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**Interim Report**

**IR-04-016**

**Measure Dynamics on a One-Dimensional Continuous Trait  
Space: Theoretical Foundations for Adaptive Dynamics**

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## **Abstract**

The measure dynamic approach to modelling single-species coevolution with a one-dimensional trait space is developed and compared to more traditional methods of adaptive dynamics and the Maximum Principle. It is shown that among monomorphisms (i.e. measures supported on a single trait value), the CSS (Continuously Stable Strategy) characterize those that are Lyapunov stable and attract all initial measures supported in an interval containing this trait value. In the cases where adaptive dynamics predicts evolutionary branching, convergence to a dimorphism is established.

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# Measure Dynamics on a One-Dimensional Continuous Trait Space: Theoretical Foundations for Adaptive Dynamics

*Ross Cressman*  
*Josef Hofbauer*

## 1 Introduction

Interest in adaptive dynamics as a means to examine stability of coevolutionary systems has grown exponentially over the past decade (see Abrams (2001) and the references therein). Cornerstones for this theory are the stability conditions (e.g. continuously stable strategy, convergence stability) developed for the mean strategy dynamic of a single species with a one-dimensional continuous trait space. We briefly summarize this approach in Section 2.1 for the special case when individual fitness is given by two-variable quadratic functions defined on the trait space through pairwise interactions. As coevolution also involves a density dynamic on the total population size, we include a background fitness (that is strategy independent and decreasing with respect to density) to limit population growth. This has the effect that stability of the coevolutionary system is completely determined by the strategy dynamic. Here, adaptive dynamics predicts stability of a monomorphic equilibrium (i.e. one where all individuals in the population are using the same strategy) if, for all other monomorphisms that are small perturbations of this equilibrium, trait substitution through nearby mutations is only successful when this substitution moves the population closer to the equilibrium.

There is a general recognition among practitioners of adaptive dynamics (e.g. Abrams and Matsuda, 1997) that the assumptions underlying this approach (e.g. maintenance of monomorphisms through trait substitution and the suppression of population size effects) are questionable, especially as the theory progresses to analyzing non equilibrium behavior. One alternative approach is to consider stability for only those coevolutionary systems where the distribution of strategies has finite support (i.e. there are only finitely many different individual strategies used by the population during the course of evolution), probably close to the monomorphic equilibrium. This approach, which in some sense ignores the possibility of continual though rare mutation, is closely related to the Maximum Principle promoted by Vincent and co-workers (Cohen et al., 1999; Vincent et al., 1996)<sup>1</sup> as summarized in Section 2.2. We give reasons in Section 4 why we do not regard this as an adequate replacement.

It is always easier to criticize existing theories than to develop an alternative. The alternative we prefer is dynamic stability in the space of measures, an extension of the concepts developed for strategy distributions to models that include density dependence. Dynamics on strategy distributions (and not just the mean) with continuous strategy

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<sup>1</sup>The literature here calls this the ESS maximum Principle. As the term ESS has several possibly different connotations, we prefer to either drop this qualification altogether or to replace it with the more neutral game-theoretic term of strict NE (Nash equilibrium).



spaces have also been considered (Bomze, 1990, 1991; Oechssler and Riedel, 2001, 2002) where quadratic interaction terms are quite commonly used. In contrast to adaptive dynamics where monomorphic populations are invaded by rare mutants, this literature considers the evolution of distributions close to the monomorphic equilibrium distribution.

For reasons discussed in Section 3, we consider this dynamic (with the addition of background fitness) to better model the coevolutionary process. In Section 4, we generate convergence and stability conditions for this measure dynamic in a general setting. These results give exact conditions in Section 5 with our assumption of quadratic pairwise interactions and background fitness which are then compared to those of adaptive dynamics and the Maximum Principle. Section 6 extends these methods to other fitness functions on a one-dimensional trait space. Extensions to multi-dimensional trait space and to general fitness functions are discussed in the final section, emphasizing the added analytic problems that arise in these circumstances.

## 2 The Quadratic Pairwise Interaction Model

Suppose individuals in our single species use strategies that are parameterized by a single real variable  $x$  belonging to a closed and bounded interval  $S = [\alpha, \beta]$ . For fitness associated with quadratic pairwise interactions, we take the payoff of an individual using strategy  $x$  against one using strategy  $y$  as

$$\pi(x, y) = ax^2 + bxy + cy^2 + dx + ey + f$$

where  $x, y \in [\alpha, \beta]$ .<sup>2</sup> Fitness of an individual using  $x$  is then the expected payoff this individual obtains in a random pairwise interaction with another individual in the population.<sup>3</sup> To avoid some mathematical complications, we want fitness to be positive for all strategy pairs when the population size  $N$  is zero (i.e. no Allee effect) and also to be negative when  $N$  is sufficiently large. The simplest way to accomplish this mathematically is to add an appropriate linear density term to the individual payoff function that is independent of the strategy pair (i.e. a “background” fitness term). That is, we take

$$\pi(x, y, N) = ax^2 + bxy + cy^2 + dx + ey + f(N) \tag{1}$$

where  $f(N)$  is a linearly decreasing function of  $N$  so  $f(0)$  is chosen to make  $\pi(x, y, 0) > 0$  for all  $x, y \in [\alpha, \beta]$ . In the remainder of this section, we briefly describe the approaches of adaptive dynamics (Section 2.1) and the Maximum Principle (Section 2.2) as they apply to the stability analysis of monomorphic populations.

### 2.1 Adaptive Dynamics

The adaptive dynamics approach (Hofbauer and Sigmund, 1990) to stability of a monomorphism is based on a concept, introduced by Eshel and coworkers (e.g. Eshel, 1983; Eshel et al., 1997) for models without density dependence, that has come to be known as *convergence stable* (Christiansen, 1991; Taylor, 1989). A monomorphism  $x^*$  is convergence stable if every  $y$  sufficiently close (but not equal) to  $x^*$  has a neighborhood  $U(y)$  such that the fitness of any  $x \in U(y)$  when playing against  $y$  should be greater than that of  $y$  against  $y$  if and only if  $x$  is closer to  $x^*$  than  $y$ .

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<sup>2</sup>Unless otherwise stated, our variables  $x, y, x^*$  etc are all assumed to belong to a closed and bounded interval  $[\alpha, \beta]$ .

<sup>3</sup>Population size is assumed sufficiently large that finite population effects, such as those arising from the fact an individual does not interact with himself, can be ignored.

With density dependent adaptive dynamics (Marrow et al., 1996; Dieckmann and Law, 1996), these fitnesses are calculated when population size is at its equilibrium value for the monomorphism  $x$ . We first find the equilibrium density  $N(x_0)$  for  $x_0$ . That is, we solve  $\pi(x_0, x_0, N(x_0)) = 0$  for  $N(x_0)$  to obtain

$$N(x_0) = f^{-1}(-ax_0^2 + bx_0^2 + cx_0^2 + dx_0 + ex_0).$$

We assume  $x^* \in (\alpha, \beta)$  (i.e. in the interior of the trait space  $S$ ). So  $x^*$  is convergence stable if and only if there exists an  $\varepsilon > 0$  such that for all  $0 < |y - x^*| < \varepsilon$  there is a  $\delta > 0$  (which is usually taken less than  $\varepsilon$  and dependent on  $y$ ) such that

$$\pi(x, y, N(y)) > \pi(y, y, N(y)) = 0 \quad (2)$$

if and only if  $0 < |x - x^*| < |y - x^*|$ .

