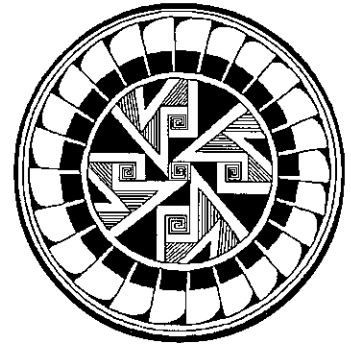


# Individual Versus Social Learning: Evolutionary Analysis in a Fluctuating Environment

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## Abstract

A model for haploid asexual inheritance of social and individual learning is proposed. Animals of one genotype, individual learners (IL), behave optimally for the current environment and, except for a fixed cost due to learning errors, have the optimal fitness in that environment. Animals of the other genotype are social learners (SL) each of whom copies a random individual from the previous generation. However, the phenotype of a social learner depends on whom it copies. If it copies an IL or a correctly behaving SL, it has the “correct” phenogenotype, SLC. Otherwise, its behavior is maladaptive and we call its phenogenotype SLW.

Different models for the environmental fluctuation produce different dynamics for the frequency of SL animals. An infinite state environment is such that when it changes, it never reverts to an earlier state. If it changes every generation, social learning can never succeed. If, however, a generation in which the environment changes is followed by  $\ell - 1$  generations of environmental stasis and  $\ell \geq 3$ , some fitness sets do allow the maintenance of social learning. Analogous results are shown for a randomly fluctuating environment, and for cyclic two-state environments.

In a second type of model, each animal can learn individually with probability  $L$ . We examine the evolutionary stability properties of this probability in the infinite state environment. When a generation of change is followed by  $\ell - 1$  generations of stasis, fitness parameters can be found that produce an evolutionarily stable nonzero probability of social learning. In all of the models treated, the greater the probability of environmental change, the more difficult it is for social learning to evolve.

## Introduction

Recent psychological surveys of animal learning suggest that local/stimulus enhancement is often the mechanism responsible for social learning (Galef, 1976, 1988; Whiten and Ham, 1992). Local/stimulus enhancement occurs when an animal has its attention drawn to a particular stimulus, by observing another animal interacting with that stimulus. The behavior itself is then acquired as the result of individual learning. If, as in this case, primitive forms of social learning can be regarded as fairly simple extensions of individual learning, the principal precursor of social learning and cultural transmission may well have been a capacity for individual learning (Laland et al., 1993). Hence, it is pertinent to ask what conditions might favor the evolution of social learning in its earliest phases from individual learning.

This question has been addressed theoretically by Boyd and Richerson (1985, 1988) and Rogers (1988). Their basic premises are as follows. The environment may change between generations, and there is an optimal behavior appropriate to each environmental state. Individual learners (animals who adopt the individual learning strategy) achieve this optimal behavior on their own. Social learners (animals who adopt the social learning strategy), on the other hand, must copy an animal of the immediately preceding generation. The term "copy" is used broadly to include all means by which an accurate transfer of information may occur. Individual learners suffer a decline in fitness due to errors made in learning. Social learners pay a smaller direct cost, but run the risk of copying an inappropriate behavior. Since only individual learners are able to accurately track the fluctuating environment, this risk increases as the frequency of individual learners decreases. Intuitively, then, one might expect that at some intermediate frequency the fitnesses of individual and social learners should be equal, and that this should define a polymorphic equilibrium.

In particular, Rogers (1988) supposes that an animal is either an obligate individual learner or an obligate social learner. He also posits a two-state environment and two possible behaviors. One behavior confers a high fitness in one environment and a low fitness in the other, with the other behavior reversing these. Individual learners always

achieve the optimal behavior corresponding to their environment. Social learners will also behave optimally if they copy individual learners of the previous generation and if the environment is unchanged. Since social learning is assumed to carry a smaller cost than individual learning, a social learner behaving optimally will have a higher fitness than an individual learner.

Assuming haploid asexual inheritance of the two types, Rogers carries out his analysis as if the frequency of social learners does not evolve. The value of this frequency at which individual and social learners have the same fitness is then defined as the evolutionary equilibrium. The justification given for this approach is that cultural change is fast enough relative to genetic evolution that the frequency of social learners "can be treated as a constant." This raises an important issue relevant to gene-culture theory. What if the problem were phrased in a truly coevolutionary framework so that the frequency of social learners changed over time? Some answers are offered in our following analysis.

