)  $p+q - 2\gamma r$  has the same sign as  $p+q$ . That is,

$$\{p, q < 0, p+q < 2\gamma r\} \quad \text{or} \quad (37)$$

$$\{p, q > 0, p+q > 2\gamma r\}.$$

Thus Eq. (37) is a necessary condition for a Hopf bifurcation to exist. See Fig. 2. We will assume that this condition is satisfied.

Notice that in the full delay case  $\gamma = 0$ , Eq. (37) is trivially satisfied whenever  $p$  and  $q$  have the same sign. That is, the Hopf occurs for any payoff matrix such that the equilibrium point lies in the interval of relevance. If  $p$  and  $q$  are both negative, the equilibrium is stable and the limit cycle resulting from the Hopf is stable. However, if  $p$  and  $q$  are both positive, the equilibrium is unstable and the limit cycle resulting from the Hopf is unstable. In either case, the Hopf occurs and a limit cycle is born with frequency given by Eq. (36) as:

$$\omega = \frac{pq}{|p+q|}. \quad (38)$$

For any nonzero value of  $\gamma$ , however, there exist payoff matrices for which the equilibrium point lies in the interval of relevance, but  $|r|$  is large enough that Eq. (37) does not hold and the Hopf does not exist.

Now, substituting Eq. (36) back into Eq. (34), we obtain the critical delay  $T_c$ :

$$T_c = \cos^{-1}\left(\frac{-\gamma r}{p+q - \gamma r}\right) \frac{1}{pq} \sqrt{\frac{(p+q)^3}{p+q - 2\gamma r}}. \quad (39)$$

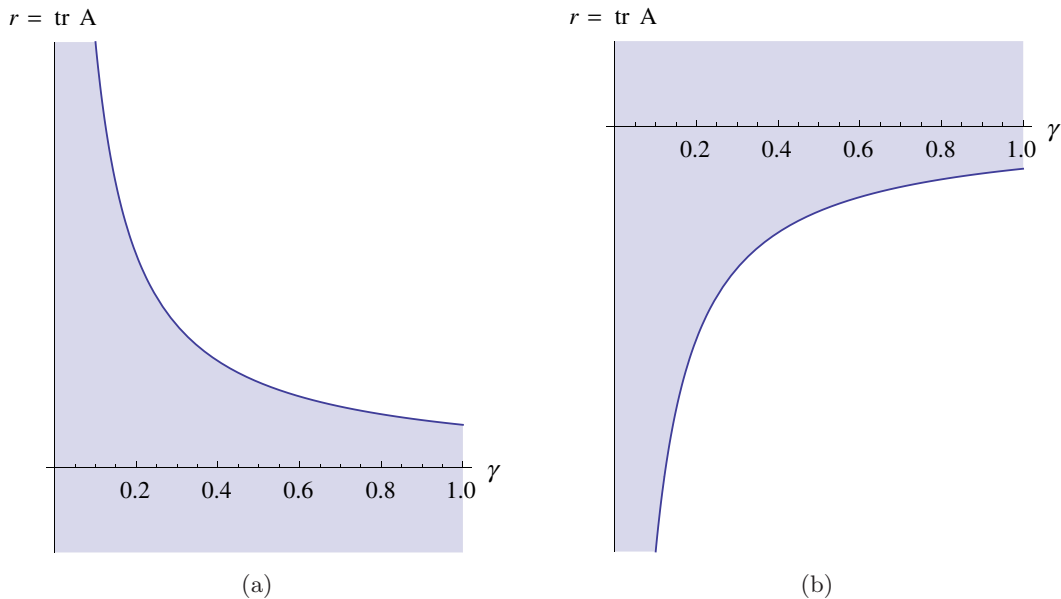


Fig. 2. The Hopf bifurcation occurs in systems lying in the shaded regions, i.e. (a) below the curve  $p+q = 2\gamma r$  if  $p+q > 0$  and (b) above the curve  $p+q = 2\gamma r$  if  $p+q < 0$ .

This result agrees with the values of  $T_c$  and  $\omega$  given by Rand and Verdugo [2007]. We also apply the results of [Rand & Verdugo, 2007] to obtain an approximation for the amplitude of the limit cycle generated by the Hopf bifurcation. See Appendix A.