The intuition here is that mutations from  $y$  will only be successful if they are closer to the monomorphism, thereby driving the population to  $x^*$ . From (2), we consider the difference

$$\begin{aligned} \pi(x, y, N(y)) - \pi(y, y, N(y)) &= ax^2 + bxy + cy^2 + dx + ey + f(N(y)) - (ay^2 + by^2 + cy^2 + dy + ey + f(N(y))) \\ &= a(x^2 - y^2) + b(x - y)y + d(x - y) \\ &= (x - y)[a(x + y) + by + d]. \end{aligned}$$

If  $2ax^* + bx^* + d > 0$ , then  $\pi(x, y, N(y)) - \pi(y, y, N(y)) < 0$  if  $x^* < x < y$  and  $y$  is sufficiently close to  $x^*$  so that  $a(x + y) + by + d > 0$ . That is,  $x^*$  is not convergence stable. By a similar argument with  $2ax^* + bx^* + d < 0$ , we have that a necessary condition for  $x^*$  to be convergence stable is

$$2ax^* + bx^* + d = 0.$$

That is, as a function of  $x$ ,  $N(x, x^*, N(x^*))$  has a critical point when  $x = x^*$ .

Furthermore, if  $2a + b = 0$ , then  $d = 0$  and so

$$\pi(x, y, N(y)) - \pi(y, y, N(y)) = (x - y)[a(x + y) - 2ay] = a(x - y)^2.$$

Thus  $2a + b \neq 0$  if  $x^*$  is convergence stable. This implies the dominating term in  $\pi(x, y, N(y)) - \pi(y, y, N(y))$  is  $(2a + b)(x - y)(y - x^*)$  and so  $x^*$  is convergence stable if and only if

$$\begin{aligned} 2ax^* + bx^* + d &= 0 \\ 2a + b &< 0. \end{aligned}$$

These conditions for convergence stability can be rewritten in their more traditional form (e.g. Marrow et al., 1996) as

$$\begin{aligned} \frac{\partial}{\partial x} \pi(x, x^*, N(x^*))|_{x=x^*} &= 0 \\ \frac{\partial^2}{\partial x^2} \pi(x, y, N(y))|_{x=y=x^*} + \frac{\partial^2}{\partial x \partial y} \pi(x, y, N(y))|_{x=y=x^*} &< 0. \end{aligned}$$

If there are non quadratic terms in  $\pi(x, y)$ , then  $x^*$  may be convergence stable even if the last inequality is not strict (in which case higher order terms need to be considered).

Adaptive dynamics is concerned with the evolution of the mean strategy of the population. If the ecological time scale (i.e. the time scale for changes in population size) is much faster than the evolutionary time scale on which the mean strategy evolves, adaptive dynamics eliminates the ecological effect by assuming the coevolutionary system tracks equilibrium population size (see also the discussion at the beginning of this section). The canonical equation for the mean strategy evolution near a monomorphic  $x^*$  is then

$$\frac{dy}{dt} = k(y) \frac{\partial}{\partial x} \pi(x, y, N(y))|_{x=y} \quad (3)$$

where  $k(y)$  is a positive function that is related to the evolutionary time scale and to equilibrium size. For our quadratic payoff model, we have  $\frac{dy}{dt} = k(y) (2ay + by + d) = k(y)(2a + b)(y - x^*)$ . We see  $y$  is asymptotically stable for the canonical equation if and only if  $y = x^*$  where  $x^*$  is convergence stable.

## 2.2 The Maximum Principle

To simplify notation somewhat, we can shift the monomorphism  $x^* = \frac{-d}{2a+b}$  to 0 (and so  $x^* = 0 \in (\alpha, \beta)$ ) by replacing  $x$  and  $y$  with  $x - \frac{d}{2a+b}$  and  $y - \frac{d}{2a+b}$  respectively. This has the effect of eliminating the  $dx$  term in (1) so we now have<sup>4</sup>

$$\pi(x, y, N) = ax^2 + bxy + cy^2 + ey + f(N).$$

Vincent and coworkers (see Cohen et al., 1999 and the references therein) take a different approach to model dynamic stability in coevolutionary systems. Following Vincent et al. (1996), the strategy  $x^* = 0$  (for them, a coalition of one) is evolutionarily stable for the equilibrium size  $N(x^*)$  if, for all choices of finitely many mutant strategies  $\{x_2, \dots, x_r\}$ , the state  $(N(x^*), 0, \dots, 0)$  is asymptotically stable for the population dynamics

$$\dot{n}_i = n_i F_i(n_1, \dots, n_r) \quad (4)$$

where  $n_i$  is the size of that part of the population where individuals use strategy  $x_i$  (here  $x_1$  is identified with  $x^*$ ) and  $F_i(n_1, \dots, n_r)$  is the expected fitness of strategy  $x_i$  when the population state is  $(n_1, \dots, n_r)$ .

When applied to our model with quadratic payoff functions and random pairwise interactions that occur once per unit time for each individual, these fitnesses behave additively to yield

$$F_i(n_1, \dots, n_r) = \sum_{j=1}^m n_j \frac{\pi(x_i, x_j, N)}{N}$$

where  $N = \sum n_j$ .

To check stability, the  $r$ -dimensional system is linearized at  $(N(x^*), 0, \dots, 0)$ . This has the form of an upper triangular  $r \times r$  matrix with diagonal entries

$$N(x^*) \frac{\partial F_1}{\partial n_1}, F_2, \dots, F_r$$

where all these functions and partial derivatives are evaluated at  $(N(x^*), 0, \dots, 0)$ . For  $i > 1$ ,  $F_i = \pi(x_i, x^*, N(x^*)) = ax_i^2$  and  $\frac{\partial F_i}{\partial n_1} = \frac{\pi(x_i, x^*, N)}{\partial N} = f'(N(x^*)) < 0$ . Thus  $x^* = 0$  is evolutionarily stable if  $a < 0$  and unstable if  $a > 0$ .

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<sup>4</sup>This change of variables does shift  $e$  and  $f(N)$  by constants but these have no effect on the mathematical analysis.

Although the case  $a = 0$  is quite important since it forms the basis of models where fitness is linear in the individual's choice of strategy (i.e. when  $\pi(x, y, N)$  is linear in  $x$ ), in our context we disregard this possibility as degenerate and so conclude that  $x^* = 0$  is evolutionarily stable<sup>5</sup> according to Vincent and coworkers if and only if

$$a < 0.$$

The Maximum Principle is then equivalent to asserting that their “fitness generating function”,  $\pi(x, x^*, N(x^*))$ , has a strict maximum at  $x = x^* = 0$  as a function of  $x$ .

This condition seems to have no immediate connection to that of convergence stability. However, in the adaptive dynamics approach, it is often assumed (Marrow et al., 1996) no mutant strategies  $x$  can invade  $x^*$  (i.e. none have higher fitness than  $x^*$  when the population is monomorphic at  $x^*$ ). This is equivalent (assuming  $a \neq 0$ ) to  $a < 0$ . In fact, the condition  $a < 0$  was already assumed by Eshel (1983) when he combined convergence stability with it to define a continuously stable strategy (CSS)  $x^*$  to be one that satisfies the two conditions,  $a < 0, 2a + b < 0$ .<sup>6</sup>

On the other hand, it should be noted that adaptive dynamics is also quite interested in the convergence stable situation with  $a > 0$  since they view this as an instance of sympatric speciation or evolutionary branching (Doebeli and Dieckmann, 2000). Furthermore, Vincent et al. (1993) (see also Cohen et al., 1999) have developed a mean strategy dynamic through their population dynamic model above that leads back to the canonical equation. Nevertheless, it is clear that there are discrepancies between these two approaches to modeling monomorphic stability in coevolutionary systems.