The way in which environmental change is modelled has strong effects on evolutionary dynamics (Haldane and Jayakar, 1963; Gillespie, 1973; Hartl and Cook, 1974; Karlin and Liberman, 1974). Rogers assigns to each genotype an (arithmetic) average of its fitnesses under changing and unchanging environments, weighted by the probabilities of change and no change. This removes most of the effect of temporal environmental change. In our analysis, the environment will either cycle deterministically between periods of change and stasis, or change with a fixed probability so that the dynamics are truly stochastic. We include a model of an infinite-state environment, namely one in which after changing, it never reverts to an earlier state. In our two state model we also include the possibility that social learners make the right choice, when the environment changes, by copying social learners who previously had it wrong. A combination of analytical and numerical approaches will be used to explore the consequences of this generalization.

A second class of models is suggested by the work of Boyd and Richerson (1985, 1988) who assume that all animals acquire their behavior by some mixture of individual and social learning, differing only in the emphasis placed on the two learning strategies. In the 1988 model, which we describe because it is simpler and more recent, the environment fluctuates between two states and there are two behaviors, as in Rogers (1988). Each animal

obtains an imperfect estimate of the state of the environment from personal experience. If it decides to trust this estimate, it matches its behavior to the presumed state. Otherwise, it copies a random animal of the previous generation. The degree of reliance placed on personal experience is treated as a quantitative variable that is genetically determined and subject to natural selection. Boyd and Richerson compute the evolutionarily stable value of this variable.

Boyd and Richerson's model is certainly more complex, and perhaps because of this, they have resorted to the same questionable expedient as Rogers (1988) of assuming that genetic change can be ignored while some cultural equilibrium is attained. Since this model does not seem amenable to a formal dynamic analysis, we have introduced an alternative model that is similar in spirit. We posit that an animal chooses to learn individually or socially with a fixed genotype-dependent probability. Once the learning mode is set, the animal acquires its behavioral phenotype and its fitness is determined in the same way as for obligate individual and social learners. We investigate the evolutionarily stable probability of individual learning and the dependence of this probability on the extent to which the environment cycles.

From our dynamic analysis we find that fixation on individual learners is possible, and, using the detailed specification of each model, we distinguish parametric ranges for this fixation, and for the stable coexistence of social and individual learning.

### Infinite State Model

Consider a fluctuating environment where the number of possible environmental states is assumed to be infinite so that when the environment changes it never reverts to an earlier state. Corresponding to each environment state there is one optimal behavior, and all other behaviors are equally maladaptive. None of the preexisting behaviors can be adaptive after an environmental change.

According to the parameters introduced by Rogers (1988), each animal has a baseline fitness  $w$ . When its behavior matches the state, its fitness is raised by an amount  $b$ . Inappropriate behavior causes an equal decline in fitness. The magnitude of the fitness

change is assumed not to depend on the particular behavior or state. An individual learner always achieves the optimal behavior. However, it suffers a fixed cost due to errors made in learning, defined as the factor  $c$  by which the fitness increment is reduced. A social learner copies a random animal of the previous generation. Provided the environment is unchanged, it acquires the optimal behavior if it copies an individual learner, or alternatively a social learner behaving optimally. Otherwise, its behavior is maladaptive. In this infinite state model, a social learner can never acquire the optimal behavior after an environmental change. A social learner also suffers a cost, defined as the factor  $s$  by which the fitness change – whether positive or negative – is reduced (see Rogers, 1988, and below). Selection is due to viability differences. The parameters satisfy the inequalities  $0 < b < w$ ,  $0 < c < 1$ , and  $0 < s < 1$ .

Posit haploid asexual inheritance of social learning and individual learning. Since the behavior of social learners can be either adaptive or maladaptive, there are a total of three phenotypes in the population. Let us use the shorthand notation SL for social learners and IL for individual learners. Also, SLC will be used for social learners behaving adaptively and SLW for social learners behaving maladaptively – C and W stand for correct and wrong. The fitnesses of SLC, SLW, and IL are therefore  $w + b(1 - s)$ ,  $w - b(1 - s)$ , and  $w + b(1 - c)$ . Economy of notation can be achieved without loss of generality by setting  $w = 1$ ,  $b(1 - c) = \gamma$ , and  $b(1 - s) = \sigma$  with  $0 < \gamma, \sigma < 1$ . The three fitnesses which we use hereafter become  $1 + \sigma$ ,  $1 - \sigma$ , and  $1 + \gamma$ , respectively. This does involve a restriction to two parameters which may influence our results, although the qualitative effect should be negligible.

