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A mixed strategy model for the emergence and intensification of social learning in a periodically changing natural environment

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Abstract

Based on a population genetic model of mixed strategies determined by alleles of small effect, we derive conditions for the evolution of social learning in an infinite-state environment that changes periodically over time. Each mixed strategy is defined by the probabilities that an organism will commit itself to individual learning, social learning, or innate behavior. We identify the convergent stable strategies (CSS) by a numerical adaptive dynamics method and then check the evolutionary stability (ESS) of these strategies. A strategy that is simultaneously a CSS and an ESS is called an attractive ESS (AESS). For certain parameter sets, a bifurcation diagram shows that the pure individual learning strategy is the unique AESS for short periods of environmental change, a mixed learning strategy is the unique AESS for intermediate periods, and a mixed learning strategy (with a relatively large social learning component) and the pure innate strategy are both AESS's for long periods. This result entails that, once social learning emerges during a transient era of intermediate environmental periodicity, a subsequent elongation of the period may result in the intensification of social learning, rather than a return to innate behavior.

Keywords: Alleles of small effect; Evolutionarily stable strategy; Convergent stable strategy; Attractive ESS; Bifurcation diagram; Adaptive dynamics

1. Introduction

The behavior of a biological organism in a particular environment—more specifically, in response to a fitness-related aspect of the environment—is a complex process involving the expression of relevant information possessed by that organism. At the risk of oversimplification (Gould and Marler, 1987), it is possible to classify behaviors in terms of the three distinct ways in which this information can be obtained (Cavalli-Sforza and Feldman, 1983; Boyd and Richerson, 1985; Laland et al., 2000; Henrich and McElreath, 2003; Alvard, 2003). This trichotomous classification labels behavior as "innate," "socially learned," or "individually learned".

A behavior is innate when it entails the direct expression of information encoded in the genes, which are inherited from the parents via the germ cells. Social learning denotes the transfer of information between socially interacting organisms, as a result of which the behavior exhibited by the "exemplar" is adopted by the "observer" (Galef, 1988; Whiten and Ham, 1992; Heyes, 1993). (We prefer the term exemplar to "model", which can be confused with mathematical model, and "demonstrator", which implies active teaching.) The rubric covers teaching, imitation, local enhancement, and various other psychological processes. Finally, individual learning refers to learning that occurs independently of any social influences. Examples are trial-and-error and insight.

Reviews of the factors contributing to the emergence of social learning emphasize the role played by a temporally changing environment (Laland et al., 2000; Richerson and Boyd, 2000; Henrich and McElreath, 2003; Alvard, 2003). These writers agree that individual learning, social learning (from the parental generation), and innate determination of behavior are favored by natural selection when environmental changes occur at short, intermediate, and long generation intervals, respectively. Theoretical studies by Boyd and Richerson (1985, 1988), Rogers (1988), and Feldman et al. (1996) have provided the motivation, and

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also some support, for this proposal. More recently, Wakano et al. (2004) and Aoki et al. (2005) rigorously showed that this consensus view is basically true for both periodically and randomly changing environments, by simultaneously comparing individual learners, social learners, and "innates" (organisms behaving innately) when they are in direct competition with each other.

Wakano et al. (2004) and Aoki et al. (2005) posited genetic variation at a tri-allelic "strategy" locus, which determines whether an organism is an individual learner, a social learner, or an innate. In other words, they assumed that the three strategies are obligate (also Rogers, 1988; Feldman et al., 1996). Clearly, a model recognizing the "facultative" nature of behavior is more realistic (Boyd and Richerson, 1985, 1988; Feldman et al., 1996; Henrich and Boyd, 1998; Kameda and Nakanishi, 2002). In the present paper, we propose a new model approximating this feature, which is an extension of the mixed strategy model of Feldman et al. (1996). The mixed strategy model assumes alleles of small effect instead of major genes.

Since we view evolution as proceeding gradually by the cumulative substitution of mutations of small effect, our interest centers on strategies that are simultaneously convergent stable (CSS) and evolutionarily stable (ESS). CSS and ESS are not equivalent concepts (Britton, 2003; Doebeli et al., 2004): an ESS that is not a CSS cannot be reached by the cumulative substitution of mutations of small effect; a CSS that is not an ESS can be reached, but is invadable by another strategy. Hence, we restrict our attention to attractive ESS's (AESS), which are defined to be strategies that are simultaneously an ESS and a CSS. We use a numerical adaptive dynamics method to identify the CCS (Geritz et al., 1997). Then, we apply analytically derived conditions to check that these strategies are also evolutionarily stable (Maynard Smith, 1982).

Many of our results are consistent with those obtained by Wakano et al. (2004) and Aoki et al. (2005), which gives us some confidence that they do indeed apply to the phenomenon being investigated, rather than being dependent on the model. However, some of our predictions are novel. For example, we find that a mixed social and individual learning strategy, once it emerges during an era of intermediate environmental stability, may be able to resist invasion by the pure innate strategy, even if an era of high environmental stability should ensue.

2. Description of the model

Feldman et al. (1996) assume an infinite population of haploid asexual organisms that can use a mixed strategy of individual and social learning. We extend their model to include innate behavior as an alternative. During development each organism commits itself to one of these three pure strategies. The "strategy" locus, with alleles A and a, determines the probabilities that behavior will be innate, individually learned, or socially learned. An organism carrying an A allele becomes an "innate" (i.e., an organism behaving innately) with probability $1-K-L$, an individual learner with probability L, and a social learner with probability K. For allele a, we substitute $L+\delta L$ for L and $K+\delta K$ for K. Here, δL and δK denote independent changes of probability (except on the boundaries of the parameter space of K and L as explained below).

The environment changes every l generations. In other words, one postchange generation experiences a different environmental state from the previous generation, and $l-1$ subsequent generations experience the same environmental state as that postchange generation. Larger values of l imply more environmental stability. We adopt the infinite environmental state model, which posits that when the environment changes it never reverts to an earlier state (Feldman et al., 1996; Wakano el al., 2004; Aoki et al., 2005).

Behavior may be adaptive (correct) or maladaptive (wrong). Individual learners always achieve a correct behavior on their own whatever the environmental state, whereas social learners and innates may get it wrong. A social learner acquires its behavior by copying a random organism of the previous generation (oblique transmission, Cavalli-Sforza and Feldman, 1981). Its behavior will be adaptive or maladaptive depending on whether the behavior it acquires is appropriate to its current environmental state. In particular, the infinite environmental state model implies that a social learner of the postchange generation has no suitable exemplars in the prechange generation from which to acquire a correct behavior (see also next paragraph).

The information needed for innate behavior is stored genetically at the "innate information" locus, with two classes of alleles M and m. If an innate carries an M allele, its behavior is adaptive. Carrying an m allele results in maladaptive behavior. Each of the two classes of alleles comprises many selectively neutral variants, which are being constantly generated by mutation. (However, we do not model the mutation process.) Hence, there may be a variety of adaptive behaviors, which by assumption are equally adaptive (i.e., have the same fitness), and similarly a variety of maladaptive behaviors. A small subset amounting to a fraction ρ of each class has the special property of being adaptive when the environment changes. (Parameter ρ is analogous to a mutation rate, and we are following standard practice in population genetics when we assume it to be a constant.) These variants can be regarded as "preadapted" alleles awaiting environmental change. Nevertheless, an innate carrying a preadapted allele behaves differently in the prechange and postchange generations—the behavior of an innate is the result of an interaction between the allele it carries and the environment it experiences—so that its behavior in the prechange generation would be maladaptive in the postchange generation. The innate information locus is not expressed when the individual or social learning strategy is adopted. These assumptions may strike the reader as arbitrary, but in fact are necessary if we are to write down a consistent and analytically tractable recursion model.