### 3 Measure Dynamic

The coevolutionary dynamic we consider is a generalization of the population dynamic (4) to the space of distributions of the population over the continuous trait space  $S = [\alpha, \beta]$ . Specifically, let  $\mu$  be a finite measure defined on the  $\sigma$ -algebra  $\mathcal{B}$  of Borel subsets of  $S$ . When the population is in state  $\mu$ , the measure  $\mu(B)$  for any  $B \in \mathcal{B}$  is interpreted as the number of individuals using strategies in  $B$ . Then  $\mu(S)$  is the total population size which we assume to be positive. The fitness of an individual using strategy  $x \in S$  (this is also denoted as the Dirac delta measure  $\delta_x$ ) is then its expected payoff (plus the background fitness); namely,

$$\pi(x, \mu) = \frac{1}{\mu(S)} \int_S \pi(x, y, \mu(S)) \mu(dy) \quad (5)$$

For our quadratic payoff functions, we obtain

$$\pi(x, \mu) = \frac{1}{\mu(S)} \int_S (ax^2 + bxy + cy^2 + ey) \mu(dy) + f(\mu(S)) \quad (6)$$

The measure dynamic becomes

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<sup>5</sup>As mentioned in the Introduction, we prefer to designate this condition as stating  $x^*$  is a strict NE.

<sup>6</sup>This again requires quadratic fitness functions or else higher order terms may need to be examined in critical cases.

$$\frac{d\mu}{dt}(B) = \int_B \pi(x, \mu) \mu(dx) \quad (7)$$

The first question that arises is whether there are solutions to this dynamic. There are if  $\mu$  has finite support<sup>7</sup> at time 0 (i.e. if  $\mu = \sum_{i=1}^r n_i \delta_{x_i}$ ). Then  $\mu(S) = \sum n_j = N$  and  $\pi(x_i, \mu) = \frac{1}{N} \sum n_j \pi(x_i, x_j, N)$ . The dynamics (5) is then the same as (4) in Section 2.2.

But we are more interested in the case where  $\mu$  does not have finite (or discrete) support, perhaps given through a continuous density function. To show there are solutions to (5) in the general case, define the measure  $P$  as

$$P(B) = \mu(B)/\mu(S).$$

This is a probability measure (i.e.  $P(S) = 1$ ) and we can rewrite individual fitness of strategy  $x \in S$  as

$$\pi(x, P, \mu(S)) = \int_S (ax^2 + bxy + cy^2 + ey)P(dy) + f(\mu(S))$$

and population mean fitness as

$$\pi(P, P, \mu(S)) = \int_S \pi(x, P, \mu(S))P(dx) + f(\mu(S)). \quad (8)$$

A straightforward calculation using the quotient rule from calculus implies the measure dynamic for the probability space is

$$\frac{dP}{dt}(B) = \int_B (\pi(x, P, \mu(S)) - \pi(P, P, \mu(S)))P(dx). \quad (9)$$

Since  $\pi(x, P, \mu(S)) - \pi(P, P, \mu(S))$  does not depend on  $\mu(S)$ , we can ignore the background fitness  $f(\mu(S))$  in (9) and take the fitness function to have the form  $\pi(x, y, \mu(S)) = \pi(x, y)$ .

Dynamics of the form (9) with  $\pi(x, y) : S \times S \rightarrow R$  continuous have been shown (e.g. Bomze, 1991; Oechssler and Riedel, 2001) to have solutions  $P_t$  for all  $t \geq 0$  for any given initial condition where the derivative on the left-hand side is taken with respect to the variational norm.

Furthermore, evolution of the total population size satisfies  $\frac{d\mu}{dt}(S) = \int_S \pi(x, P_t, \mu(S))P_t(dx)\mu(S)$ . This is a one-dimensional non-autonomous dynamic with continuous vector field and so has a unique solution for every initial condition. Also, since  $\pi(x, P_t, 0) > 0$  and  $\pi(x, P_t, \mu(S)) < 0$  for all  $P_t$  if  $\mu(S)$  is sufficiently large, the solution is bounded. Moreover, if  $P_t$  evolves to  $P^*$ , then  $\mu_t$  converges to  $N^*P^*$  where  $N^*$  is the unique positive population size for which  $\int_S \pi(x, P^*, N^*)P^*(dx) = 0$ . That is, for convergence and stability of the measure dynamic (5), we can restrict attention to analyzing these same properties for (9) instead.

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<sup>7</sup>The support  $\text{supp } \mu$  of a measure  $\mu$  is the closed set of those  $x$  for which every open neighbourhood of  $x$  has positive measure.

## 4 The Dynamic on the Space of Probability Measures

Our primary aim in the next section is the complete characterization of the convergence and stability properties of the probability dynamic (9) for all quadratic payoff functions and  $S = [\alpha, \beta]$ . However, many of our results that lead to this characterization in Section 5 are true for more general classes of payoff functions and other trait spaces  $S$ . These general results are collected in the present section. They rely on two Lyapunov functions, the relative (or cross) entropy and the mean payoff that are developed in Sections 4.1 and 4.2 respectively.

For the sake of concreteness, we assume  $S$  is a compact metric space and  $\pi(x, y)$  is a continuous payoff function on  $S \times S$ . The measure dynamic is then the *replicator equation*

$$\frac{dP}{dt}(B) = \int_B (\pi(x, P) - \pi(P, P)) P(dx) \quad (10)$$

on the set of probability measures  $\Delta(S)$  on the Borel  $\sigma$ -algebra. This again has a unique solution  $P_t$  for all initial  $P_0 \in \Delta(S)$ .

An important issue is the topology to be used on  $\Delta(S)$ . We feel the *weak topology* captures best the essence of convergence in coevolutionary systems. This topology will mostly be applied to neighborhoods of monomorphic and dimorphic  $P^*$ . For a probability measure  $P^*$  with finite support  $\{x_1, \dots, x_m\}$ , we can take  $\varepsilon$ -neighbourhoods in the weak topology to be of the form

$$\{Q \in \Delta(S) : |Q(B_\varepsilon(x_i)) - P^*(x_i)| < \varepsilon \quad \forall i = 1, \dots, m\}$$

where  $B_\varepsilon(x)$  is the open ball of radius  $\varepsilon$  centered at  $x$ . In particular, two monomorphisms  $\delta_{x_1}$  and  $\delta_{x_2}$  are within  $\varepsilon$  of each other if and only if the Euclidean distance between these points is less than  $\varepsilon$ . In the following all topological notions are taken for this weak topology, unless otherwise stated.

### 4.1 Local Superiority

When  $S = \{x_1, \dots, x_m\}$  is finite, the space of probability measures  $\Delta(S)$  is the set  $\{q = (q_1, \dots, q_m) \mid \sum_{j=1}^m q_j = 1\}$  of probability vectors where  $q_i$  is the proportion of the population using the  $i$ th strategy. The probability measure dynamic is then the standard replicator game dynamic (Hofbauer and Sigmund, 1998) with  $m \times m$  payoff matrix whose entries are  $\pi(x_i, x_j)$ . A standard way to prove the local asymptotic stability of a strategy  $p^*$  is by showing that it is a “matrix-ESS”,<sup>8</sup> i.e., that

$$\pi(p^*, q) > \pi(q, q) \quad (11)$$

for all  $q$  close to  $p^*$ . Here closeness is meant either on each ray connecting  $p^*$  with another strategy  $p$ , or simply in a Euclidean neighborhood. Whereas these various versions of closeness are all equivalent in finite games, there are many different versions for games with an infinite trait space  $S$  (see also the Remark in Section 5.1). The weaker the topology (or more general nearness concept) on  $\Delta(S)$ , the stronger the corresponding version of “ESS”. Although it is our contention that the generalization of (11) to infinite

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<sup>8</sup>As mentioned earlier, the term ESS is overused in the literature and so may have several meanings for some readers. On the other hand, for games with a finite trait space, there is one universally accepted meaning originating with Maynard Smith (1982) as an evolutionarily stable strategy of the  $m \times m$  payoff matrix  $A$  (hence a matrix-ESS).

trait spaces with respect to the weak topology deserves the ESS designation, we have used the phrase “locally superior in the weak topology” instead for this concept in the following definition to avoid confusion. Also, the notion of local superiority (Weibull, 1995) is now well-established for the case of a finite trait space  $S$  as an alternative phrase to denote a matrix-ESS.<sup>9</sup>

**Definition 1**  $P^* \in \Delta(S)$  is a locally superior strategy (in the weak topology) if, for all  $Q \neq P^*$  sufficiently close to  $P^*$ ,

$$\pi(P^*, Q) > \pi(Q, Q) \quad (12)$$

We say  $P^*$  is globally superior if this inequality is true for all  $Q \neq P^*$ .