Denote the frequencies of SLC, SLW, and IL among reproductive adults by  $x, y, z$ . The life cycle is reproduction, learning, and selection. Then, after an environmental change, these frequencies become

$$x' = 0 \tag{1a}$$

$$y' = (1 - \sigma)(1 - z)/T \tag{1b}$$

$$z' = (1 + \gamma)z/T \tag{1c}$$

where

$$T = (1 + \gamma)z + (1 - \sigma)(1 - z). \quad (1d)$$

If this recursion were to operate forever, we could rewrite (1c) as

$$T(z_{n+1} - z_n) = z_n(1 - z_n)(\gamma + \sigma) > 0. \quad (2)$$

Hence  $\{z_n\}$  is an increasing sequence bounded above so that it must converge. If  $z_0 > 0$  this limit must be  $\hat{z} = 1$ , a population of only IL. Obviously  $\hat{y} = 1$  is an equilibrium of the system (1), but it is always unstable.

After a generation with no environmental change, the frequencies  $x, y, z$  would instead become

$$x' = (1 + \sigma)(x + y)(x + z)/T \quad (2a)$$

$$y' = (1 - \sigma)(x + y)y/T \quad (2b)$$

$$z' = (1 + \gamma)z/T \quad (2c)$$

where

$$T = (1 + \gamma)z + [1 + \sigma(x + z - y)](1 - z). \quad (2d)$$

Here, the offspring of SL ( $x+y$ ) copy those who behaved correctly in the previous generation ( $x + z$ ) to give  $x'$ , and they copy those who behaved incorrectly ( $y$ ) to give  $y'$ . In this case it is clear that  $y' < y$ . The equilibria associated with repeated operation of (2) are (a)  $\hat{z} = 0, \hat{x} = 1, \hat{y} = 0$ , (b)  $\hat{z} = 0, \hat{x} = 0, \hat{y} = 1$ , and (c)  $\hat{z} = 1, \hat{x} = 0, \hat{y} = 0$ . If the system (2) operated over a sufficiently long time, then with  $y$  initially very small and  $\sigma > \gamma$ , there would be global convergence to equilibrium (a) with  $\hat{x} = 1$ . With  $\gamma > \sigma$ , on the other hand, there is global convergence to equilibrium (c) with individual learners fixed. Equilibrium (b) with only SLW present can never be stable.

### Two-generation cycle

Suppose that a generation in which the environment changes, so that recursion system (1) operates, is followed by one in which there is no environmental change, so that system (2) operates. This cycle with period two then continues ad infinitum. In this infinite state

model, after a generation with an environmental change  $x$ , the frequency of SLC is reset to zero so that the recursions (2) may be modified to read

$$T'x'' = (1 + \sigma)y'z' \quad (3a)$$

$$T'y'' = (1 - \sigma)(y')^2 \quad (3b)$$

$$T'z'' = (1 + \gamma)z' \quad (3c)$$

with

$$T' = 1 + \sigma y'(z' - y') + \gamma z'. \quad (3d)$$

Here  $x'$ ,  $y'$ , and  $z'$  are given by the recursions (1).

Write  $\phi$  for the transformation (1) and  $\phi'$  for the transformation (2). Then at equilibrium of the combined transformation ( $\phi'\phi$ ) we have

$$TT'z = (1 + \gamma)^2 z, \quad (4)$$

and, if  $\hat{z} = 0$ , then from (3a) and (1c),  $\hat{x} = 0$  and  $\hat{y} = 1$ . If  $\hat{z} \neq 0$ , then either  $\hat{z} = 1$  or

$$(1 + \gamma)^2 = (1 - \sigma)[1 + \sigma(z' - y')]$$

which is impossible. Hence, there exists no equilibrium value  $\hat{z} \in (0, 1)$ . The same is clearly true of the transformation ( $\phi\phi'$ ).

Near  $\hat{x} = 0$ ,  $\hat{y} = 1$ ,  $\hat{z} = 0$ ,  $T \approx 1 - \sigma$ , and  $T' \approx 1 - \sigma$ . When  $x$  and  $z$  are small enough, from (3) and (1) we have

$$x'' = \frac{(1 + \sigma)(1 + \gamma)}{(1 - \sigma)^2} z$$

$$z'' = \frac{(1 + \gamma)^2}{(1 - \sigma)^2} z,$$

so that  $\hat{y} = 1$  must be locally unstable as an equilibrium of the two generation cycle.

Near  $\hat{x} = \hat{y} = 0$ ,  $\hat{z} = 1$ ,  $T \approx 1 + \gamma$ , and  $T' \approx 1 + \gamma$ . With  $x$  and  $y$  sufficiently small, we have

$$y' = \frac{1 - \sigma}{1 + \gamma} (x + y); \quad y'' = O(x + y)^2.$$

$$x'' = \frac{1 + \sigma}{1 + \gamma} y' = \frac{1 - \sigma^2}{(1 + \gamma)^2} (x + y).$$

Clearly, therefore,  $\hat{z} = 1$  is a locally stable fixation for the two generation cycle.