Let us illustrate what we mean by a preadapted allele with two textbook examples from human genetics. An allele in our haploid asexual organism corresponds, albeit imperfectly, to a genotype in diploid sexual humans. The hemoglobin S allele is recessive to the A allele in a malaria-free environment, so that the fitnesses of genotypes AA and AS are identical (and greater than the fitness of genotype SS). If the population is exposed to malaria, however, genotype AS now has a higher fitness than genotype AA due to overdominance. Hence, in so far as the allele S is present at a low frequency before malaria becomes a selective factor, it can be regarded as a preadapted allele. Our second example is adult lactose absorber, which shows that the behavior associated with a genetic trait may depend on the environment in a way that affects fitness. In the incipient stage of animal domestication, the amount of milk available to an absorber is likely small and not sufficient to make a difference in fitness. As domestication proceeds and milk becomes more abundant, an absorber who persists in limiting intake is behaving maladaptively compared to one who increases consumption.

The fitnesses are relative viabilities and are assigned in the following way. There is a baseline fitness of 1 for adaptive behavior. Maladaptive behavior causes the fitness to be reduced by s. Social learners bear a direct cost of developing and maintaining a nervous system supportive of learning, which is translated into a fitness loss d. Individual learners suffer a similar—though not necessarily equivalent—direct cost and are also adversely affected by mistakes made before the mature behavior is realized; the total penalty is c. The fitnesses associated with each of the three strategies when the behavior is correct or wrong are summarized in Table 1. We assume $0<d<c<s<d+s<1$ (Aoki et al., 2005).

There are four genotypes AM, Am, aM, and am, each of which may express either of two phenotypes, i.e., adaptive or maladaptive behavior. The frequencies of the eight phenogenotypes (genotype–phenotype combinations, Feldman and Cavalli-Sforza, 1984) are listed in Table 2. The life cycle events are asexual reproduction, learning, and natural selection in that order. The recursions relating the frequencies of the eight phenogenotypes in the offspring generation (with primes) to those in the parental generation (without primes) can be written as follows.

Table 1
Strategy/behavior combinations with associated fitnesses

Strategy/behavior	Fitness
Innate/correct	1
Innate/wrong	$1-s$
Social learning/correct	$1-d$
Social learning/wrong	$1-d-s$
Individual learning/correct	$1-c$

$0<d<c<s<d+s<1$.

Table 2
Notation for the frequencies of the eight phenogenotypes

Phenogenotype		Frequency
Genotype	Behavior	
AM	Correct	u
AM	Wrong	$\bar{u}$
Am	Correct	v
Am	Wrong	$\bar{v}$
aM	Correct	x
aM	Wrong	$\bar{x}$
am	Correct	y
am	Wrong	$\bar{y}$

First, when the environment changes between generations they are:

$$
\begin{aligned}
Vu' &= (u+\bar{u}+v+\bar{v})\rho[1-K-L+L(1-c)],\\
V\bar{u}' &= (u+\bar{u}+v+\bar{v})\rho K(1-d-s),\\
Vv' &= (u+\bar{u}+v+\bar{v})(1-\rho)L(1-c),\\
V\bar{v}' &= (u+\bar{u}+v+\bar{v})(1-\rho)[(1-K-L)\\
&\quad\times(1-s)+K(1-d-s)],\\
Vx' &= (x+\bar{x}+y+\bar{y})\rho[1-K-\delta K\\
&\quad-L-\delta L+(L+\delta L)(1-c)],\\
V\bar{x}' &= (x+\bar{x}+y+\bar{y})\rho(K+\delta K)(1-d-s),\\
Vy' &= (x+\bar{x}+y+\bar{y})(1-\rho)(L+\delta L)(1-c),\\
V\bar{y}' &= (x+\bar{x}+y+\bar{y})(1-\rho)[(1-K-\delta K-L-\delta L)\\
&\quad\times(1-s)+(K+\delta K)(1-d-s)].
\end{aligned}
\tag{1}
$$

Second, when the environment remains constant between generations they are:

$$
\begin{aligned}
Wu' &= (u+\bar{u})[1-K-L+L(1-c)\\
&\quad+K(u+v+x+y)(1-d)],\\
W\bar{u}' &= (u+\bar{u})K(\bar{u}+\bar{v}+\bar{x}+\bar{y})(1-d-s),\\
Wv' &= (v+\bar{v})[L(1-c)+K(u+v+x+y)(1-d)],\\
W\bar{v}' &= (v+\bar{v})[(1-K-L)(1-s)\\
&\quad+K(\bar{u}+\bar{v}+\bar{x}+\bar{y})(1-d-s)],\\
Wx' &= (x+\bar{x})[1-K-\delta K-L-\delta L+(L+\delta L)\\
&\quad\times(1-c)+(K+\delta K)(u+v+x+y)(1-d)],\\
W\bar{x}' &= (x+\bar{x})(K+\delta K)(\bar{u}+\bar{v}+\bar{x}+\bar{y})(1-d-s),\\
Wy' &= (y+\bar{y})[(L+\delta L)(1-c)\\
&\quad+(K+\delta K)(u+v+x+y)(1-d)],\\
W\bar{y}' &= (y+\bar{y})[(1-K-\delta K-L-\delta L)(1-s)\\
&\quad+(K+\delta K)(\bar{u}+\bar{v}+\bar{x}+\bar{y})(1-d-s)].
\end{aligned}
\tag{2}
$$

The quantities V and W in (1) and (2) are the mean fitnesses that normalize the equations. Their explicit forms are not given, but can be obtained by summing the right-hand sides. Corresponding to the environmental periodicity of l, one set of iterations entails one application of (1) followed by $l-1$ applications of (2).

We now explain the derivation of these recursions, which are a direct extension of (20) and (21) of Feldman et al. (1996). First, we note that the first four lines of (1) and (2) describe changes in the frequencies of genotypes AM and Am, which have the A allele at the strategy locus, while the last four lines describe changes in the frequencies of genotypes aM and am, which have the a allele. Since the derivation of the last four lines is identical to that of the first four lines except for the substitution of $L+\delta L$ for L and $K+\delta K$ for K, the argument will not be repeated.

The recursions with stasis (2) are easier to explain, so we will deal with them first. Since reproduction is asexual, each offspring is genetically identical to its parent. Hence the frequencies of the genotypes AM and Am among newborns are $u+\bar{u}$ and $v+\bar{v}$, respectively. Since these genotypes have the A allele at the strategy locus, innate behavior, individual learning, and social learning occur with probabilities $1-K-L$, L, and K, respectively. When the innate strategy is adopted, the behavior of genotype AM is adaptive since it has an M allele at the innate information locus (fitness equals 1, first line), whereas the behavior of genotype Am is maladaptive since it has an m allele (fitness equals $1-s$, fourth line). With individual learning, behavior is always adaptive (fitness equals $1-c$, first and third lines). Socially learned behavior is adaptive if an adaptively behaving member of the previous generation, whose frequency is $u+v+x+y$, is copied (fitness equals $1-d$, first and third lines), and maladaptive if a maladaptively behaving member, whose frequency is $\bar{u}+\bar{v}+\bar{x}+\bar{y}$, is copied (fitness equals $1-d-s$, second and fourth lines).