Our first main result given in the following theorem uses the concept of *cross entropy*,<sup>10</sup> as developed by Bomze (1991) for probability measure dynamics. If  $P$  is absolutely continuous with respect to  $Q$ , and whose Radon-Nikodym derivative  $\phi = \frac{dP}{dQ}$  is bounded (i.e., there is a  $C > 0$  such that  $P(A) \leq CQ(A)$  for all Borel sets  $A \subset S$ ) then the cross entropy

$$L(Q) := K_{Q:P} = \int_S \log \frac{dP}{dQ} P(dx) = \int_S \phi \log \phi Q(dx)$$

is defined, nonnegative and finite. Lemma 2 in Bomze (1991) shows that  $L(Q_t)$  is defined along the orbit of  $Q$ , and its time derivative satisfies

$$\frac{d}{dt} L(Q_t) = -\pi(P, Q_t) + \pi(Q_t, Q_t) \quad (13)$$

for all  $t \geq 0$ . In particular, the cross entropy is decreasing if  $P$  is locally superior and  $Q_t$  is sufficiently close to  $P$ , a key fact in the proof of the following theorem.

**Theorem 2** If  $P^*$  is a locally superior strategy, which is Lyapunov stable, then for any initial  $Q$  sufficiently close to  $P^*$  with  $\text{supp } Q \supseteq \text{supp } P^*$ ,  $Q_t \rightarrow P^*$  as  $t \rightarrow +\infty$ . Moreover, if  $P^*$  is globally superior and Lyapunov stable then for any initial  $Q \in \Delta(S)$  with  $\text{supp } Q \supseteq \text{supp } P^*$ ,  $Q_t \rightarrow P^*$  as  $t \rightarrow +\infty$ .

*Proof.* Let  $U_1$  be a compact neighborhood of  $P^*$  such that  $\pi(P^*, P) - \pi(P, P) > 0$  holds for all  $P \in U_1 \setminus \{P^*\}$ . Since  $P^*$  is Lyapunov stable there is a neighborhood  $U_2$  of  $P^*$  such that for all  $Q \in U_2$  and  $t \geq 0$  we have  $Q_t \in U_1$ .

Suppose now that  $P^*$  is not an  $\omega$ -limit point of such a  $Q$ . Then there is an open neighborhood  $U_3$  of  $P^*$  with  $Q_t \notin U_3$  for all  $t \geq 0$ . By compactness  $\pi(P^*, P) - \pi(P, P) \geq 2c > 0$  for some  $c > 0$  and all  $P \in U_1 \setminus U_3$ . By continuity, for all  $\tilde{P}$  close enough to  $P^*$  (in the weak topology) we have

$$\pi(\tilde{P}, P) - \pi(P, P) \geq c > 0 \quad \forall P \in U_1 \setminus U_3. \quad (14)$$

Since  $\text{supp}(P^*) \subseteq \text{supp}(Q)$ , there is such a  $\tilde{P}$  which is absolutely continuous with respect to  $Q$  and whose Radon-Nikodym derivative  $\frac{d\tilde{P}}{dQ}$  is bounded.<sup>11</sup> By (13) and (14), the cross

<sup>9</sup>In Oechssler and Riedel (2002), locally superior with respect to the weak topology is called “evolutionarily robust”.

<sup>10</sup>In the finite case this cross entropy corresponds to the function  $L(q) = \sum_i p_i^* \log \frac{p_i^*}{q_i}$  which like  $\prod_i q_i^{p_i^*}$  is the well-known Lyapunov function near a matrix-ESS  $p^*$ .

<sup>11</sup>Such a  $\tilde{P}$  exists since the weak\* closure of the set of probability measures that are absolutely continuous with respect to  $Q$  and have bounded Radon-Nikodym derivative is the set of all probability measures whose support is contained in  $\text{supp } Q$ . For example, for  $s \in \text{supp } Q$ , and  $U_n$  the  $\frac{1}{n}$ -neighborhood of  $s$ , the measures with density  $\frac{1}{Q(U_n)} \chi_{U_n}$  converge to  $\delta_s$ .

entropy  $L(Q) := K_{Q;\bar{P}}$  is defined and satisfies

$$\frac{d}{dt}L(Q_t) \leq -c < 0$$

along the solution  $Q_t$  for  $t \geq 0$ . Hence  $L(Q_t) \rightarrow -\infty$ , a contradiction to  $L(Q) \geq 0$ .

This shows that  $P^*$  is an  $\omega$ -limit point of  $Q$ . Since  $P^*$  is Lyapunov stable, it is the unique  $\omega$ -limit point of  $Q$  and hence  $Q_t \rightarrow P^*$ . Finally, if  $P^*$  is globally superior then take  $U_1 = U_2 = \Delta(S)$ . This completes the proof.

This result generalizes Theorem 3 of Oechssler and Riedel (2002) who proved it for monomorphisms  $P^* = \delta_{x^*}$  and initial  $Q$  with  $Q(\{x^*\}) > 0$  in place of our weaker assumption  $x^* \in \text{supp } Q$ . It is an open problem whether the additional assumption of Lyapunov stability is really needed. When the trait space is finite, Lyapunov stability follows from local superiority.

It is essential  $\text{supp } Q \supseteq \text{supp } P^*$  for the conclusions given in Theorem 2 to be valid. This is due to the fact that the measure dynamic (10) shares the same property as (4) in that its support is invariant for all  $t \geq 0$ .<sup>12</sup> However, local asymptotic stability of  $x^*$  in the dynamic (4) does not imply the corresponding discrete measure converges weakly to  $\delta_{x^*}$  since this would require (4) to be globally asymptotically stable for all finite choices of strategies that are sufficiently close to  $x^*$ .

**Remark.** The following observations are useful to identify locally/globally superior strategies. First, every locally superior strategy  $P^*$  is a Nash equilibrium (NE) (i.e.  $\pi(P^*, P^*) \geq \pi(Q, P^*)$  for all  $Q \in \Delta(S)$ ). Indeed, given  $Q \in \Delta(S)$ , for all  $\varepsilon$  sufficiently close to zero

$$\begin{aligned} 0 &\leq \pi(P^*, P^* + \varepsilon(Q - P^*)) - \pi(P^* + \varepsilon(Q - P^*), P^* + \varepsilon(Q - P^*)) \\ &= \varepsilon\pi(P^* - Q, P^* + \varepsilon(Q - P^*)) \end{aligned}$$

Thus, for  $\varepsilon \rightarrow 0$ , we get  $0 \leq \pi(P^* - Q, P^*)$ .

Second, if the game is negative definite (i.e.  $\pi(P - Q, P - Q) < 0$  for all  $Q \neq P$ ) then there exists a globally superior strategy. To see this, let  $P^*$  be any NE. Then, for all  $Q \neq P^*$

$$\begin{aligned} \pi(P^*, Q) - \pi(Q, Q) &= \pi(P^* - Q, P^*) + \pi(P^* - Q, Q - P^*) \\ &\geq \pi(P^* - Q, Q - P^*) > 0. \end{aligned}$$

Conversely, if  $P^*$  is locally superior (on each ray connecting  $P^*$  with another strategy  $Q$ ) with full support then the game is negative definite.<sup>13</sup>

## 4.2 Potential Games

Consider now a symmetric payoff function  $\pi : S \rightarrow S$ , i.e.  $\pi(x, y) = \pi(y, x)$ , that is assumed to be continuous. Note that, for quadratic fitness functions and  $S = [\alpha, \beta]$ , the dynamic (9) is unchanged if we take the symmetric version  $\pi(x, y) = ax^2 + bxy + ay^2$  as our payoff function. By common game-theoretic usage, games with symmetric payoff matrices are known as ‘‘potential’’ games.