If  $T = T_c + \mu$ , the amplitude  $R$  of the limit cycle produced by the Hopf bifurcation is given by

$$R = \sqrt{\frac{\mu P}{Q}} \tag{40}$$

where

$$P = -\frac{4p^7q^7(5(p+q) - 9\gamma r)(p+q - 2\gamma r)(p+q - \gamma r)^3}{(p+q)^{12}} \tag{41}$$

$$Q = -\frac{p^4q^4\sqrt{\frac{p+q - 2\gamma r}{(p+q)^3}}(p+q - \gamma r)^3}{(p+q)^8} \\ \times \left[ (p^2 - q^2)^2(p+q - 3\gamma r)\sqrt{\frac{p+q - 2\gamma r}{(p+q)^3}} + [-3\gamma r(2p^2 - pq + 2q^2)(p+q) \right. \\ \left. + (3p^2 - pq + 3q^2)(p+q)^2 + 3\gamma^2r^2(p-q)^2] \cos^{-1}\left(-\frac{\gamma r}{p+q - \gamma r}\right) \right]. \tag{42}$$

When  $\gamma = 0$ , this reduces to

$$P = -\frac{20p^7q^7}{(p+q)^7}, \tag{43}$$

$$Q = -\frac{p^4q^4(\pi(3p^2 - pq + 3q^2)|p+q| + 2(p+q)(p-q)^2)}{2(p+q)^5}. \tag{44}$$

Since  $R$  is real,  $\mu$  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  $T < T_c$  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.

#### 4. Example: Hawk–Dove Games

As an example, consider the Hawk–Dove system described by Nowak [2006]. 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 benefit  $b$ , 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

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$$A = \begin{pmatrix} \frac{b-c}{2} & b \\ 0 & \frac{b}{2} \end{pmatrix} \tag{45}$$

where  $b$  and  $c$  are positive numbers. (Note that  $b, c$  in Eq. (45) are not the same as  $b, c$  in Eq. (5).)

In this case, we have

$$p = \frac{b-c}{2}, \quad q = -\frac{b}{2}, \quad r = b - \frac{c}{2} \tag{46}$$

and Eq. (25) becomes

$$\dot{x} = \frac{1}{2}x(x-1)(c\bar{x} - b + \gamma(2b-c)(\bar{x}-x)). \tag{47}$$

The equilibria of the system are

$$x = 0, \quad x = 1, \quad x = \frac{b}{c}. \tag{48}$$

The condition for the third equilibrium to lie in the interval of physical relevance  $(0, 1)$ , which is that  $p$

and  $q$  must have the same sign, reduces to

$$0 < b < c. \quad (49)$$

Notice that this means there is an equilibrium point where both  $x$  and  $y$  are nonzero (i.e. both strategies coexist), if and only if the expected payoff  $\frac{1}{2}(b - c)$  for a hawk versus another hawk is negative.

If we let

$$z = x - \frac{b}{c} \quad (50)$$

then the linearization about  $z = 0$  is

$$\dot{z} = \frac{b(b - c)(c\bar{z} - (c - 2b)(\bar{z} - z)\gamma)}{2c^2}. \quad (51)$$

In the case of no delay ( $T = 0$  and  $\bar{z} = z$ ) this becomes

$$\dot{z} = \frac{b(b - c)z}{2c}. \quad (52)$$

Therefore, if Eq. (49) holds — that is, if the third equilibrium lies in the interval of relevance — then the point  $z = 0$  is stable for  $T = 0$ , for any value of  $\gamma$ .

If there is a Hopf bifurcation, its critical frequency Eq. (36) is

$$\omega = \frac{b(c - b)}{2c^{3/2}} \sqrt{4b\gamma - 2\gamma c + c}. \quad (53)$$

From Eq. (37), we see that the condition for  $\omega$  to be real — i.e. for the point  $z = 0$  to have a Hopf bifurcation — is

$$(2\gamma - 1)c < 4\gamma b. \quad (54)$$

If  $\gamma \leq 1/2$ , then Eq. (54) is trivially true, so  $\omega$  is real for all Hawk–Dove games such that Eq. (49)

holds. If  $\gamma > 1/2$ , however,  $\omega$  is real only if

$$c < \frac{4b\gamma}{2\gamma - 1}. \quad (55)$$

It is instructive to define a new parameter  $k$ , such that

$$c = kb. \quad (56)$$

Intuitively,  $k$  is the *cost per unit of benefit* that the hawks are willing to incur. We can enforce conditions Eqs. (49) and (54) by stipulating that  $k > 1$ , and if  $\gamma > 1/2$ ,

$$k < \frac{4\gamma}{2\gamma - 1}. \quad (57)$$

Then in terms of  $b$  and  $k$ , the frequency  $\omega$  is

$$\omega = \frac{b(k - 1)\sqrt{4\gamma - 2\gamma k + k}}{2k^{3/2}}. \quad (58)$$

The critical delay Eq. (39) is

$$T_c = \frac{2c^{3/2}}{b(c - b)\sqrt{4b\gamma - 2\gamma c + c}} \times \cos^{-1} \left( 1 - \frac{c}{2b\gamma - \gamma c + c} \right) \quad (59)$$

$$= \frac{2k^{3/2}}{b(k - 1)\sqrt{4\gamma - 2\gamma k + k}} \times \cos^{-1} \left( \frac{k}{(\gamma - 1)k - 2\gamma} + 1 \right) \quad (60)$$