The recursions with environmental change (1) can be obtained by modifying the above argument. Among the newborns of the postchange generation the frequencies of genotypes AM and Am are $\rho(u+\bar{u}+v+\bar{v})$ and $(1-\rho)(u+\bar{u}+v+\bar{v})$, respectively. Using the innate strategy, behavior is adaptive for genotype AM (first line), but maladaptive for genotype Am (fourth recursion). All individual learners behave adaptively (first and third lines), and all social learners behave maladaptively (second and fourth lines).

3. Analysis

Recall that the A and a alleles at the strategy locus determine two strategies that differ in the probabilities that behavior is innate, individually learned, or socially learned. These differences are expressed in terms of the parameters δL and δK. Our purpose in Sections 3–5 is to obtain the conditions for local stability of a monomorphism in the "wild type" allele A to invasion by the "mutant" allele a. In particular, if this genetic monomorphism is locally stable for all combinations of δL and δK, then by definition it corresponds to an ESS (Maynard Smith, 1982). We focus on the case of small δL and δK in this paper.

First, when the population is monomorphic for allele A, there exists a globally stable equilibrium solution of period l (Appendix A). Next, as shown in Appendix B, the dominant eigenvalue determining the local stability to invasion by allele a is

$$\lambda=\alpha\prod_{i=1}^{l-1}\gamma^{(i)}+\beta\prod_{i=1}^{l-1}\xi^{(i)}, \tag{3a}$$

where

$$\begin{aligned}
\alpha&=\rho\frac{\hat{V}+(1-K-L)(1-\rho)s}{\hat{V}}\\
&\quad\times\left[1-\frac{c\delta L+(d+s)\delta K}{\hat{V}+(1-K-L)(1-\rho)s}\right],\\
\beta&=(1-\rho)\frac{\hat{V}-(1-K-L)\rho s}{\hat{V}}\\
&\quad\times\left[1+\frac{(s-c)\delta L-d\delta K}{\hat{V}-(1-K-L)\rho s}\right],\\
\gamma^{(i)}&=\frac{W^{(i)}+(1-K-L)(\hat{v}^{(i)}+\hat{\bar{v}}^{(i)})s}{\hat{W}^{(i)}}\\
&\quad\times\left\{1-\frac{c\delta L+[d+(\bar{u}^{(i)}+\hat{\bar{v}}^{(i)})s]\delta K}{W^{(i)}+(1-K-L)(\hat{v}^{(i)}+\hat{\bar{v}}^{(i)})s}\right\},\\
\xi^{(i)}&=\frac{\hat{W}^{(i)}-(1-K-L)(\hat{u}^{(i)}+\hat{\bar{u}}^{(i)})s}{\hat{W}^{(i)}}\\
&\quad\times\left\{1+\frac{(s-c)\delta L-[d-(\hat{u}^{(i)}+\hat{v}^{(i)})s]\delta K}{\hat{W}^{(i)}-(1-K-L)(\hat{u}^{(i)}+\hat{\bar{u}}^{(i)})s}\right\}.
\end{aligned} \tag{3b}$$

Superscript i in (3) denotes the number of generations that have elapsed since an environmental change and the hat indicates monomorphic equilibrium. When $|\lambda|<1$, the periodic solution for the monomorphism in allele A (see (A.1), (A.2) of Appendix A) is locally stable to invasion by allele a.

For small δL and δK we approximate (3) by

$$\lambda\approx 1+C_L\delta L+C_K\delta K, \tag{4a}$$

where

$$\begin{aligned}
C_L&=\left\{\frac{\rho[\hat{V}+(1-K-L)(1-\rho)s]}{\hat{V}}\right.\\
&\quad\left.\times\prod_{i=1}^{l-1}\frac{\hat{W}^{(i)}+(1-K-L)(\hat{v}^{(i)}+\hat{\bar{v}}^{(i)})s}{\hat{W}^{(i)}}\right\}\\
&\quad\times\left\{-\frac{c}{\hat{V}+(1-K-L)(1-\rho)s}\right.\\
&\quad\left.-\sum_{i=1}^{l-1}\frac{c}{\hat{W}^{(i)}+(1-K-L)(\hat{v}^{(i)}+\hat{\bar{v}}^{(i)})s}\right\}\\
&\quad+\left\{\frac{(1-\rho)[\hat{V}-(1-K-L)\rho s]}{\hat{V}}\right.\\
&\quad\left.\times\prod_{i=1}^{l-1}\frac{\hat{W}^{(i)}-(1-K-L)(\hat{u}^{(i)}+\hat{\bar{u}}^{(i)})s}{\hat{W}^{(i)}}\right\}
\end{aligned}$$

$$\times\left\{\frac{s-c}{\hat{V}-(1-K-L)\rho s}+\sum_{i=1}^{l-1}\frac{s-c}{\hat{W}^{(i)}-(1-K-L)(\hat{u}^{(i)}+\hat{\tilde{u}}^{(i)})s}\right\}, \tag{4b}$$

$$\begin{aligned}C_K=&\left\{\frac{\rho[\hat{V}+(1-K-L)(1-\rho)s]}{\hat{V}}\times\prod_{i=1}^{l-1}\frac{\hat{W}^{(i)}+(1-K-L)(\hat{v}^{(i)}+\hat{\tilde{v}}^{(i)})s}{\hat{W}^{(i)}}\right\}\\&\times\left\{-\frac{d+s}{\hat{V}+(1-K-L)(1-\rho)s}-\sum_{i=1}^{l-1}\frac{d+(\hat{\tilde{u}}^{(i)}+\hat{\tilde{v}}^{(i)})s}{\hat{W}^{(i)}+(1-K-L)(\hat{v}^{(i)}+\hat{\tilde{v}}^{(i)})s}\right\}\\&+\left\{\frac{(1-\rho)[\hat{V}-(1-K-L)\rho s]}{\hat{V}}\times\prod_{i=1}^{l-1}\frac{\hat{W}^{(i)}-(1-K-L)(\hat{u}^{(i)}+\hat{\tilde{u}}^{(i)})s}{\hat{W}^{(i)}}\right\}\\&\times\left\{-\frac{d}{\hat{V}-(1-K-L)\rho s}-\sum_{i=1}^{l-1}\frac{d-(\hat{u}^{(i)}+\hat{v}^{(i)})s}{\hat{W}^{(i)}-(1-K-L)(\hat{u}^{(i)}+\hat{\tilde{u}}^{(i)})s}\right\}.\end{aligned} \tag{4c}$$

4. Special case of $K=L=0$

When allele A defines a strategy of pure innate behavior, (A.1), (A.2) of Appendix A can be explicitly solved to yield the periodic solution shown in Appendix C.

If $\rho\ll(1-s)^l$ holds, we have from (4) to leading order in ρ:

$$\lambda\approx 1+\frac{l}{1-s}[(s-c)\delta L-d\delta K] \tag{5}$$

(Appendix D). Since $s>c$ and $d>0$, we observe that $\lambda>1$ only if $\delta L>0$. In other words, a small amount of social learning in isolation ($\delta L=0$, $\delta K>0$) confers no advantage over the pure innate strategy (since $C_K=-\frac{ld}{1-s}<0$), so that a successful mutant allele a must have an individual learning component ($\delta L>0$).

In fact, we can show that $C_K<0$ is true in general (Appendix E). Hence, a necessary condition for instability is $C_L>0$. From (4b)

$$\begin{aligned}\hat{V}\prod_{i=1}^{l-1}\hat{W}^{(i)}\cdot C_L&=l[-\rho c+(1-\rho)(s-c)(1-s)^{l-1}]\\&=l[(1-c)\eta(l-1)-\eta(l)],\end{aligned} \tag{6a}$$

where

$$\eta(l)=\rho+(1-\rho)(1-s)^l. \tag{6b}$$

Hence, $C_L>0$ if and only if

$$\frac{\eta(l)}{\eta(l-1)}<1-c. \tag{7}$$

Thus, provided

$$\rho+(1-\rho)(1-s)<1-c, \tag{8}$$

there exists a unique integer $l_m^*(\geqslant 1)$ such that (7) is satisfied for $l\leqslant l_m^*$ (Appendix F).