<sup>12</sup>In fact,  $Q_0$  and  $Q_t$  are mutually absolutely continuous measures, as shown by Bomze (1991).

<sup>13</sup>If  $P^*$  is globally superior but does not have full support then the game is not necessarily negative definite, as already games with two strategies show. A game is negative definite if and only if the mean payoff function  $P \mapsto \pi(P, P)$  is strictly concave on  $\Delta$ . Our quadratic games are negative semi-definite if and only if  $b \leq 0$ .



By the symmetry of  $\pi$ , the expected payoff satisfies

$$\begin{aligned} \frac{d}{dt}\pi(P, P) &= 2 \int_S \int_S \pi(x, y) [\pi(x, P) - \pi(P, P)] P(dx) P(dy) \\ &= 2 \int_S (\pi(x, P) - \pi(P, P))^2 P(dx) \geq 0. \end{aligned} \quad (15)$$

By the continuity of  $\pi(x, P)$  in  $x$ , there is equality if and only if  $\pi(x, P) = \pi(P, P)$  for all  $x$  in the support of  $P$  if and only if  $P$  is a rest point of (10).<sup>14</sup> Thus  $\pi(P, P)$  is a strict Lyapunov function on  $\Delta(S)$  in that it is strictly increasing under (10) unless at equilibrium.

Since  $\Delta(S)$  is compact in the weak topology and  $\pi(P, P)$  is a continuous function,  $P^*$  will be Lyapunov stable if it is an isolated local maximizer of  $\pi(P, P)$  with respect to the weak topology. For finite games, a strategy  $P^*$  is a local maximizer of  $\pi(P, P)$  if and only if it is locally superior, see e.g. Hofbauer and Sigmund (1998). In general only the following direction is true, as shown by the counterexample given in Remark of Section 5.1.

**Lemma 3** *If  $P^*$  is locally superior then it is an isolated local maximizer of the mean fitness function  $\pi(P, P)$ .*

*Proof.* Since  $P^*$  is a Nash equilibrium,  $\pi(P^*, P^*) \geq \pi(Q, P^*) = \pi(P^*, Q) > \pi(Q, Q)$  for all  $Q$  sufficiently close to  $P^*$ .

Combining the above with Theorem 2 we get

**Theorem 4** *If  $P^*$  is a locally superior strategy (with respect to the weak topology) in a potential game, then  $P^*$  is Lyapunov stable and for any initial  $Q$  sufficiently close to  $P^*$  with  $\text{supp } Q \supseteq \text{supp } P^*$ ,  $Q_t \rightarrow P^*$ . If  $P^*$  is globally superior with  $\text{supp } Q \supseteq \text{supp } P^*$ , then  $Q_t \rightarrow P^*$ .*

This theorem was proved by Bomze (1990) in the special case where  $\pi(x, y)$  depends only on  $x$  and by Oechssler and Riedel (2002) when  $\pi(x, y)$  is symmetric and  $P^*$  is a monomorphism.

## 5 Dynamic Stability for Quadratic Payoff Functions

Let us apply the general theory above to our quadratic payoff function  $\pi(x, y) = ax^2 + bxy + ay^2$  where the interesting monomorphism is  $x^* = 0$  and we assume  $a \neq 0$ . For this, the following formulas for  $\pi(P, Q)$  etc. in terms of the mean  $E(P)$  and the variance  $\text{Var}(P)$  of a probability measure  $P$  are useful. It is even convenient to consider higher order moments: let  $P_k = \int x^k P(dx)$  be the  $k$ th moment of  $P$ . Then  $P_1 = E(P)$  and  $P_2 = \text{Var}(P) + P_1^2$ . We get  $\pi(x, P) = ax^2 + bxP_1 + aP_2$ ,

$$\begin{aligned} \pi(P, Q) &= aP_2 + bP_1Q_1 + aQ_2 = \\ &= a(\text{Var}(P) + E(P)^2 + \text{Var}(Q) + E(Q)^2) + bE(P)E(Q). \end{aligned} \quad (16)$$

$$\pi(P, P) = 2a\text{Var}(P) + (2a + b)E(P)^2, \quad (17)$$

$$\pi(x, P) - \pi(P, P) = a(x^2 - P_2) + b(xP_1 - P_1^2), \quad (18)$$

$$\pi(P - Q, P - Q) = b(E(P) - E(Q))^2. \quad (19)$$

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<sup>14</sup>This is the extension to continuous strategy spaces of one part of the Fundamental Theorem of Natural Selection that states mean fitness increases unless at equilibrium.

Our classification of the stability of  $\delta_0$  in Sections 5.1 and 5.2 is based first on whether  $a$  is negative or positive and then on subclasses depending on the value of  $b$ . This classification scheme is similar to that given by Geritz et al. (1997) and Diekmann (2002) for the adaptive dynamics approach.

One reason for using this classification scheme is that the subspace of probability measures that are symmetric about 0 is invariant for our quadratic payoff functions, and on this subspace, the variance is increasing if  $a > 0$  and decreasing if  $a < 0$ . To see this, we derive from (18) and

$$\dot{P}_k = \int x^k d\dot{P} = \int x^k [\pi(x, P) - \pi(P, P)] P(dx)$$

the differential equations for the moments

$$\dot{P}_1 = aP_3 + (b - a)P_1P_2 - bP_1^3 \quad (20)$$

$$\dot{P}_2 = aP_4 - aP_2^2 + bP_1P_3 - bP_1^2P_2 \quad (21)$$

$$\dot{P}_3 = aP_5 - aP_2P_3 + bP_1P_4 - bP_1^2P_3 \quad (22)$$

...

Obviously, if the initial  $P$  is symmetric around 0, then so is  $P_t$ , hence the odd moments vanish and the variance satisfies  $\dot{P}_2 = a(P_4 - P_2^2)$ . Since  $P_4 \geq P_2^2$  (with equality for point measures), variance increases if  $a > 0$  and decreases if  $a < 0$ . In particular, this shows instability of  $\delta_0$  for  $a > 0$ .

## 5.1 Case 1: $a < 0$

This is the case where  $x^* = 0$  is a strict NE, i.e.  $\pi(0, 0) > \pi(x, 0)$  for all  $x \neq 0$ .

### 5.1.1 Case 1a: $a + b < 0$ .

From (17), we see that  $\pi(P, P) \leq 0$  with equality if and only if  $P = P^* = \delta_0$ . Thus  $P^*$  is the unique global maximizer of the mean fitness function (and there are no other local maximizers). Hence  $P^* = \delta_0$  is Lyapunov stable by section 4.2. Furthermore, from (18), if  $Q \neq P^*$ , then

$$\pi(\delta_0, Q) - \pi(Q, Q) = -a\text{Var}(Q) - (a + b)E(Q)^2 > 0.$$

Thus  $P^* = \delta_0$  is globally superior and by Theorem 2 it attracts all initial  $Q_0$  that have  $0 \in \text{supp } Q_0$ .

### 5.1.2 Case 1b: $2a + b < 0 \leq a + b$ .

We still have  $P^* = \delta_0$  as the unique global maximizer of mean fitness and so Lyapunov stable but it is no longer locally superior. However, the following theorem that uses an iterated domination argument between pure strategies shows  $P^*$  still attracts all initial  $Q_0$  with full support.