In the infinite state model, with a 2-generation cycle there are, therefore, no interior equilibria and social learning should disappear.

### Cycles of period $\ell > 2$

It is natural to ask whether increasing the number of generations of stasis surrounding one of environmental change allows for the stable existence of social learners that was not possible with period 2. Here we allow transformation (2) to operate  $\ell - 1$  times after an environmental change in which transformation (1) occurred. The overall recursion is then  $[(\phi')^{(\ell-1)}\phi]$ . As in the two-generation cycle, the fixation states  $\hat{z} = 1$  on IL and  $\hat{y} = 1$  on SLW must be considered. (We use the notation  $\hat{z} = 1$  and  $\hat{y} = 1$  here because these fixation states remain as fixation states at all points in the cycle.) In order to determine whether polymorphism is possible, note that at equilibrium  $\hat{z}^{(\ell)} = \hat{z}^{(0)}$  and

$$T^{(0)}T^{(1)} \dots T^{(\ell-1)}\hat{z}^{(\ell)} = (1 + \gamma)^\ell \hat{z}^{(0)}. \quad (5)$$

From (3d),

$$T^{(1)}T^{(2)} \dots T^{(\ell-1)} = \prod_{i=1}^{\ell-1} \left\{ (1 + \gamma)z^{(i)} + [1 + \sigma(1 - 2y^{(i)})](1 - z^{(i)}) \right\}.$$

Hence

$$T^{(1)}T^{(2)} \dots T^{(\ell-1)} = (1 + \gamma)^{\ell-1} z^{(1)} + (1 - z^{(1)}) \prod_{i=1}^{\ell-1} [1 + \sigma(1 - 2y^{(i)})].$$

Now operate with  $T^{(0)}$  from (1) to give

$$T^{(0)}T^{(1)} \dots T^{(\ell-1)} = (1 + \gamma)^\ell z^{(0)} + (1 - z^{(0)})(1 - \sigma) \prod_{i=1}^{\ell-1} [1 + \sigma(1 - 2y^{(i)})].$$

Using (5) at equilibrium we are left with

$$(1 + \gamma)^\ell = (1 - \sigma) \prod_{i=1}^{\ell-1} [1 + \sigma(1 - 2\hat{y}^{(i)})]. \quad (6)$$

Equation (6) must be satisfied by the sequence  $\hat{y}^{(i)}$  for a valid equilibrium to exist.

Now let us consider the two boundary equilibria  $\hat{x} = \hat{y} = 0, \hat{z} = 1$ , and  $\hat{x} = 0, \hat{y} = 1, \hat{z} = 0$ . It is straightforward to see that near  $\hat{z} = 1$ , when  $x^{(0)}$  and  $y^{(0)}$  are small

$$\left(x^{(\ell)} + y^{(\ell)}\right) = \frac{(1 + \sigma)^{\ell-1}(1 - \sigma)}{(1 + \gamma)^\ell} \left(x^{(0)} + y^{(0)}\right).$$

For social learners to increase when rare, we therefore require

$$\ell \ln \left[ \frac{1 + \sigma}{1 + \gamma} \right] > \ln \left[ \frac{1 + \sigma}{1 - \sigma} \right] \quad (7)$$

which is impossible if  $\gamma > \sigma$ . Near  $\hat{y} = 1$ , on the other hand, with  $z^{(0)}$  small enough,

$$z^{(\ell)} = \frac{(1 + \gamma)^\ell}{(1 - \sigma)^\ell} z^{(0)},$$

so that  $\hat{y} = 1$  can never be locally stable.

When inequality (7) is false,  $\hat{z} = 1$  is locally stable and we expect the population to fix on individual learners. For any positive fixed value of  $\sigma = b(1 - s)$ , as  $\gamma = b(1 - c)$  approaches zero, the inequality (7) will be satisfied for  $\ell$  large enough. We have already seen that it fails for  $\ell = 2$ . It may, however, hold for  $\ell = 3$  or larger. In other words, a sufficiently long period of environmental stasis will support the maintenance of social learning if its cost is not too high relative to that of individual learning.