and the amplitude of the limit cycle that is born in this bifurcation is given by Eqs. (40)–(42):

$$R = \sqrt{\frac{\mu P}{Q}} \quad (61)$$

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

$$\frac{P}{Q} = [2bk^{-5/2}(k - 1)^3(2\gamma(k - 2) - k)(9\gamma(k - 2) - 5k)] \Bigg/ \left[ \sqrt{k}(k - 2)^2(-k^2 - 6\gamma^2(k - 2)^2 + 5\gamma(k - 2)k) + \sqrt{4\gamma - 2\gamma k + k}(k^2(k(3k - 7) + 7) + 3\gamma^2(k - 2)^4 - 3\gamma k(k(2k - 5) + 5)(k - 2)) \cos^{-1} \left( \frac{k}{(\gamma - 1)k - 2\gamma} + 1 \right) \right]. \quad (62)$$

In the full delay case ( $\gamma = 0$ ), the critical frequency and delay become

$$\omega = \frac{b(k - 1)}{2k} \quad (63)$$

and

$$T_c = \frac{\pi k}{b(k-1)} \quad (64)$$

and the ratio  $P/Q$  reduces to

$$\frac{P}{Q} = \frac{20b(k-1)^3}{k^3(\pi(k(3k-7)+7)-2(k-2)^2)}. \quad (65)$$

In the off-diagonal case ( $\gamma = 1$ ), these values are

$$\omega = \frac{b\sqrt{4-k}(k-1)}{2k^{3/2}} \quad (66)$$

and

$$T_c = \frac{2k^{3/2} \cos^{-1}\left(1 - \frac{k}{2}\right)}{b\sqrt{4-k}(k-1)} \quad (67)$$

and

$$\frac{P}{Q} = \frac{-2b\sqrt{4-k}(k-1)^3(2k-9)k^{-5/2}}{(k-3)\sqrt{-(k-4)k}(k-2)^2 + (24 - (k-3)k(2k-11)) \cos^{-1}\left(1 - \frac{k}{2}\right)}. \quad (68)$$

Note that in terms of  $b$  and  $k$ , for all values of  $\gamma$

$$\omega \propto b, \quad T_c \propto \frac{1}{b}, \quad \frac{P}{Q} \propto b. \quad (69)$$

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

Observe (Figs. 3–5) that when  $k = 2$ ,  $\omega$ ,  $T_c$  and  $P/Q$  do not change as  $\gamma$  varies. In fact, for  $k = 2$  they reduce to

$$\omega = \frac{b}{4}, \quad T_c = \frac{2\pi}{b}, \quad \frac{P}{Q} = \frac{b}{2\pi}. \quad (70)$$

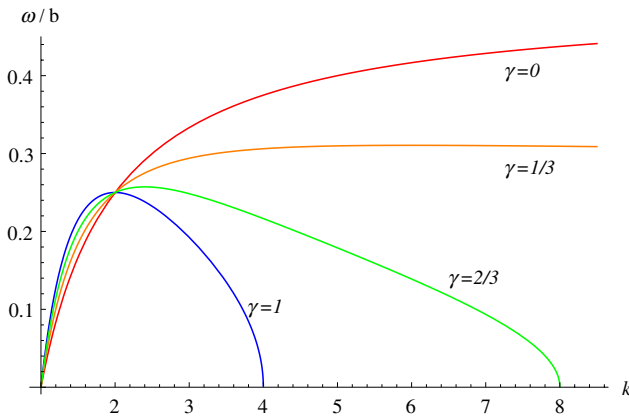


Fig. 3. Normalized frequency  $\omega/b$ , at the Hopf bifurcation in the Hawk–Dove system, as a function of  $k = c/b$ . Red: full type delay ( $\gamma = 0$ ). Blue: off-diagonal delay ( $\gamma = 1$ ). Orange:  $\gamma = 1/3$ . Green:  $\gamma = 2/3$ .

This is to be expected, since for this value of  $k$  the Hawk–Dove replicator equation (47) does not depend on  $\gamma$ . It reduces to

$$\dot{x} = \frac{1}{2}b(x-1)x(2\bar{x}-1). \quad (71)$$

We see by plotting the normalized version of Eq. (62) (Fig. 5) that  $P/Q > 0$ , so for the amplitude  $R$  to be real,  $\mu$  must also be positive. Thus the Hopf bifurcation is supercritical, and the limit cycle is stable. Numerical simulation using NDSOLVE in Mathematica confirms the stability of the limit