**Theorem 5** *Suppose  $a < 0$  and  $a + 2b < 0 \leq a + b$ . If the support of  $Q_0$  is an interval that contains  $x^* = 0$ , then  $Q_t$  converges to  $\delta_0$  (in the weak topology).*

**Proof.** Without loss of generality, assume  $\text{supp } Q \supseteq [0, \beta]$ . Let  $x_0 = -\frac{b\beta}{2a}$ . Then  $0 < x_0 < \beta$ . Take  $A = [x_0 + 3\varepsilon, \beta]$  and  $B = [x_0 + \varepsilon, x_0 + 2\varepsilon]$  where  $x_0 + 3\varepsilon < \beta$  and  $\varepsilon$  is positive.

Then, another application of the quotient rule yields

$$\frac{d}{dt} \left( \frac{Q(B)}{Q(A)} \right) = \frac{1}{Q(A)^2} \int_S \left[ \int_A \int_B (\pi(x, z) - \pi(y, z)) Q(dx) Q(dy) \right] Q(dz). \quad (23)$$

For  $x \in B, y \in A, z \in S$ , we have

$$\pi(x, z) - \pi(y, z) = ax^2 + bxz - ay^2 - byz = (x - y)[a(x + y) + bz] > -2a\varepsilon^2 > 0. \quad (24)$$

Thus,  $\frac{d}{dt} \left( \frac{Q(B)}{Q(A)} \right) \geq -\frac{Q(B)}{Q(A)} 2a\varepsilon^2 > 0$ . Thus  $\frac{d}{dt} \left( \frac{Q(B)}{Q(A)} \right)$  grows to infinity with exponential order. In particular,  $\lim Q_t(A)$  is 0 as  $t$  approaches infinity. Now choose  $\varepsilon$  so that  $x_0 + 3\varepsilon = (x_0 + \beta)/2$  (i.e.  $\varepsilon = (\beta - x_0)/6$ ). Then  $\lim Q_t([x_0 + \beta)/2, \beta]$  is 0. Now suppose we have shown  $\lim Q_t[\gamma, \beta] = 0$  for some  $0 < \gamma < \beta$ . We will iterate the above argument to show  $\lim Q_t[\frac{x_0 + \beta}{2}\gamma, \gamma] = 0$ . Take  $A = [-\beta\gamma/2a + 3\varepsilon, \gamma]$  and  $B = [-\beta\gamma/2a + \varepsilon, -\beta\gamma/2a + 2\varepsilon]$  where  $-\beta\gamma/2a + 3\varepsilon < \gamma$ . Then

$$\begin{aligned} \frac{d}{dt} \left( \frac{Q(B)}{Q(A)} \right) &= \frac{1}{Q(A)^2} \int_{[\gamma, \beta]} \left[ \int_A \int_B (\pi(x, z) - \pi(y, z)) Q(dx) Q(dy) \right] Q(dz) \\ &\quad + \frac{1}{Q(A)^2} \int_{S - [\gamma, \beta]} \left[ \int_A \int_B (\pi(x, z) - \pi(y, z)) Q(dx) Q(dy) \right] Q(dz) \\ &\geq -(Q([\gamma, \beta]2K + Q(S - [\gamma, \beta])2a\varepsilon^2) \frac{Q(B)}{Q(A)}) \\ &\geq -a\varepsilon^2 \frac{Q(B)}{Q(A)} \end{aligned}$$

for  $t$  sufficiently large. Here  $K = \max_{x, y \in S} |\pi(x, y)|$ . In particular,  $\lim Q_t(A) = 0$ . Thus, by iteration, we can take  $\gamma = [(x_0 + \beta)/2]^n \beta$  for all  $n \in \mathbb{Z}$  and so  $\lim Q_t([\gamma, \beta]) = 0$  for all  $\gamma > 0$ .

A similar argument on the interval  $[\alpha, \gamma]$  with  $\gamma < 0$  completes the proof.

In game-theoretic terms, inequality (24) asserts that every  $x \in B$  strictly dominates every  $y \in A$ . The proof is then essentially the iterated elimination of strictly dominated pure strategies. This technique is well-known for games with finite trait space (e.g. Samuelson and Zhang, 1992; Hofbauer and Weibull, 1996) but this seems to be the first instance where it is used in games with a continuum of pure strategies.

The method of proof can extend the statement of the Theorem to measures that do not have full support as long as the ‘‘gap’’ between points in the support of  $Q_0$  is not too great. This gap must decrease as we get closer to  $x^*$ . In particular, if one wants to approximate the measure dynamic with a discrete version similar to (4), then one needs the grid to become finer as we approach  $x^*$ . Otherwise, say if the grid is uniform, the most we can expect is that the support of  $Q_t$  will approach an interval containing  $x^*$  and that this interval will approach  $x^*$  as the number of points in the grid increases.

### 5.1.3 Case 1c: $2a + b = 0$ .

$\pi(P, P) = 0$  for all  $P = \delta_x$  with  $x \in [\alpha, \beta]$ . In this degenerate case the payoff function  $\pi(x, y) = a(x - y)^2$  is translation invariant. Every  $\delta_s$  is a strict NE and maximizer of  $\pi(P, P)$ .

### 5.1.4 Case 1d: $2a + b > 0$ .

Here  $P = \delta_0$  is a saddle point, and  $P = \delta_\alpha$  and  $P = \delta_\beta$  are the only local maximizers of  $\pi(P, P)$ . These endpoints are also locally superior with respect to those  $Q$  whose support is either  $[\alpha, -\varepsilon]$  or  $[\varepsilon, \beta]$  respectively. This gives us a bistable situation where some initial  $Q_0$  close to  $\delta_0$  evolve to one monomorphism supported at one endpoint and some to the other. In fact, by continuity of  $\pi(Q, Q)$ ,  $\delta_\beta$  attracts those  $Q_0$  with full support that have  $Q_0([\alpha, 0])$  sufficiently small.

**Remark.** The four subcases of this section clarify the relevance of the CSS concept and the importance of the topology chosen for  $\Delta(S)$ .

First, Cases 1a and 1b combine to show that a CSS  $x^* = 0$  in the interior of  $[\alpha, \beta]$  (i.e.  $a < 0$  and  $2a + b < 0$ ) is Lyapunov stable and every initial  $Q$  with full support converges to  $\delta_0$  in the weak topology. Moreover, it is already clear from (17) that  $\delta_0$  is unstable if  $2a + b > 0$ . These results give a strong measure theoretic justification of the CSS concept that lies at the heart of adaptive dynamics.

It must be pointed out, however, that there is a significant difference between the basins of attraction of  $\delta_0$  that are CSS depending on the sign of  $a + b$ . If  $a + b < 0$ ,  $\delta_0$  is known as a *good invader* (Kisdi and Meszéna, 1995) or a *neighborhood invader strategy* (NIS) (McKelvey and Apaloo, 1995; Apaloo, 1997). This latter condition can be used to prove convergence in Case 1a with a single domination argument (Cressman, 2003) that avoids the entropy technique used in the proof of Theorem 2. To illustrate this difference, suppose  $Q_0$  is a dimorphism with support  $\{0, s\}$ , with  $0 < s \leq \beta$ . Then  $a + b < 0$  implies  $Q_t$  converges to  $\delta_0$  in the weak topology.