Restated, the pure innate strategy is an ESS if inequality (8) is reversed or if $l>l_m^*$.

5. Special case of $K+L=1$

Allele A defines a mixed strategy of individual and social learning ($0<K=1-L<1$), a pure individual learning strategy ($L=1$), or a pure social learning strategy ($K=1$).

It is convenient to rewrite (4) by applying the transformation

$$\delta P=\frac{\delta K+\delta L}{2},\quad \delta Q=\frac{\delta K-\delta L}{2}. \tag{9}$$

In the parameter space of K and L (Fig. 1), δP and δQ are the components perpendicular and parallel to the line $K+L=1$, respectively. Clearly $\delta P\leqslant 0$, since the parameter space is a simplex. A mutant allele, a, that introduces a small innate component is characterized by $\delta P<0$. On the other hand, if the probabilities of individual and social learning are slightly altered without adding an innate component, then $\delta P=0$ and $\delta Q\neq 0$.

In terms of δP and δQ, the approximate eigenvalue (4a) becomes

$$\lambda\approx 1+C_P\delta P+C_Q\delta Q, \tag{10a}$$

where

$$\begin{aligned}C_P=&-\rho\left[\frac{s+c+d}{\hat{V}}+\sum_{i=1}^{l-1}\frac{s(\hat{\tilde{u}}^{(i)}+\hat{\tilde{v}}^{(i)})+c+d}{\hat{W}^{(i)}}\right]\\&+(1-\rho)\left[\frac{s-c-d}{\hat{V}}+\sum_{i=1}^{l-1}\frac{s(1+\hat{u}^{(i)}+\hat{v}^{(i)})-c-d}{\hat{W}^{(i)}}\right],\end{aligned} \tag{10b}$$

$$C_Q=-\frac{s-c+d}{\hat{V}}-\sum_{i=1}^{l-1}\frac{s(\hat{\tilde{u}}^{(i)}+\hat{\tilde{v}}^{(i)})-c+d}{\hat{W}^{(i)}}, \tag{10c}$$

with

$$\begin{aligned}\hat{V}&=L(1-c)+K(1-d-s),\\\hat{W}^{(i)}&=\hat{V}+K(\hat{u}^{(i)}+\hat{v}^{(i)})s.\end{aligned} \tag{10d}$$

In Appendix G, the binary sums of the phenogenotypes frequencies, $\hat{u}^{(i)}+\hat{v}^{(i)}$ and $\hat{\tilde{u}}^{(i)}+\hat{\tilde{v}}^{(i)}$, are obtained, which permits explicit evaluation of (10) (also (11) below).

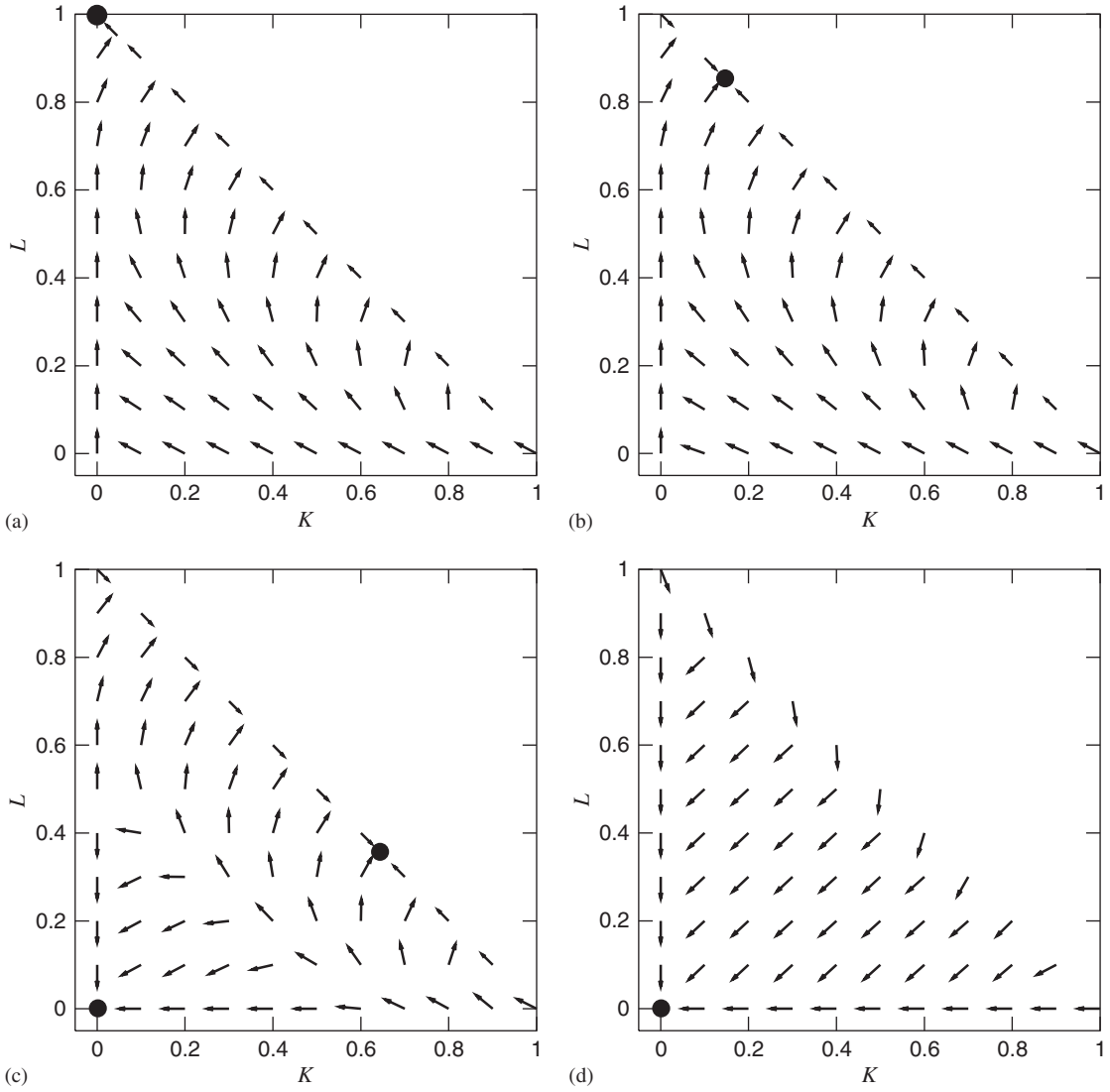

Fig. 1. Parameter space of K (probability of social learning) and L (probability of individual learning) is shown, with vector field (arrows) indicating the most likely direction that evolution by the cumulative substitution of mutations of small effect will take. Filled circles denote the convergent stable strategies (CSS), which are also evolutionarily stable (ESS). Other parameters are: for (a)–(c) $s = 0.3$, $c = 0.2$, $d = 0.19$, $\rho = 10^{-6}$, (a) $l = 20$, (b) $l = 35$, (c) $l = 70$, and for (d) $s = 0.3$, $c = 0.29$, $d = 0.28$, $\rho = 0.05$, $l = 100$.