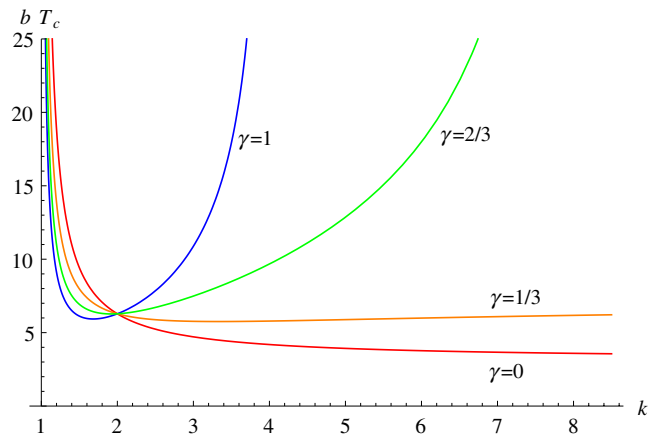


Fig. 4. Normalized critical delay  $bT_c$ , for the Hopf, as a function of  $k = c/b$ . Red: full type delay ( $\gamma = 0$ ). Blue: off-diagonal delay ( $\gamma = 1$ ). Orange:  $\gamma = 1/3$ . Green:  $\gamma = 2/3$ .



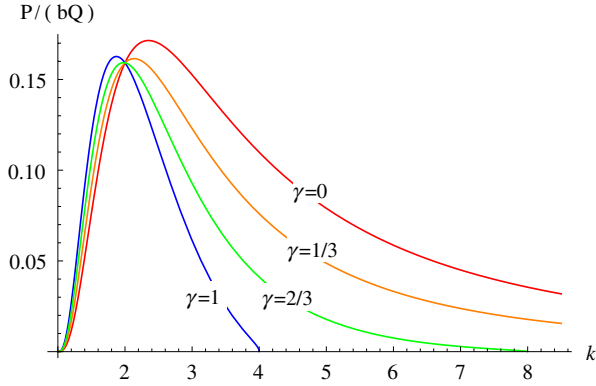


Fig. 5. Normalized growth coefficient  $\frac{P}{bQ}$ , for the Hopf, as a function of  $k = c/b$ . Red: full type delay ( $\gamma = 0$ ). Blue: off-diagonal delay ( $\gamma = 1$ ). Orange:  $\gamma = 1/3$ . Green:  $\gamma = 2/3$ .

cycle. See Figs. 6 and 7, in which we show numerical solutions for the particular case  $b = 1$  and  $c = k = 3$ , corresponding to the payoff matrix

$$A = \begin{pmatrix} -1 & 1 \\ 0 & \frac{1}{2} \end{pmatrix} \quad (72)$$

for values of  $T$  above and below  $T_c$ .

Finally, we compare the results of this perturbation method to those obtained by continuation in DDE-BIFTOOL. (The latter method is outlined by Heckman [2012].) As in Figs. 6 and 7, we take  $b = 1$ ,  $c = k = 3$ . We have plotted the results for  $\gamma = 0$ ,  $\gamma = 1/3$ ,  $\gamma = 2/3$ , and  $\gamma = 1$ . See Fig. 8.

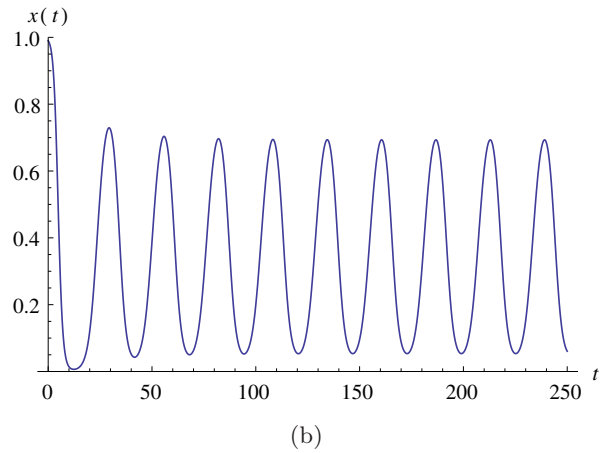
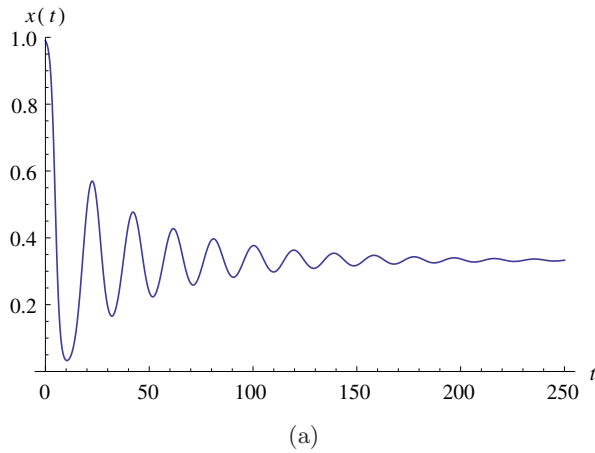


Fig. 6. Numerical solutions of the Hawk–Dove system with  $b = 1$ ,  $c = k = 3$  and  $\gamma = 1/3$  for values of  $T$  above and below  $T_c$ . (a) Delay 5 =  $T < T_c$ . Interior equilibrium is stable and (b) delay 7 =  $T > T_c$ . Limit cycle is stable.