On the other hand, if  $a + b > 0$ , the dynamic (10) restricted to the support  $\{0, s\}$  is bistable: with  $q = Q_t(\{0\})$  and  $1 - q = Q_t(\{s\})$  we get

$$\begin{aligned} \dot{q} &= q(1 - q)[q(\pi(0, 0) - \pi(s, 0)) + (1 - q)(\pi(0, s) - \pi(s, s))] \\ &= q(1 - q)s^2[bq - (a + b)] \end{aligned} \quad (25)$$

Hence  $\dot{q} < 0$  if  $0 < q < (a + b)/b$ . (Note that  $0 < (a + b)/b < 1/2$  which means that  $\delta_0$  has the larger basin of attraction on this line than  $\delta_s$ .) Thus,  $q \rightarrow 0$  if  $q$  is sufficiently small initially. This result also follows from (17) since  $\pi(q\delta_0 + (1 - q)\delta_s, q\delta_0 + (1 - q)\delta_s) = s^2(bq^2 - 2(a + b)q + 2a + b)$  which is a quadratic function of  $q$  with minimum at  $q = (a + b)/b$ . Since  $\pi(Q, Q)$  is increasing,  $Q_t \rightarrow \delta_s$  if  $0 < Q_0(\{0\}) < (a + b)/b$ . Furthermore, by continuity of  $\pi(Q, Q)$  in the weak topology, for  $\varepsilon$  sufficiently small, if  $\text{supp } Q_0 = [-\varepsilon, \varepsilon] \cup [s - \varepsilon, s + \varepsilon]$  and  $Q_0([s - \varepsilon, s + \varepsilon]) < (a + b)/b$ , then  $Q_t([s - \varepsilon, s + \varepsilon]) \rightarrow 1$  as  $t \rightarrow \infty$  (actually,  $Q_t$  converges weakly to  $\delta_{s-\varepsilon}$  by the argument in the proof of Theorem 5).

The above analysis also shows that the convergence results of Theorem 4 need not be true if we only assume  $P^*$  is the unique global maximizer of the expected payoff  $\pi(P, P)$ .

Cases 1c and 1d illustrate the importance of the chosen topology for convergence and stability results. Specifically,  $\delta_0$  is locally superior with respect to the variational norm<sup>15</sup> if

<sup>15</sup>This norm corresponds to the strong topology with respect to which local superiority is often called “strongly uninventable” (e.g. Bomze, 1991).

and only if  $a < 0$ . That is, even in these last two cases when mean fitness at  $\delta_0$  is less than that of any other monomorphism,  $\delta_0$  is locally superior in the strong topology (in fact, every  $\delta_s$  in Case 1c is locally superior). Thus,  $\delta_0$  is Lyapunov stable in this strong topology, and further  $Q_t$  converges weakly to  $\delta_0$ , if  $Q_0(\{0\})$  is close to 1 as shown by Oechssler and Riedel (1990).

## 5.2 Case 2: $a > 0$

From (17), any local maximizer of  $\pi(P, P)$  must have as large a variance as possible given  $E(P^*) =: E$ . Thus the support of  $P^*$  is contained in  $\{\alpha, \beta\}$ . In fact,  $P_E^* = p_1^* \delta_\beta + p_2^* \delta_\alpha$  where  $p_1^* = \frac{E-\alpha}{\beta-\alpha}$  and  $p_2^* = \frac{\beta-E}{\beta-\alpha}$ . Thus, we need to maximize

$$f(E) = \text{Var}(P_E^*) = 2a(p_1^*(E - \beta)^2 + p_2^*(E - \alpha)^2) + (2a + b)E^2$$

for  $E \in [\alpha, \beta]$ . This expression simplifies to

$$f(E) = -2a(E - \alpha)(E - \beta) + (2a + b)E^2 = bE^2 + 2a(\alpha + \beta)E - 2a\alpha\beta.$$

If  $b < 0$ , this is a downwards parabola that has a unique maximum at  $E^* = -\frac{a}{b}(\alpha + \beta)$ . Depending on whether  $E^*$  is outside or inside the interval  $S$ , the unique local maximizer is given by  $P^* = \delta_\beta$  if  $(a + b)\beta + a\alpha \geq 0$ , by  $P^* = \delta_\alpha$  if  $(a + b)\alpha + a\beta \leq 0$  and by the above dimorphism if  $(a + b)\beta + a\alpha < 0$  and  $(a + b)\alpha + a\beta > 0$ . Since  $P^*$  is a NE and the game is negative semidefinite by (19),

$$\begin{aligned} \pi(P^*, Q) - \pi(Q, Q) &= \pi(P^* - Q, P^*) + \pi(P^* - Q, Q - P^*) \\ &\geq \pi(P^* - Q, Q - P^*) = -b(E(P^*) - E(Q))^2 \geq 0. \end{aligned}$$

Furthermore, if  $E(P^*) = E(Q)$ , then  $\pi(P^*, Q) - \pi(Q, Q) = a(\text{Var}(P^*) - \text{Var}(Q))$  from (16) and (17). Thus,  $\pi(P^*, Q) - \pi(Q, Q) > 0$  unless  $P^*$  and  $Q$  have the same mean and variance. Since  $P^*$  is the unique probability measure that has the largest variance for a given mean,  $P^*$  is globally superior. By Theorem 4,  $P^*$  is Lyapunov stable and attracts every  $Q_0$  whose support contains that of  $P^*$ .

### 5.2.1 Case 2a: $2a + b < 0$ .

In this case we have the situation which is often referred to in the adaptive dynamics literature as *evolutionary branching* (Geritz et al, 1997). It is straightforward to show that  $P^*$  is then a dimorphism. By the above reasoning for  $b < 0$ ,  $P^*$  is Lyapunov stable and attracts any initial  $Q(0)$  whose support includes  $\{\alpha, \beta\}$  since it is globally superior.

### 5.2.2 Case 2b: $2a + b \geq 0$ and $b < 0$ .

$P^*$  is still globally superior but could be either a dimorphism or one of the monomorphisms  $\delta_\beta$  or  $\delta_\alpha$ .

### 5.2.3 Case 2c: $b > 0$ .

In this final case,  $f(E)$  is an upwards parabola which has  $\delta_\beta$  and  $\delta_\alpha$  as the local maximizers of  $\pi(P, P)$ . This is again the bistable situation as in Case 1d.

### 5.3 Normal Distributions with $S = \mathbf{R}$

Following Oechssler and Riedel (2002), we consider special solutions  $Q_t$  of (10) with  $S = \mathbf{R}$  that are normal distributions with mean  $m(t)$  and variance  $V(t)$ , i.e.,

$$\frac{dQ_t}{dx} = \frac{1}{\sqrt{2\pi V(t)}} e^{-\frac{(x-m(t))^2}{2V(t)}} \quad (26)$$

From  $\frac{dP}{dP}(x) = \pi(x, P) - \pi(P, P)$  we obtain

$$-\frac{d}{dt} \left[ \frac{(x - m(t))^2}{2V(t)} + \frac{1}{2} \log V(t) \right] = a(x^2 - m(t)^2) + bm(t)(x - m(t)) - aV(t)$$

which reduces to

$$\dot{V} = 2aV^2 \quad \dot{m} = (2a + b)mV \quad (27)$$

Hence (26) are solutions of (10) if and only if the mean and variance satisfy the differential equations (27).

This illustrates nicely the meaning of the two crucial parameters  $a$  and  $2a + b$ : the equation for the mean resembles the canonical equation of adaptive dynamics. Note that, for  $a > 0$ , the variance goes to infinity in finite time. Such a blow up is possible only for non-compact  $S$ .

## 6 Non-Quadratic Payoff Functions

The method developed in Section 4 and the proof of Theorem 5 can be used to analyze probability measure dynamics beyond the quadratic payoff functions considered in Section 5. For instance, the domination argument used in the proof of Theorem 5 remains valid if we restrict the support of  $Q_0$  to be an interval sufficiently close to  $x^*$  so that the quadratic terms in the Taylor expansion of  $\pi(x, y)$  about  $(x^*, x^*)$  are predominant. In particular, a CSS that is not an NIS continues to attract all such initial  $Q_0$ . Moreover, the one-time domination argument of Cressman (2003) (see Remark in Section 5.1) shows the same result for arbitrary support sufficiently close to  $x^*$  when  $x^*$  is CSS and NIS. Thus, the CSS condition will continue to guarantee local convergence in the absence of the symmetry implied by only quadratic terms in the payoff function - what is lost is whether the CSS remains Lyapunov stable. Conversely, if  $x^*$  is not CSS then a reverse domination argument shows instability of  $\delta_{x^*}$ .