Eq. (10) shows that a mixed learning strategy ($0<K=1-L<1$) can be locally stable against all alternative strategies with $\delta P = 0$ and $\delta Q \neq 0$ only if $C_Q = 0$, i.e.,

$$\frac{s-c+d}{\hat{V}}+\sum_{i=1}^{l-1}\frac{s(\hat{\tilde{u}}^{(i)}+\hat{\tilde{v}}^{(i)})-c+d}{\hat{W}^{(i)}}=0. \tag{11}$$

In addition, we require $C_P>0$ (to first order) when $\delta P<0$. Hence, a mixed learning strategy is an ESS (to first order) only if inequality $C_P>0$ and equality (11) are both satisfied ((11) can be solved numerically for L; Figs. 1 and 2).

Similarly, the pure individual learning strategy ($L = 1$) is locally stable against alternative strategies with $\delta P = 0$ and $\delta Q>0$ if $C_Q<0$, i.e.,

$$l<\frac{s}{c-d}. \tag{12}$$

Our assumption $0<d<c<s$ entails that (12) is satisfied for l sufficiently small. If (8) and (12) both hold, the pure individual learning strategy is an ESS (Appendix H).

Finally, the pure social learning strategy ($K = 1$) is always unstable. Conditions (11) and (12) were obtained by Feldman et al. (1996, p. 227).

6. Numerical work

For general K and L, we investigate the model numerically. The periodic equilibrium solution for the monomorphism in allele A is uniquely determined by iterating (A.1) and (A.2) of Appendix A. Moreover, local stability to invasion by allele a can be resolved by evaluating the eigenvalue (4). Let us represent the wild type strategy by a point (K, L) in the parameter space of K

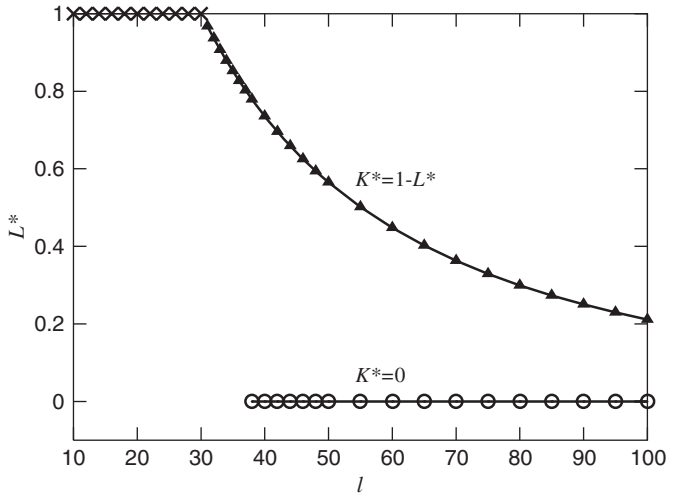

Fig. 2. A bifurcation diagram of AESS's. Attractive evolutionarily stable probability of individual learning, L^*, is plotted against the period of environmental change, l. For $l<\frac{s}{c-d}$, the pure individual learning strategy ($K^*=0$, $L^*=1$) is the unique AESS (crosses). For $\frac{s}{c-d}<l\leqslant l_m^*$, a mixed learning strategy ($0<L^*<1$, $K^*=1-L^*$) is the unique AESS (triangles). For $l>l_m^*$, the pure innate strategy ($K^*=0$, $L^*=0$) coexists as an AESS (circles) with a mixed learning strategy. Hence, the model exhibits "bistability" when $l>l_m^*$. Parameters are: $s=0.3$, $c=0.2$, $d=0.19$, $\rho=10^{-6}$. Critical values of the period are $\frac{s}{c-d}=30$, $l_m^*=37$, $l_M^*=61$.

and L (Fig. 1) and the mutant strategy by a neighboring point $(K+\delta K, L+\delta L)$. If (K, L) is an interior point, then $(K+\delta K,\ L+\delta L)$ may occupy any one of the four quadrants centered on (K, L). For a boundary point (K, L), there are restrictions on $(\delta K, \delta L)$, for example as noted in Section 5 and Appendix H. With each point (K, L) there is associated a vector of coefficients (C_K, C_L) defined by (4b) and (4c), which in conjunction with the vector of differences $(\delta K, \delta L)$ determines whether the mutant strategy will invade.

The wild type strategy is locally stable to invasion by any mutant strategy for which $C_L\delta L+C_K\delta K$ (the inner product of the two vectors) is negative. This will be the case when the angle between $(\delta K, \delta L)$ and (C_K, C_L) exceeds 90°. On the other hand, the wild type strategy will be invaded by any mutant strategy for which $C_L\delta L+C_K\delta K>0$. This inequality will hold if the angle between $(\delta K, \delta L)$ and (C_K, C_L) is less than 90°. Hence, if we view evolution as proceeding gradually by the cumulative substitution of mutations of small effect (not necessarily at the same genetic locus), the vector (C_K, C_L) serves as a rough indicator of the direction in parameter space that evolution will take.

In Fig. 1 we have drawn "vector fields" obtained by plotting the vectors (C_K, C_L) at various interior and boundary points of the parameter space. Thus, an orbit in this vector field represents an evolutionary path. A CSS is obtained numerically as the stable equilibrium to which the dynamical system

$$\dot{K}=C_K,\ \ \dot{L}=C_L \tag{13}$$

converges in the simplex $0\leqslant K\leqslant 1$, $0\leqslant L\leqslant 1$, and $0\leqslant K+L\leqslant 1$ (Fig. 1). The dots over K and L in (13) signify differentiation by a time variable, and of course the CSS may depend on the initial conditions. The method described here is similar to the adaptive dynamics approach (e.g., Geritz et al., 1997), where the gradient of the fitness landscape is (C_K, C_L). We first solve (13) numerically to locate the CSS's. Then we check that these equilibria are also ESS's. As shown in Sections 4 and 5, tests of evolutionary stability are available in the special cases $K=L=0$ and $K+L=1$. (Appendix I illustrates the difference between CSS and ESS.)

The numerical work suggests that there are no interior CSS's, which would require $C_K=C_L=0$. Neither do we find CSS's on the L-axis ($K=0$, $0<L<1$) or the K-axis ($L=0$, $0<K\leqslant 1$). Thus, a strategy with both an innate and a learning (whether individual or social) component cannot be a CSS. The CSS's are the pure individual learning strategy, a mixed learning strategy, and the pure innate strategy. In fact, as we see below, each CSS is also an ESS, hence an AESS.

Fig. 1a illustrates the case where the pure individual learning strategy is the unique CSS. Fig. 1b shows that a mixed learning strategy can be the unique CSS. In Fig. 1c there are two CSS's, the pure innate strategy and a mixed learning strategy. Although not shown, the pure innate CSS may coexist with the pure individual learning CSS. Finally, the pure innate strategy can be the sole CSS as shown in Fig. 1d. Each pure individual learning CSS and pure innate CSS is also an ESS, as can be verified by application of (7), (8), and (12). In addition, numerical work using (10b) and (11) suggests that each mixed learning CSS is an ESS; since (11) is necessary but not sufficient, local stability against mutant strategies represented by neighboring points of the parameter space was checked by iterating (1) and (2).

Fig. 2 is a "bifurcation diagram" illustrating the dependence of the AESS's on parameter l (the environmental periodicity). Inequality (8) holds in this figure (other parameter are: $s=0.3$, $c=0.2$, $d=0.19$, $\rho=10^{-6}$), whence the pure individual learning strategy is an ESS for $l<\frac{s}{c-d}$ (i.e., when (12) is satisfied), and the pure innate strategy is an ESS for $l>l_m^*$ (i.e., when (7) is reversed). Numerical work using (10b) and (11) suggests that a mixed learning ESS exists for each $l>\frac{s}{c-d}$. All points indicated by crosses, triangles, or circles have been shown numerically to be CSS's. Hence, there are apparently two AESS's when $l>l_m^*$.