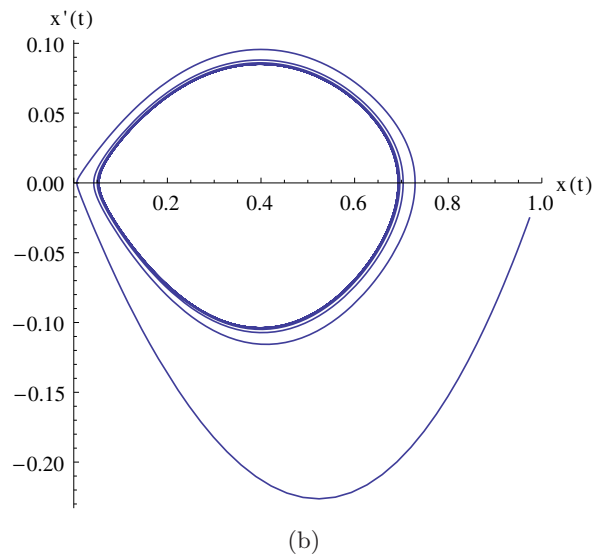
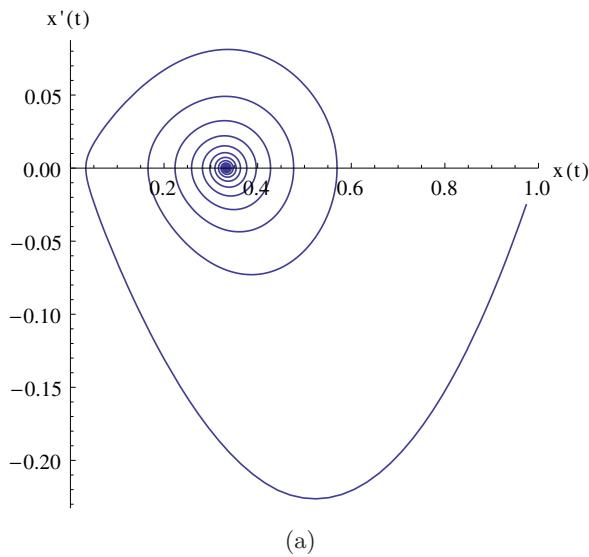


Fig. 7. Parametric ( $\dot{x}$  versus  $x$ ) representation of numerical solutions of Hawk–Dove system with  $b = 1$ ,  $c = k = 3$  and  $\gamma = 1/3$  for values of  $T$  above and below  $T_c$ . (a) Delay 5 =  $T < T_c$ . Interior equilibrium is stable and (b) delay 7 =  $T > T_c$ . Limit cycle is stable.