In the other case of particular interest to adaptive dynamics (i.e. the evolutionary branching of Case 2a), a convergence stable  $x^*$  with  $\pi_{xx}(x^*, x^*) > 0$  will be unstable in the measure dynamic whether  $\pi(x, y)$  is quadratic or not. What is not so clear is what the measure dynamic will evolve to in this situation without the quadratic payoffs that imply a globally stable dimorphism emerges that is supported on the endpoints of the trait space  $S$  since mean fitness grows as variance increases. However, our results apply to nonquadratic payoff functions of the form  $\pi(x, y) = \phi(x) + bxy + \phi(y)$  with  $b < 0$  and  $\phi$  an arbitrary smooth function. Since such games are negative semidefinite, if there is a unique maximizer  $P^*$  of the mean fitness then  $P^*$  is globally superior and hence attracts all initial  $Q$  with full support. If  $\phi_{xx}(0) > 0$  then there is no monomorphic NE, and hence  $P^*$  is supported on at least two traits. As an example take  $b = -5$  and  $\phi(x) = 2x^2 - x^4$  on the trait space  $S = \mathbf{R}$ . If  $\text{supp } Q_0$  contains both maxima of  $\phi$  (i.e.  $\{-1, 1\}$ ), the theory

from Section 4 proves  $Q_t$  converges to the Lyapunov stable dimorphism  $P^* = \frac{1}{2}\delta_1 + \frac{1}{2}\delta_{-1}$  in the weak topology. This follows from the fact  $P^*$  is globally superior since

$$\begin{aligned} & \pi(P^*, Q) - \pi(Q, Q) = \\ &= \int_S \int_S (\phi(x) - 5xy + \phi(y)) P^*(dx) Q(dy) - \int_S \int_S (\phi(x) - 5xy + \phi(y)) Q(dx) Q(dy) \\ &= \frac{1}{2}(\phi(1) + \phi(-1)) + \int_S \phi(y) Q(dy) - (2 \int_S \phi(y) Q(dy) - E(Q)^2) > 0 \end{aligned}$$

unless  $\text{supp } Q = \{-1, 1\}$  and  $E(Q) = 0$  (i.e. unless  $Q = P^*$ .)

## 7 Discussion

This paper is meant to introduce measure dynamics as a means to model coevolutionary systems and to compare this theory to other, more established, approaches such as adaptive dynamics. The comparison is most complete in the basic model of coevolution where stability of a monomorphism in a single species with a one-dimensional continuous trait space is analyzed. This necessarily entailed several simplifying assumptions that we would like to address in this concluding section.

We have already discussed to some extent the issue of symmetric payoff functions in Section 6. There is no doubt symmetry is an important tool in our development of the theory for a general setting in Section 4 (see especially Lemma 3 and its proof that shows a locally superior strategy is Lyapunov stable). On the other hand, the quadratic approximation to fitness functions about a monomorphism  $x^*$  provide this symmetry and can be used to describe local behavior of the dynamics of probability measures with support near  $x^*$ .

Dependence on total population size (i.e. density dependence) is included in our model by assuming a background fitness that is strategy independent. This has the effect that density dependence essentially disappears from the measure space dynamic of Section 3 (as well as the adaptive models summarized in Section 2). General density dependence is more difficult from a technical perspective. One attempt to avoid this problem is to assume, as in the adaptive dynamics approach, that the population instantaneously tracks its equilibrium density for a given probability measure. This assumption is usually justified by appealing to a dichotomy between the time scales for the population dynamics (ecological time scale) versus strategy evolution (evolutionary time scale). That is, it is assumed ecological changes are much faster than evolutionary ones. The dynamic is then reduced to one on the “stationary density surface” (SDS) where the fitness  $\pi(x, P)$  is assumed to be given by  $\pi(x, P, N(P))$  where  $N(P)$  is on the stationary density surface. We feel such an assumption is unwarranted if adaptive dynamics is to be put on firm theoretical ground. However, there is some evidence the SDS continues to play an important role when there is no separation of time scales, at least when there is a finite number of strategies as in Section 2.2. The SDS can then be used to separate the density effect from the local asymptotic stability analysis of the mean strategy dynamic for both monomorphisms and polymorphisms in single species (Cressman, 1992) or multiple species (Cressman and Garay, 2003) models of coevolution. Of particular relevance for us is the result for monomorphisms; namely, a monomorphism is locally asymptotically stable in the coevolutionary model of combined density and strategy evolution when there is a finite number of strategies if and only if the monomorphic density dynamic is asymptotically stable at equilibrium strategy and the induced strategy dynamic on the stationary density

surface is asymptotically stable (no matter what the relative rates of ecology and evolution are). For our measure dynamic models, we conjecture a stationary density surface will continue to predict local behavior near a monomorphism but not for general equilibria  $P^*$  distributed over the trait space (see also our comments on higher dimensional trait space below).

Mutation has not been explicitly added to our model since our perspective is that this effect is already included by considering arbitrary initial population distributions over the strategy space. In this sense, all potential mutations are already present in the system to start with and, if this “mutation” is successful, it will grow in relative size compared to other possible strategies. In particular, our formalism includes systems that are initially concentrated near a monomorphic equilibrium with a small subpopulation concentrated around a “mutant” strategy. On the other hand, our results also allow one to introduce rare mutations in the more traditional sense by letting the system evolve arbitrarily close to a stable equilibrium between mutation events. Theorems 2 and 4 then show the perturbed system will stay close to a locally superior equilibrium distribution  $P^*$  that is Lyapunov stable and eventually return to it.

The adaptive dynamics approach has also been extended to multi-dimensional strategy spaces (e.g. Meszéna et al., 2001) and/or multi-species models (e.g. Marrow et al., 1996). For a single-species monomorphic equilibrium  $x^*$  in a compact trait space in  $R^n$  (such as a ball or hypercube), the measure dynamic approach applied here suggests the method of assuming the CSS conditions hold along any ray (as in Meszéna et al., 2001) from  $x^*$  is particularly relevant. Indeed, it is straightforward to see that the CSS conditions along any ray are necessary for stability of  $\delta_0$  (simply take initial measures supported on this ray). On the other hand, under the additional condition corresponding to NIS, convergence to  $x^*$  can be shown in the weak topology when initial distributions have support sufficiently close to  $x^*$  (this uses an argument similar to Cressman (2003)). A precise characterization of stability is an open problem.

However, in other multi-dimensional or multi-species situations (e.g. non-monomorphic  $P^*$  or especially if there is non-equilibrium behavior of the adaptive dynamics such as cyclic behavior in a single-species model or in a two-species predator-prey system), we are quite skeptical that the conclusions from the measure dynamic approach will correspond to that from adaptive dynamics where it is again assumed population size(s) tracks its equilibrium value. There is in fact evidence from coevolutionary models based on finite trait spaces (e.g. Abrams and Matsuda, 1997) that questions the relevance of the adaptive dynamics approach in these circumstances. Models that exhibit non-equilibrium behavior also call into question the assumption that fitness functions are based on pairwise interactions. It seems more reasonable that in such situations,  $\pi(x, \mu)$  should depend on the measure in a more complicated way than simply averaging the payoffs between individual interactions. In fact, such non-pairwise fitness functions were proposed from the outset of coevolutionary models (e.g. Roughgarden, 1979) where Lotka-Volterra type models were proposed with interaction coefficients given by Gaussian distributions depending on the separation of strategies from the mean.

We view this paper as a first, but crucial, step to give the adaptive dynamics approach a solid theoretical foundation as a means to predict long term behavior in coevolutionary systems. From this perspective, our results (see especially the Remark in Section 5.1 that the CSS plays a central role in understanding convergence and stability of the measure dynamic at a monomorphism) shows the adaptive method is clearly a valid shortcut to analyzing coevolutionary models when there are quadratic pairwise interactions. As discussed above, there are many obstacles to a general theory, but the end results should be equally rewarding.



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