Equilibrium condition (5) is very difficult to analyse formally so we have investigated the properties of the  $\ell$ -cycle numerically. In Table 1, we show how the mean and variance of the frequency of social learners across the equilibrium cycling values change with the length of the cycle. For a given cycle length, it might be suspected that the mean frequency of all social learners should decrease with increasing  $\gamma$  all other parameters being constant, and this is seen in Table 1. Also, the fraction of SLC ( $x$ ) increases as  $\gamma$  increases. This is shown in Table 2, which reports the frequencies of social learners as  $\sigma$  and  $\ell$  vary. Within a given cycle length, the frequency of SLC increases as  $\sigma$  increases except for short cycle lengths, with large  $\sigma$ , polymorphism is not maintained. Figure 1 gives a pictorial representation of an example of the dependence on  $\ell$ .

**Tables 1 and 2 here.**

**Figure 1 here.**

## Random environmental changes

Suppose that a change in the environment occurs with probability  $u$  and that it remains unchanged with complementary probability  $1 - u$ . Thus, with probability  $u$ , the phenotypes change according to recursion (1), and with  $(1 - u)$  according to recursion (2). Although general solutions to polymorphic “equilibria” are not usually available for this kind of problem, analysis of the boundary equilibria in terms of stochastic local stability (Karlin and Liberman, 1974) is usually very informative.

Near  $\hat{z} = 1$ , the local change in  $x + y$  is given by (see (1))

$$(x' + y') \approx \frac{1 - \sigma}{1 + \gamma} (x + y)$$

with probability  $u$  and

$$(x' + y') \approx \frac{1 + \sigma}{1 + \gamma} (x + y)$$

with probability  $(1 - u)$ . The theory developed by Gillespie (1973), Hartl and Cook (1974), and Karlin and Liberman (1974) tells us to expect that  $(x + y)$  will increase when small if

$$u \ln \left\{ \frac{1 - \sigma}{1 + \gamma} \right\} + (1 - u) \ln \left\{ \frac{1 + \sigma}{1 + \gamma} \right\} > 0. \quad (8)$$

Notice that if we set  $u = 1/\ell$ , this condition reduces exactly to inequality (7), and, like (7) cannot be true unless  $\sigma > \gamma$ .

Near  $\hat{y} = 1$ , a similar argument produces the conclusion that  $z$  and  $x$  are always expected to increase when rare, as was the case in the  $\ell$ -generation cycle.

In order to investigate the dynamics of this stochastic model away from the boundary fixations, we simulated the process with various values of the parameters. Figure 2 shows an example of the dependence on  $u$ ; for  $u$  small (as we saw with  $\ell$  large) stable coexistence of social and individual learners is possible. Again this requires that the cost of individual learning is high relative to that for social learning.

Figure 2 here.

## A Two State Model

This model differs from the infinite state model in that the environment is now assumed to exist in one of two states. A behavior that is correct for one of the environmental states is incorrect for the other. Thus, social learners will behave incorrectly if they copy SLC or IL animals from the previous generation and the environment changes. The recursions for phenogentotype frequencies with environmental change become

$$Tx' = (1 + \sigma)(x + y)y \quad (9a)$$

$$Ty' = (1 - \sigma)(x + y)(x + z) \quad (9b)$$

$$Tz' = (1 + \gamma)z \quad (9c)$$

with

$$T = (1 + \gamma)z + [1 - \sigma(1 - 2y)](1 - z), \quad (9d)$$

which replaces the system (1). Notice that social learners may now behave appropriately if they copy SLW animals from the previous generation and the environment changes.

The properties of (9) under continued iteration are expected to differ from those of (1). Indeed, suppose that  $\hat{z} = 0$  at equilibrium of (9). Then

$$\hat{x}/\hat{y} = \left( \frac{1 + \sigma}{1 - \sigma} \right) \hat{y}/\hat{x}$$

so that

$$\hat{x} = \frac{\sqrt{1 + \sigma}}{\sqrt{1 + \sigma} + \sqrt{1 - \sigma}}, \quad \hat{y} = \frac{\sqrt{1 - \sigma}}{\sqrt{1 + \sigma} + \sqrt{1 - \sigma}}. \quad (10)$$

The only other equilibrium of (9) is  $\hat{z} = 1$ . At the equilibrium (10),  $T = 1 - \sigma(\hat{x} - \hat{y})$  in (9d). Hence, from (9c), the equilibrium (10) cannot be a stable outcome of iterating (9). In the same way, near  $\hat{z} = 1$ ,  $(x' + y') = \{(1 - \sigma)/(1 + \gamma)\}(x + y)$ , so that social learning disappears when rare under continued iteration of (9).

The frequency dynamics for the phenogentotypes when the environment does not change are the same in this two state model as for the infinite state case.