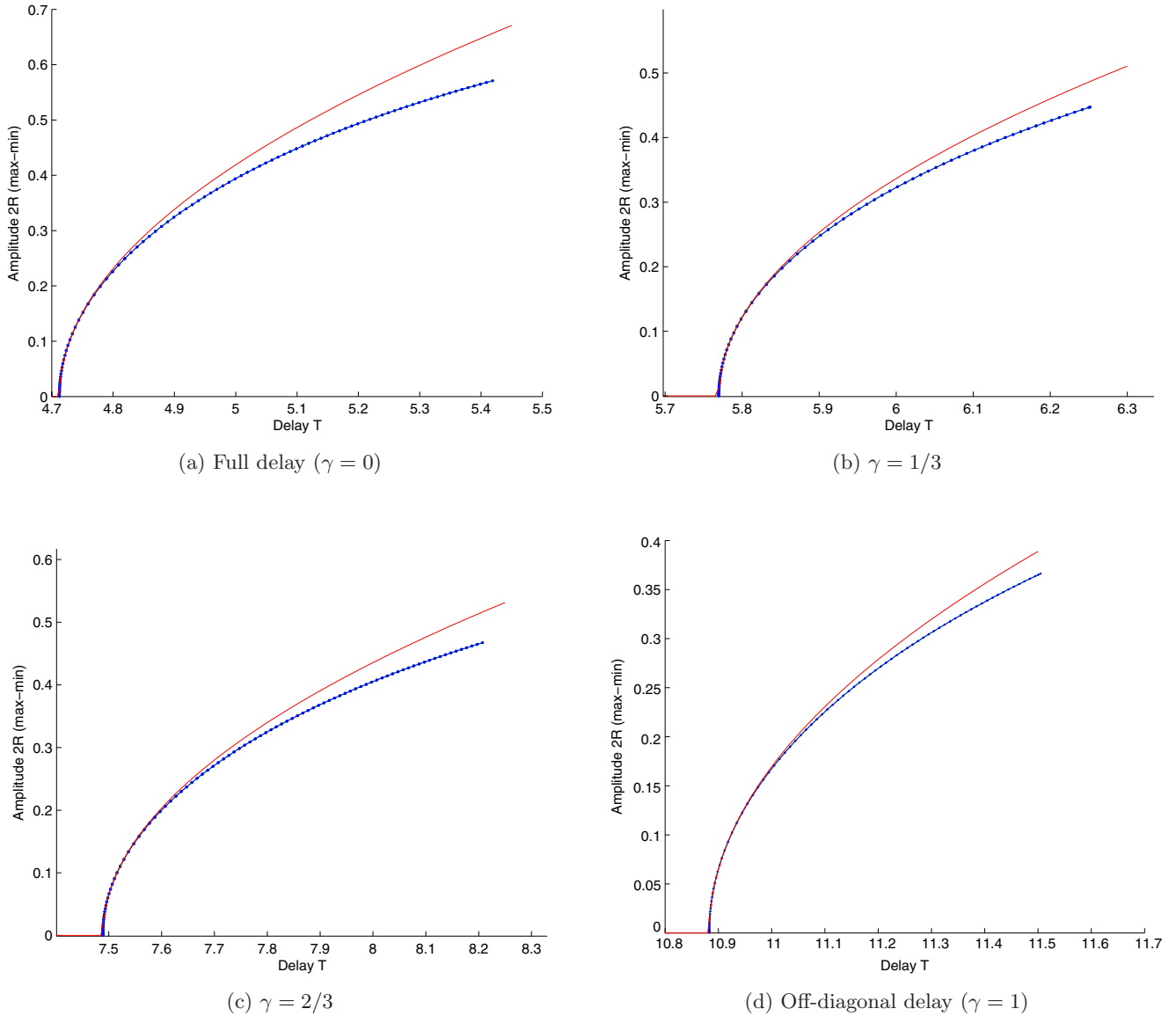


Fig. 8. Amplitude of limit cycle versus  $T$  in the Hawk–Dove system with  $b = 1$ ,  $c = k = 3$  given by Lindstedt (upper curve, red) and continuation in DDE-BIFTOOL (lower curve, blue), for various values of  $\gamma$ .

Note that the amplitude given by DDE-BIFTOOL is the full width of the limit cycle, twice the amplitude predicted by Lindstedt’s method, which is the average displacement from the equilibrium point. We observe from Fig. 8 that for all tested values of  $\gamma$  the results of the two methods are in good agreement for values of  $T$  reasonably close to  $T_c$ .

## 5. Conclusion

We have investigated the dynamics of two-strategy replicator systems with delay. We have considered a range of models indexed by a homotopy

parameter  $\gamma$ , which determines the relative weights of delayed and nondelayed terms when determining the fitness arising from interactions with agents having the same strategy. (Interactions between agents with different strategies are always delayed.) At one extreme ( $\gamma = 0$ ) the model describes a full-type delay in which the fitness of each strategy is the delayed expected payoff of that strategy. At the other extreme ( $\gamma = 1$ ) only the opposite-strategy terms in each fitness function are delayed.

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

The introduction of delay makes the system into a DDE, so the phase space is infinite-dimensional.

In this work, we have shown that, for all values of  $\gamma$ , there exist two-strategy games for which non-degenerate Hopf bifurcations and limit cycles occur. In the full delay case ( $\gamma = 0$ ), Hopf bifurcations occur for all two-strategy games. For  $\gamma > 0$ , there exist two-strategy games for which there is no Hopf bifurcation.

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. That is, for such systems, the population dynamics converge to a periodic oscillation in the proportions of hawks versus doves. We have used Lindstedt’s method to approximate the amplitude of the limit cycles, and we have shown that this approximation agrees with the results of numerical continuation.

If  $\gamma \leq 1/2$ , i.e. closer to full delay than off-diagonal delay, the Hopf bifurcation occurs for all Hawk–Dove systems in which the cost  $c$  of fighting is greater than the benefit  $b$  attained. If  $\gamma > 1/2$ , i.e. closer to off-diagonal delay, there is a maximum cost-benefit ratio above which the bifurcation does not occur, and limit cycles in the population frequencies are not observed.

This generalization of the replicator equation may be useful in modeling a range of scenarios, given the ubiquity and heterogeneity of delay in real-world applications. It is often the case that people have more accurate and up-to-date information about those who are more similar to themselves, and that organisms which have the same phenotype are located closer to each other. Thus it may well be that delay plays a bigger role in interactions between agents with different strategies than agents with the same strategy. The framework we introduce here demonstrates the important consequences such heterogeneous delays can have on the system’s evolutionary dynamics.

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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 [2007].