On the basis of extensive numerical work, we have identified two other bifurcation patterns when l is varied. First, if inequality (8) is reversed (because the penalty suffered by individual learners, c, is almost as large as the cost of maladaptive behavior, s), the pure innate strategy appears to be the only ESS. In this case, learning cannot evolve whatever the value of l. Second, if $l_m^*<\frac{s}{c-d}$ (e.g., for parameter values $s=0.4$, $c=0.39$, $d=0.38$, $\rho=10^{-6}$), the pure individual learning ESS coexists with the pure innate

ESS for $l_m^* < l < \frac{s}{c-d}$, whereas a mixed learning ESS and the pure innate ESS coexist for $l > \frac{s}{c-d}$. All ESS's are also CSS's, hence AESS's.

It is also possible to plot bifurcation diagrams against other parameters. Let us briefly note the effect of parameter ρ. The pure innate strategy is an ESS if $C_L < 0$ in (6a), or equivalently

$$\rho > \frac{(s-c)(1-s)^{l-1}}{c+(s-c)(1-s)^{l-1}}. \tag{14}$$

In words, the frequency of preadapted alleles at the innate information locus must be sufficiently high. From (11) we see that the probability of individual learning, L, at a mixed learning strategy is independent of ρ. Evolutionary stability, however, requires that $C_P > 0$ in (10b). A necessary but not sufficient condition for this inequality to hold is that ρ be sufficiently small. Numerical work shows that an ESS is also a CSS, hence an AESS. Thus, a possible bifurcation pattern comprises two horizontal straight lines, one representing the pure innate strategy, which is an AESS when (14) is satisfied, and the other a mixed learning strategy, which is an AESS for sufficiently small values of ρ.

7. Discussion

We studied the evolution of social learning in a model where small genotypic differences occur in the probabilities that an organism will commit itself to individual learning, social learning, or innate determination of behavior. Analytical and numerical methods were employed to identify the evolutionarily stable pure or mixed strategies (ESS) that are also CSS. The possible AESS are the pure innate strategy ($K = 0$, $L = 0$), a mixed learning strategy ($0 < L < 1$, $K = 1 - L$), and the pure individual learning strategy ($K = 0$, $L = 1$).

It is perhaps surprising that no AESSs are found with both an innate and a learning component. This result apparently contradicts the observation that some strategies currently used by humans, for example in language acquisition, involve learning subject to innate constraints (Chomsky, 1975; Bickerton, 1983). We can think of at least three reasons for the discrepancy. First, the present model may be too simple—we have assumed that each organism commits itself during development to one of three pure strategies, whereas actual examples of a mixed strategy often involve the simultaneous application of two or more pure strategies by the same organism—which is the most likely explanation. Second, a current strategy may not be an AESS, since the waiting time for the appropriate mutations may be prohibitively long. Third, the fault may lie with our reliance on numerical method alone to locate the CSS's—no numerical survey can claim to be complete.

According to the bifurcation diagram of Fig. 2, the pure individual learning strategy is the unique AESS if the environmental periodicity is short $\left(l < \frac{s}{c-d}\right)$, a mixed learning strategy is the unique AESS if changes occur with intermediate frequency $\left(\frac{s}{c-d} < l \leqslant l_m^*\right)$, and two AESSs—a mixed learning strategy (with a relatively large social learning component, K) and the pure innate strategy—coexist if the environment is highly stable $\left(l > l_m^*\right)$. Except for the continued presence of a mixed learning AESS beyond the threshold l_m^*, with implications discussed below, the dependence on the environmental periodicity is essentially the same as that noted by Wakano et al. (2004) and Aoki et al. (2005).

Let us assume the bifurcation diagram of Fig. 2. Then, to reiterate, the pure innate strategy is an AESS if the environmental periodicity $l > l_m^*$. On the other hand, if the environment is sufficiently changeable so that $l \leqslant l_m^*$ (i.e., when (7) holds), the pure innate strategy is invadable, but only by a mutant strategy with an individual learning component that is large relative to the social learning component ($0 \leqslant \delta K < \delta L$, see Section 4). Hence, the initial evolution of learning from an ancestral state of innate behavior likely involves a stage in which learning, on the rare occasions that it occurs, is entirely or predominantly individual. Nevertheless, by the cumulative substitution of mutations of small effect, the relative reliance on social learning will subsequently increase if $\frac{s}{c-d} < l \leqslant l_m^*$ (depending on the parameter set, this interval may not be as narrow as Fig. 2 would suggest). Ultimately, a mixed learning strategy with a non-negligible social learning component will evolve, as this is the unique AESS (Fig. 1b) in this case.

Still assuming the same bifurcation diagram, suppose that a population at this mixed learning AESS (Fig. 1b) now experiences a more stable environment ($l > l_m^*$). Two AESS's, the pure innate strategy and a mixed learning strategy with a relatively larger social learning component (Fig. 1c), replace the previous unique AESS (Fig. 1b). This population will not necessarily evolve back to the pure innate condition ($K = 0$, $L = 0$,). Rather, the vector field of Fig. 1c suggests it is more likely to evolve along the edge $K + L = 1$ toward the new AESS with the greater reliance on social learning (a larger value of K). Hence, the model exhibits "irreversibility". Once social learning emerges during a temporary era of intermediate environmental stability, a subsequent elongation of the environmental periodicity toward increased stability may result in the intensification of social learning, rather than a return to innate behavior.

Richerson and Boyd (2005) note a possible connection between the evolution of social learning in humans and the increased variability of the world's climate during the Pleistocene (beginning about 2 million years ago). On the other hand, the climate has been very stable according to the ice core data for the last 10,000 years, or about 500 generations. (Nevertheless, even in a stable climate, range expansion and migration may have caused drastic and rapid changes in the environment governing the evolution of early humans.) The irreversibility of our model may account for the observation that our social learning ability has not been lost.

In stark contrast, the Wakano et al. (2004) major gene model predicts a sharp threshold, l_M^*, above and below which obligate innate behavior and a polymorphism of obligate individual and social learners, respectively, are globally stable. Here, l_M^* is defined as the largest integer that satisfies the inequality

$$\eta(l)<(1-c)^l \tag{15}$$

where $\eta(l)$ is given by (6b). Incidentally, $l_m^*<l_M^*$ (Appendix F), which entails more stringent conditions for the invadability of the pure innate strategy in the present model.

We have begged the question of the accuracy of social learning, by assuming that the behavior of the exemplar is faithfully reproduced in the observer. However, a more fundamental analysis would require us to show that social learning does indeed evolve toward greater precision. Given that it does, when the reliability of social learning has attained a level sufficient for the development of a cumulative culture, we would expect that culture to affect the environment, in particular render it more, or less, stable. Clearly, such "cultural niche construction" (Laland et al., 2000; Odling-Smee et al., 2003; Ihara and Feldman, 2004) could have far reaching implications. (We say *more*, or *less*, because it is not obvious what the long-term, as opposed to the immediate effects, of an innovation will be. For example, the control of fire and the making of clothing greatly modified the hominid niche, but these innovations also provided protection against temperature fluctuations.) To fully understand the nature of human social learning, it is necessary to take into account the fact that a significant part of our environment is, and has been, "man-made". Note our use of the adjective "natural" in the title of the present paper to emphasize the limitations of the research described here.