### Two-generation cycle

Suppose that the transformation (9), represented by  $\tilde{\phi}$ , acts first, followed by  $\phi'$  given by (2). Then at equilibrium of  $(\phi' \tilde{\phi})$  we have

$$TT'z = (1 + \gamma)^2 z$$

where  $T$  is given by (9d) and  $T'$  by (2d). Suppose first that  $\hat{z} = 0$ , which is preserved by both (9) and (2). Then at equilibrium

$$TT'x = (1 + \sigma)^2 y \quad (11a)$$

$$TT'y = (1 - \sigma)^2 x \quad (11b)$$

so that

$$\hat{x} = \frac{1 + \sigma}{2}, \quad \hat{y} = \frac{1 - \sigma}{2}. \quad (12)$$

An argument analogous to that following eqn. (4) then demonstrates that the only way for  $\hat{z}$  to be positive is that  $\hat{z} = 1$ . Thus, this two-generation cycle cannot support a polymorphism with all phenogenotypes present.

Applying the transformation (9) to the point (12) we see that after each generation of environmental change  $\hat{x}$  and  $\hat{y}$  both become  $1/2$ . They then revert to the values (12) after each generation without change. In other words, the two equilibrium cycles are

$$\left. \begin{array}{l} \hat{x} = 0 \rightarrow 0 \rightarrow 0 \rightarrow 0 \dots \\ \hat{y} = 0 \rightarrow 0 \rightarrow 0 \rightarrow 0 \dots \\ \hat{z} = 1 \rightarrow 1 \rightarrow 1 \rightarrow 1 \dots \end{array} \right\} A$$

and

$$\left. \begin{array}{l} \hat{x} = (1 + \sigma)/2 \rightarrow 1/2 \rightarrow (1 + \sigma)/2 \rightarrow 1/2 \dots \\ \hat{y} = (1 - \sigma)/2 \rightarrow 1/2 \rightarrow (1 - \sigma)/2 \rightarrow 1/2 \dots \\ \hat{z} = 0 \rightarrow 0 \rightarrow 0 \rightarrow 0 \dots \end{array} \right\} B.$$

For the stability of  $\hat{z} = 1$ , note that after one generation of environmental stasis

$$(x' + y') = \frac{1 + \sigma}{1 + \gamma} (x + y), \quad (13a)$$

while after a generation of change,

$$(x' + y') = \frac{1 - \sigma}{1 + \gamma} (x + y). \quad (13b)$$

Thus with a two-generation cycle

$$(x'' + y'') = \frac{1 - \sigma^2}{(1 + \gamma)^2} (x + y), \quad (14)$$

so that social learners cannot invade a population of individual learners.

Now consider the transformation in the neighborhood of  $\hat{z} = 0$  with  $\hat{x}$  and  $\hat{y}$  given by eqn. (12). Write  $\hat{y}^{(0)} = (1 - \sigma)/2$ ,  $\hat{y}^{(1)} = 1/2$ , where  $\hat{y}^{(1)}$  is the equilibrium after a generation of change and  $\hat{y}^{(0)}$  that after a generation of stasis. Set  $y^{(1)} = \hat{y}^{(1)} + \varepsilon_y^{(1)}$ ,  $z^{(1)} = \varepsilon_z^{(1)}$  with  $\varepsilon_y^{(1)}$  and  $\varepsilon_z^{(1)}$  small. Linearizing (9) near  $\hat{z}^{(0)} = 0$ ,  $\hat{y}^{(0)}$ ,  $\hat{x}^{(0)} = 1 - \hat{y}^{(0)}$ , we find

$$\varepsilon_y^{(1)} = \frac{-1}{1 - \sigma^2} \varepsilon_y^{(0)} + \text{term in } \varepsilon_z^{(0)} \quad (14a)$$

$$\varepsilon_z^{(1)} = \frac{1 + \gamma}{1 - \sigma^2} \varepsilon_z^{(0)}. \quad (14b)$$

After this generation with a changed environment, there is a generation of stasis with  $y^{(2)} = \hat{y}^{(2)} + \varepsilon_y^{(2)}$ ,  $z^{(2)} = \varepsilon_z^{(2)}$  and  $\hat{y}^{(2)} = \hat{y}^{(0)} = (1 - \sigma)/2$ . Linearizing the system (2) near  $\hat{z}^{(1)} = 0$ ,  $\hat{y}^{(1)}$ ,  $\hat{x}^{(1)} = (1 - \hat{y}^{(1)})$  we find

$$\varepsilon_y^{(2)} = (1 - \sigma^2)\varepsilon_y^{(1)} + \text{term in } \varepsilon_z^{(1)} \quad (15a)$$

$$\varepsilon_z^{(2)} = (1 + \gamma)\varepsilon_z^{(1)}. \quad (15b)$$

Applying the matrix of (15) to that in (14), the local two-generation stability of the equilibrium  $B$  is governed by the matrix

$$\left\| \begin{array}{cc} -1 & * \\ 0 & \frac{(1 + \gamma)^2}{1 - \sigma^2} \end{array} \right\|.$$

whose larger eigenvalue is clearly greater than unity. In other words, in the two state model, the two-generation cycle allows only  $\hat{z} = 1$  to be locally stable.