Consider a differential delay equation (DDE)

$$\begin{aligned} \frac{dx}{dt} = & \alpha x + \beta \bar{x} + a_1 x^2 + a_2 x \bar{x} + a_3 \bar{x}^2 + b_1 x^3 \\ & + b_2 x^2 \bar{x} + b_3 x \bar{x}^2 + b_4 \bar{x}^3 \end{aligned} \quad (\text{A.1})$$

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

$$\frac{dx}{dt} = \alpha x + \beta \bar{x}. \quad (\text{A.2})$$

Assume that Eq. (A.1) has a critical delay  $T_c$  for which it has a pair of pure imaginary eigenvalues  $\pm i\omega_c$  and the linearized problem Eq. (A.2) has the general solution

$$x = c_1 \cos \omega_c t + c_2 \sin \omega_c t. \quad (\text{A.3})$$

Since the system is autonomous, we can without loss of generality choose the initial conditions so that the periodic solution has only one term,

$$x = c_1 \cos \omega_c t. \quad (\text{A.4})$$

The goal of Lindstedt's method is to find a periodic solution of the full nonlinear DDE Eq. (A.1) for values of  $T$  close to  $T_c$  by detuning the frequency off  $\omega_c$ . First, we introduce a small parameter  $\epsilon$  via the scaling

$$x = \epsilon u. \quad (\text{A.5})$$

We detune  $T$  by a term of order  $\epsilon^2$ :

$$T = T_c + \mu = T_c + \epsilon^2 \mu_2. \quad (\text{A.6})$$

Next we stretch time by the change of variables

$$\tau = \omega t \quad (\text{A.7})$$

where  $\omega$  is detuned from  $\omega_c$ :

$$\omega = \omega_c + \epsilon^2 k_2 + \dots \quad (\text{A.8})$$

This gives us

$$\frac{du}{dt} = \omega \frac{du}{d\tau} = (\omega_c + \epsilon^2 k_2 + \dots) \frac{du}{d\tau} \quad (\text{A.9})$$

and

$$\begin{aligned} \bar{u} &= u(\tau - \omega T) \\ &= u(\tau - (\omega_c + \epsilon^2 k_2 + \dots)(T_c + \epsilon^2 \mu_2)) \end{aligned} \quad (\text{A.10})$$

$$= u(\tau - \omega_c T_c - \epsilon^2 (k_2 T_c + \mu_2 \omega_c) + \dots) \quad (\text{A.11})$$

$$\begin{aligned} &= u(\tau - \omega_c T_c) - \epsilon^2 (k_2 T_c + \mu_2 \omega_c) u' \\ &\quad \times (\tau - \omega_c T_c) + \dots \end{aligned} \quad (\text{A.12})$$

Finally, we expand  $u$  as a series in  $\epsilon$ :

$$u(\tau) = u_0(\tau) + \epsilon u_1(\tau) + \epsilon^2 u_2(\tau) + \dots \quad (\text{A.13})$$

Collecting similar orders of  $\epsilon$ , we find that the lowest-order equation has the solution

$$u_0(\tau) = A \cos \tau. \quad (\text{A.14})$$

By substituting this into the next higher-order equation and eliminating secular terms, we can find  $A$  as a function of  $\mu_2$ . Multiplying through by  $\epsilon^2$ , we thus find that the limit cycle solution of Eq. (A.1) can be approximated by

$$x = R \cos \omega t \quad (\text{A.15})$$

where the amplitude  $R = \epsilon^2 A$  as a function of  $\mu = \epsilon^2 \mu_2$  is given by

$$R^2 = \frac{\mu P}{Q} \quad (\text{A.16})$$

where

$$P = 4\beta^3(4\alpha - 5\beta)(\beta - \alpha)(\alpha + \beta)^2 \quad (\text{A.17})$$