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Appendix A

Using superscripts to denote the number of generations that have elapsed after an environmental change, we observe from (1) that

$$\begin{aligned}
\hat{u}^{(1)} &= \rho[1-K-L+L(1-c)]/\hat{V},\\
\hat{\tilde{u}}^{(1)} &= \rho K(1-d-s)/\hat{V},\\
\hat{v}^{(1)} &= (1-\rho)L(1-c)/\hat{V},\\
\hat{\tilde{v}}^{(1)} &= (1-\rho)[(1-K-L)(1-s)+K(1-d-s)]/\hat{V},
\end{aligned} \tag{A.1a}$$

where

$$\begin{aligned}
\hat{V} &= (1-K-L)[\rho+(1-\rho)(1-s)]\\
&\quad + L(1-c)+K(1-d-s),
\end{aligned} \tag{A.1b}$$

and from (2) that

$$\begin{aligned}
\hat{u}^{(i)} &= (\hat{u}^{(i-1)}+\hat{\tilde{u}}^{(i-1)})[1-K-L+L(1-c)\\
&\quad + K(\hat{u}^{(i-1)}+\hat{v}^{(i-1)})(1-d)]/\hat{W}^{(i-1)},\\
\hat{\tilde{u}}^{(i)} &= (\hat{u}^{(i-1)}+\hat{\tilde{u}}^{(i-1)})K(\hat{\tilde{u}}^{(i-1)}+\hat{\tilde{v}}^{(i-1)})\\
&\quad \times(1-d-s)/\hat{W}^{(i-1)},\\
\hat{v}^{(i)} &= (\hat{v}^{(i-1)}+\hat{\tilde{v}}^{(i-1)})[L(1-c)\\
&\quad + K(\hat{u}^{(i-1)}+\hat{v}^{(i-1)})(1-d)]/\hat{W}^{(i-1)},\\
\hat{\tilde{v}}^{(i)} &= (\hat{v}^{(i-1)}+\hat{\tilde{v}}^{(i-1)})[(1-K-L)(1-s)\\
&\quad + K(\hat{\tilde{u}}^{(i-1)}+\hat{\tilde{v}}^{(i-1)})(1-d-s)]/\hat{W}^{(i-1)},
\end{aligned} \tag{A.2a}$$

where

$$\begin{aligned}
\hat{W}^{(i-1)} &= (1-K-L)[\hat{u}^{(i-1)}+\hat{\tilde{u}}^{(i-1)}\\
&\quad + (\hat{v}^{(i-1)}+\hat{\tilde{v}}^{(i-1)})(1-s)]\\
&\quad + L(1-c)+K[(\hat{u}^{(i-1)}+\hat{v}^{(i-1)})(1-d)\\
&\quad + (\hat{\tilde{u}}^{(i-1)}+\hat{\tilde{v}}^{(i-1)})(1-d-s)]
\end{aligned} \tag{A.2b}$$

for $2\leqslant i\leqslant l$. Recursions (A.2) can be solved iteratively with (A.1) as the initial conditions to yield a periodic solution. Global stability in the genetically monomorphic subspace is assured, since the phenogenotype frequencies in the postchange generation assume fixed values (see formulae for $\hat{u}^{(1)}, \hat{\tilde{u}}^{(1)}, \hat{v}^{(1)}, \hat{\tilde{v}}^{(1)}$ in (A.1)).

Appendix B

Take $x^{(i)}+\bar{x}^{(i)}$ and $y^{(i)}+\bar{y}^{(i)}$ as the small variables. Let $x^{(0)}+\bar{x}^{(0)}$ and $y^{(0)}+\bar{y}^{(0)}$ be the initial deviations from the equilibrium point $(\hat{u}^{(0)}, \hat{\tilde{u}}^{(0)}, \hat{v}^{(0)}, \hat{\tilde{v}}^{(0)})$, where the superscript 0 denotes the prechange generation. Then, after one application of (1) followed by $l-1$ applications of (2), we have

$$\begin{pmatrix} x^{(l)}+\bar{x}^{(l)} \\ y^{(l)}+\bar{y}^{(l)} \end{pmatrix} = \prod_{i=1}^{l-1} \begin{pmatrix} \gamma^{(i)} & 0 \\ 0 & \xi^{(i)} \end{pmatrix} \times \begin{pmatrix} \alpha & \alpha \\ \beta & \beta \end{pmatrix} \begin{pmatrix} x^{(0)}+\bar{x}^{(0)} \\ y^{(0)}+\bar{y}^{(0)} \end{pmatrix},$$

where the elements of the coefficient matrices are (3b). Clearly, the dominant eigenvalue is (3a).

Appendix C

Substitute $K=L=0$ in (A.1) and (A.2). Then,

$$\hat{\tilde{u}}^{(i)} = \hat{v}^{(i)} = 0 \quad \text{for } 1\leqslant i\leqslant l, \tag{C.1a}$$

$$\hat{V} = \rho+(1-\rho)(1-s), \tag{C.1b}$$

$$\hat{W}^{(i)} = \hat{u}^{(i)}+\hat{\tilde{v}}^{(i)}(1-s) \quad \text{for } 1\leqslant i\leqslant l-1. \tag{C.1c}$$

Next, taking the ratio of the first and fourth lines of (A.2a) yields the linear recursion

$$\frac{\hat{u}^{(i)}}{\hat{\tilde{v}}^{(i)}}=\frac{\hat{u}^{(i-1)}}{\hat{\tilde{v}}^{(i-1)}}\frac{1}{1-s},$$

which can be solved with the initial condition

$$\frac{\hat{u}^{(1)}}{\hat{\tilde{v}}^{(1)}}=\frac{\rho}{(1-\rho)(1-s)}.$$

Thus

$$\frac{\hat{u}^{(i)}}{\hat{\tilde{v}}^{(i)}}=\frac{\rho}{1-\rho}\left(\frac{1}{1-s}\right)^{i},$$

or equivalently

$$\hat{u}^{(i)}=\frac{\rho}{\rho+(1-\rho)(1-s)^{i}}. \tag{C.2}$$

Substituting (C.2) in (C.1) gives

$$\hat{W}^{(i)}=\frac{\rho+(1-\rho)(1-s)^{i+1}}{\rho+(1-\rho)(1-s)^{i}}\quad \text{for } 1\leqslant i\leqslant l-1. \tag{C.3}$$

Appendix D

Substituting $K=L=0$ and (C.1) in (4b) gives

$$C_L=[-\rho lc+(1-\rho)l(s-c)(1-s)^{l-1}]\frac{1}{\hat{V}}\prod_{i=1}^{l-1}\frac{1}{\hat{W}^{(i)}}. \tag{D.1a}$$

Similarly from (4c)

$$C_K=-\left\{\rho\left[ld+s\left(1+\sum_{i=1}^{l-1}\hat{\tilde{v}}^{(i)}\right)\right]+(1-\rho)(1-s)^{l-1}\times\left[ld-s\sum_{i=1}^{l-1}\hat{u}^{(i)}\right]\right\}\frac{1}{\hat{V}}\prod_{i=1}^{l-1}\frac{1}{\hat{W}^{(i)}}. \tag{D.1b}$$

Using (C.1b) and (C.3), we achieve the simplification

$$\frac{1}{\hat{V}}\prod_{i=1}^{l-1}\frac{1}{\hat{W}^{(i)}}=\frac{1}{\rho+(1-\rho)(1-s)^{l}}. \tag{D.2}$$

We now use the assumption $\rho\ll(1-s)^{l}$ to obtain the zeroth order approximation in the small quantity ρ. First, (D.2) reduces to $\frac{1}{(1-s)^{l}}$. Second, (C.2) shows that $\hat{u}^{(i)}$ in (D.1b) are first order in ρ, and hence can be neglected. Thus,

$$C_L=\frac{l(s-c)}{1-s},\quad C_K=-\frac{ld}{1-s}$$

as required.