### $\ell$ -generation cycle

Here we suppose that a generation of environmental change is followed by  $\ell - 1$  generation of environmental stasis during which transformation (2) operates. For the local stability of the fixation point  $\hat{z} = 1$  for all generations, the eigenvalue is

$$\frac{(1 + \sigma)^{\ell-1}(1 - \sigma)}{(1 + \gamma)^\ell},$$

exactly as it was in the infinite state model. The condition for social learners to increase when rare is again given by inequality (6), and entails that  $\sigma$  be large compared to  $\gamma$  and, in view of the previous paragraph,  $\ell \geq 3$ .

The equilibrium given by  $\hat{z} = 0$  in the two state case differs from that in the infinite-state model. In the latter, we had  $\hat{y} = 1$ ; in the two state case,  $\hat{z} = 0$  entails that  $\hat{x} \neq 0$  as well as  $\hat{y} \neq 0$ . Thus, the  $\ell$ -cycle equilibrium could be represented as  $(\hat{x}^{(i)}, \hat{y}^{(i)}, 0)$  for  $i = 0, 1, 2, \dots, \ell - 1$ , with  $(\hat{x}^{(0)}, \hat{y}^{(0)}, 0)$  corresponding to the generation of environmental change. From (9d) we have

$$\hat{T}^{(0)} = 1 - \sigma(1 - 2\hat{y}^{(0)})$$

and from (2)

$$\hat{T}^{(i)} = 1 + \sigma(1 - 2\hat{y}^{(i)}) \quad i = 1, 2, \dots, \ell - 1.$$

Continuing the argument for the two-generation cycle, the local stability matrix is

$$\begin{aligned} & \left\| \begin{array}{cc} \frac{1 - \sigma(1 - 2\hat{y}^{(1)})}{\hat{T}^{(0)}} & * \\ 0 & \frac{1 + \gamma}{\hat{T}^{(0)}} \end{array} \right\| \times \\ & \prod_{i=1}^{\ell-1} \left\| \begin{array}{cc} \frac{1 - \sigma(1 - 2\hat{y}^{(i+1)})}{\hat{T}^{(i)}} & * \\ 0 & \frac{1 + \gamma}{\hat{T}^{(i)}} \end{array} \right\|, \end{aligned} \quad (16)$$

where the matrix entries marked \* are not relevant to our calculation. The eigenvalues of this product matrix are

$$\lambda_1 = -\frac{1 - \sigma(1 - 2\hat{y}^{(1)})}{1 - \sigma(1 - 2\hat{y}^{(0)})} \prod_{i=1}^{\ell-1} \frac{1 - \sigma(1 - 2\hat{y}^{(i+1)})}{1 + \sigma(1 - 2\hat{y}^{(i)})} \quad (17)$$

and

$$\lambda_2 = \frac{(1 + \gamma)^\ell}{\prod_{i=0}^{\ell-1} \hat{T}^{(i)}}. \quad (18)$$

At this equilibrium, from (9) we have  $\hat{z} = 0$  and

$$\frac{\hat{x}^{(1)}}{\hat{y}^{(1)}} = \frac{1 + \sigma}{1 - \sigma} \frac{\hat{y}^{(0)}}{\hat{x}^{(0)}}$$

$$\frac{\hat{x}^{(i+1)}}{\hat{y}^{(i+1)}} = \frac{1 + \sigma}{1 - \sigma} \frac{\hat{x}^{(i)}}{\hat{y}^{(i)}}, \quad i = 1, 2, \dots, \ell - 1.$$

So that

$$\frac{\hat{x}^{(0)}}{\hat{y}^{(0)}} = \frac{\hat{x}^{(\ell)}}{\hat{y}^{(\ell)}} = \left[ \frac{1 + \sigma}{1 - \sigma} \right]^\ell \frac{\hat{y}^{(0)}}{\hat{x}^{(0)}},$$

whence

$$\frac{\hat{x}^{(0)}}{\hat{y}^{(0)}} = \left[ \frac{1 + \sigma}{1 - \sigma} \right]^{\ell/2}; \quad \frac{\hat{x}^{(i)}}{\hat{y}^{(i)}} = \left[ \frac{1 + \sigma}{1 - \sigma} \right]^{i - \ell/2}, \quad i = 1, 2, \dots, \ell.$$