$$\begin{aligned} Q &= 5b_2 T_c \beta^6 + 15b_4 T_c \beta^6 + 15b_1 \beta^5 + 5b_3 \beta^5 - 4a_1^2 T_c \beta^5 - 3a_2^2 T_c \beta^5 - 22a_3^2 T_c \beta^5 \\ &\quad - 7a_1 a_2 T_c \beta^5 - 14a_1 a_3 T_c \beta^5 - 7a_2 a_3 T_c \beta^5 - 15\alpha b_1 T_c \beta^5 + \alpha b_2 T_c \beta^5 - 15\alpha b_3 T_c \beta^5 \\ &\quad + 3\alpha b_4 T_c \beta^5 - 18a_1^2 \beta^4 - a_2^2 \beta^4 - 4a_3^2 \beta^4 - 9a_1 a_2 \beta^4 - 18a_1 a_3 \beta^4 - 9a_2 a_3 \beta^4 \\ &\quad + 3\alpha b_1 \beta^4 - 15\alpha b_2 \beta^4 + \alpha b_3 \beta^4 - 15\alpha b_4 \beta^4 + 18\alpha a_1^2 T_c \beta^4 + 7\alpha a_2^2 T_c \beta^4 \\ &\quad + 12\alpha a_3^2 T_c \beta^4 + 19\alpha a_1 a_2 T_c \beta^4 + 30\alpha a_1 a_3 T_c \beta^4 + 37\alpha a_2 a_3 T_c \beta^4 - 3\alpha^2 b_1 T_c \beta^4 \\ &\quad + 6\alpha^2 b_2 T_c \beta^4 - 3\alpha^2 b_3 T_c \beta^4 - 12\alpha^2 b_4 T_c \beta^4 + 12\alpha a_1^2 \beta^3 + 11\alpha a_2^2 \beta^3 + 26\alpha a_3^2 \beta^3 \\ &\quad + 33\alpha a_1 a_2 \beta^3 + 30\alpha a_1 a_3 \beta^3 + 19\alpha a_2 a_3 \beta^3 - 12\alpha^2 b_1 \beta^3 - 3\alpha^2 b_2 \beta^3 + 6\alpha^2 b_3 \beta^3 \\ &\quad - 3\alpha^2 b_4 \beta^3 - 8\alpha^2 a_1^2 T_c \beta^3 - 12\alpha^2 a_2^2 T_c \beta^3 + 4\alpha^2 a_3^2 T_c \beta^3 - 26\alpha^2 a_1 a_2 T_c \beta^3 - 16\alpha^2 a_1 a_3 T_c \beta^3 \\ &\quad - 20\alpha^2 a_2 a_3 T_c \beta^3 + 12\alpha^3 b_1 T_c \beta^3 - 12\alpha^2 a_1 a_3 \beta^2 - 32\alpha^2 a_2 a_3 \beta^2 + 12\alpha^3 b_2 \beta^2 + 2\alpha^3 b_3 \beta^2 \\ &\quad + 2\alpha^3 b_4 \beta^2 + 12\alpha^3 b_3 T_c \beta^3 - 14\alpha^2 a_2^2 \beta^2 - 8\alpha^2 a_3^2 \beta^2 - 18\alpha^2 a_1 a_2 \beta^2 \\ &\quad + 12\alpha^3 b_4 \beta^2 + 8\alpha^3 a_2^2 T_c \beta^2 + 8\alpha^3 a_1 a_2 T_c \beta^2 - 4\alpha^3 a_2 a_3 T_c \beta^2 - 8\alpha^4 b_2 T_c \beta^2 \\ &\quad + 4\alpha^3 a_2^2 \beta - 8\alpha^3 a_3^2 \beta + 8\alpha^3 a_2 a_3 \beta - 8\alpha^4 b_3 \beta + 8\alpha^4 a_2 a_3. \end{aligned} \quad (\text{A.18})$$

The critical delay  $T_c$  and frequency  $\omega_c$  may be expressed in terms of  $\alpha$  and  $\beta$  by considering the linear equation (A.2). Substituting Eq. (A.4) into Eq. (A.2) and setting the coefficients of  $\sin \omega_c t$  and  $\cos \omega_c t$  equal to zero give

$$\beta \sin \omega_c T_c = -\omega_c, \quad \beta \cos \omega_c T_c = -\alpha. \quad (\text{A.19})$$

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

$$\omega_c = \sqrt{\beta^2 - \alpha^2} \quad (\text{A.20})$$

and

$$T_c = \frac{\cos^{-1}\left(-\frac{\alpha}{\beta}\right)}{\sqrt{\beta^2 - \alpha^2}}. \quad (\text{A.21})$$

The system in question, the two-strategy replicator equation (30), can be written as

$$\begin{aligned} \dot{z} = & \alpha z + \beta \bar{z} + a_1 z^2 + a_2 z \bar{z} + a_3 \bar{z}^2 \\ & + b_1 z^3 + b_2 z^2 \bar{z} + b_3 z \bar{z}^2 + b_4 \bar{z}^3 \end{aligned} \quad (\text{A.22})$$

where

$$\alpha = \frac{\gamma p q r}{(p+q)^2} \quad (\text{A.23})$$

$$\beta = \frac{p q (p+q - \gamma r)}{(p+q)^2} \quad (\text{A.24})$$

$$a_1 = \frac{\gamma r (p-q)}{p+q} \quad (\text{A.25})$$

$$a_2 = \frac{(p-q)(p+q - \gamma r)}{p+q} \quad (\text{A.26})$$

$$b_1 = -r\gamma, \quad (\text{A.27})$$

$$b_2 = -p - q + \gamma r \quad (\text{A.28})$$

$$a_3 = b_3 = b_4 = 0. \quad (\text{A.29})$$

We substitute these values into Eqs. (A.16)–(A.18) to obtain the amplitude of the limit cycle, Eqs. (40)–(42).