Appendix E

The terms multiplied by d or $d+s$ on the right-hand side of (4c) are negative. Hence,

$$\begin{aligned}C_K<&\left\{\frac{\rho[\hat{V}+(1-K-L)(1-\rho)s]}{\hat{V}}\times\prod_{i=1}^{l-1}\frac{\hat{W}^{(i)}+(1-K-L)(\hat{v}^{(i)}+\hat{\tilde{v}}^{(i)})s}{\hat{W}^{(i)}}\right\}\\&\times\left\{-\sum_{i=1}^{l-1}\frac{(\hat{\tilde{u}}^{(i)}+\hat{\tilde{v}}^{(i)})s}{\hat{W}^{(i)}+(1-K-L)(\hat{v}^{(i)}+\hat{\tilde{v}}^{(i)})s}\right\}\\&+\left\{\frac{(1-\rho)[\hat{V}-(1-K-L)\rho s]}{\hat{V}}\times\prod_{i=1}^{l-1}\frac{\hat{W}^{(i)}-(1-K-L)(\hat{u}^{(i)}+\hat{\tilde{u}}^{(i)})s}{\hat{W}^{(i)}}\right\}\\&\times\left\{\sum_{i=1}^{l-1}\frac{(\hat{u}^{(i)}+\hat{v}^{(i)})s}{\hat{W}^{(i)}-(1-K-L)(\hat{u}^{(i)}+\hat{\tilde{u}}^{(i)})s}\right\}.\end{aligned}$$

Since $K+L=0$, and Appendix C informs us that $\hat{\tilde{u}}^{(i)}=\hat{v}^{(i)}=0$, $\hat{V}=\rho+(1-\rho)(1-s)$, and $\hat{W}^{(i)}=\hat{u}^{(i)}+\hat{\tilde{v}}^{(i)}(1-s)$, this simplifies to

$$\hat{V}\prod_{i=1}^{l-1}\hat{W}^{(i)}\cdot C_K<-\rho\sum_{i=1}^{l-1}\hat{\tilde{v}}^{(i)}s+(1-\rho)(1-s)^{l}\sum_{i=1}^{l-1}\frac{\hat{u}^{(i)}s}{1-s}.$$

Thus, substituting the explicit values of $\hat{u}^{(i)}$ and $\hat{\tilde{v}}^{(i)}$ from Appendix C, we obtain

$$\hat{V}\prod_{i=1}^{l-1}\hat{W}^{(i)}\cdot C_K<\rho(1-\rho)s\sum_{i=1}^{l-1}\frac{(1-s)^{l-1}-(1-s)^{i}}{\rho+(1-\rho)(1-s)^{i}}<0.$$

Appendix F

The ratio $\frac{\eta(l)}{\eta(l-1)}$, where $\eta(l)$ is defined in (6b), is monotone increasing in l. Moreover, $\frac{\eta(1)}{\eta(0)}=\rho+(1-\rho)(1-s)$ and $\lim_{l\to\infty}\frac{\eta(l)}{\eta(l-1)}=1$. Hence, provided (8) holds, there exists a unique root, θ, of the equation

$$\frac{\eta(\theta)}{\eta(\theta-1)}=1-c$$

Next, we show that (7) is more stringent than (15). Suppose $l\leqslant l_m^*$. Then

$$\eta(l)=\frac{\eta(1)}{\eta(0)}\times\frac{\eta(2)}{\eta(1)}\times\cdots\times\frac{\eta(l)}{\eta(l-1)}<(1-c)^{l},$$

since $\eta(0)=1$. Hence, $l\leqslant l_m^*$ implies $l\leqslant l_M^*$.

Appendix G

Setting $K+L=1$ in (A.1a) and taking the ratio of the binary sums of appropriate lines yields

$$\frac{\hat{u}^{(1)}+\hat{v}^{(1)}}{\hat{\bar{u}}^{(1)}+\hat{\bar{v}}^{(1)}}=\frac{L(1-c)}{K(1-d-s)}.$$

Next, doing the same with (A.2a) gives

$$\begin{aligned}\frac{\hat{u}^{(i)}+\hat{v}^{(i)}}{\hat{\bar{u}}^{(i)}+\hat{\bar{v}}^{(i)}}&=\frac{L(1-c)+K(\hat{u}^{(i-1)}+\hat{v}^{(i-1)})(1-d)}{K(\hat{\bar{u}}^{(i-1)}+\hat{\bar{v}}^{(i-1)})(1-d-s)}\\&=\frac{L(1-c)+K(1-d)}{K(1-d-s)}\frac{\hat{u}^{(i-1)}+\hat{v}^{(i-1)}}{\hat{\bar{u}}^{(i-1)}+\hat{\bar{v}}^{(i-1)}}\\&\quad+\frac{L(1-c)}{K(1-d-s)}.\end{aligned}$$

Hence, setting $a=\frac{L(1-c)+K(1-d)}{K(1-d-s)}$ and $b=\frac{L(1-c)}{K(1-d-s)}$, we obtain

$$\frac{\hat{u}^{(i)}+\hat{v}^{(i)}}{\hat{\bar{u}}^{(i)}+\hat{\bar{v}}^{(i)}}=b\frac{1-a^i}{1-a},$$

or equivalently

$$\hat{u}^{(i)}+\hat{v}^{(i)}=\frac{b(1-a^i)}{1-a+b(1-a^i)}.$$

Appendix H

Any alternative to the pure individual learning strategy has $\delta P\leqslant 0$ and $\delta Q>0$, where consistency requires $-\delta Q<\delta P\leqslant 0$. When $L=1$,

$$C_P=\frac{[2l(1-\rho)-1]s-l(c+d)}{1-c},$$

$$C_Q=-\frac{s-c+d-(l-1)(c-d)}{1-c},$$

where (12) entails $C_Q<0$. If $C_P>0$, then clearly $\lambda<1$, and we are done. If $C_P<0$, the constraint $-\delta Q<\delta P\leqslant 0$ implies $C_P\delta P<-C_P\delta Q$, so that $\lambda<1-(C_P-C_Q)\delta Q$. But $C_P-C_Q=2l[(1-\rho)s-c]/(1-c)$. Hence, $\lambda<1$ when $c<(1-\rho)s$, or equivalently (8).

Appendix I

The eigenvalue (3) is a function of the wild type strategy (K, L) and the mutant strategy $(K+\delta K, L+\delta L)$. As a purely hypothetical example, suppose

$$\lambda=1+a[(K-K^*)\delta K+(L-L^*)\delta L]+b[(\delta K)^2+(\delta L)^2],$$

where (K^*, L^*) is an interior point, and a, b are constants. Then, $C_K=a(K-K^*)$ and $C_L=a(L-L^*)$. Clearly, (K^*, L^*) is an ESS if $b<0$, i.e., if the quadratic form in δK and δL is negative definite. However, if $a>0$, then all vectors originating at neighboring points $(K^*+\delta K, L^*+\delta L)$ are directed outward from (K^*, L^*). Hence, (K^*, L^*) is not a CSS. Conversely, if $a<0$ but $b>0$, then (K^*, L^*) is a CSS but not an ESS, since all vectors originating at neighboring points $(K^*+\delta K, L^*+\delta L)$ are directed toward (K^*, L^*), but the eigenvalue at (K^*, L^*) is greater than one.

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