From this we infer that  $\hat{y}^{(i)} + \hat{y}^{(\ell-i)} = 1$ ,  $\hat{y}^{(0)} < 1/2$  and, if  $\ell$  is even,  $\hat{y}^{(\ell/2)} = 1/2$ . Now in  $\lambda_1$  substitute  $1 - 2\hat{y}^{(i)} = -(1 - 2\hat{y}^{(\ell-i)})$ . This gives us  $\lambda_1 = -1$ . Finally,

$$\begin{aligned} \prod_{i=0}^{\ell-1} T^{(i)} &= \left[ 1 - \sigma(1 - 2\hat{y}^{(0)}) \right] \prod_{i=1}^{\ell-1} \left[ 1 + \sigma(1 - 2\hat{y}^{(i)}) \right] \\ &= \left[ 1 - \sigma(1 - 2\hat{y}^{(0)}) \right] \left[ 1 + \sigma(1 - 2\hat{y}^{(\ell/2)}) \right] \times \\ &\quad \prod_{i=1}^{\ell/2-1} \left\{ 1 - \left[ \sigma(1 - 2\hat{y}^{(i)}) \right]^2 \right\} \end{aligned} \quad (19a)$$

for  $\ell$  even, and

$$\left[ 1 - \sigma(1 - 2\hat{y}^{(0)}) \right] \prod_{i=1}^{(\ell-1)/2} \left\{ 1 - \left[ \sigma(1 - 2\hat{y}^{(i)}) \right]^2 \right\} \quad (19b)$$

for  $\ell$  odd. Thus,  $\lambda_2 > 1$  and the equilibrium with  $\hat{z} = 0$  is unstable.

### A Strategy Model for Mode of Learning

In this model, each animal can learn individually or socially. However, it cannot simultaneously use both strategies so that once the learning mode is set, the animal acquires its behavioral phenotype and its fitness is determined in the same way as for obligate individual and social learners in the first model. There are two haploid asexual types of animals that differ in their probability of adopting the individual learning strategy. For

type 1 animals, this probability is  $L$ , and for type 2 animals, it is  $L + dL$ . The environment fluctuates as in the infinite state model described previously. Each of two types of animals may behave in an appropriate manner for the environment it confronts, which we call adaptive behavior, or maladaptively. Thus, there are four types of individuals, type 1 behaving adaptively, type 1 behaving maladaptively, type 2 behaving adaptively, and type 2 behaving maladaptively. Denote their frequencies by  $x, \bar{x}, y, \bar{y}$ , respectively.

When the environment changes, only individual learners behave adaptively so that the recursion for environmental change is

$$Tx' = (x + \bar{x})L(1 + \gamma) \quad (20a)$$

$$T\bar{x}' = (x + \bar{x})(1 - L)(1 - \sigma) \quad (20b)$$

$$Ty' = (y + \bar{y})(L + dL)(1 + \gamma) \quad (20c)$$

$$T\bar{y}' = (y + \bar{y})(1 - L - dL)(1 - \sigma), \quad (20d)$$

with

$$T = (x + \bar{x}) \{L(1 + \gamma) + (1 - L)(1 - \sigma)\} \\ + (y + \bar{y}) \{(L + dL)(1 + \gamma) + (1 - L - dL)(1 - \sigma)\}. \quad (20e)$$

Here  $\gamma$  and  $\sigma$  have the same meanings as before.

When the environment does not change, any animal may learn adaptive behavior by copying those who behave correctly in the previous generation. After a generation of environmental stasis, the recursion is

$$Tx' = (x + \bar{x}) \{L(1 + \gamma) + (1 - L)(1 + \sigma)(x + y)\} \quad (21a)$$

$$T\bar{x}' = (x + \bar{x})(1 - L)(1 - \sigma)(\bar{x} + \bar{y}) \quad (21b)$$

$$Ty' = (y + \bar{y}) \{(L + dL)(1 + \gamma) + (1 - L - dL)(1 + \sigma)(x + y)\} \quad (21c)$$

$$T\bar{y}' = (y + \bar{y})(1 - L - dL)(1 - \sigma)(\bar{x} + \bar{y}) \quad (21d)$$

where

$$T = (x + \bar{x}) \{L(1 + \gamma) + (1 - L)(1 + \sigma)(x + y) \\ + (1 - L)(1 - \sigma)(\bar{x} + \bar{y})\}$$