The evolution of conformist transmission in social learning when the environment changes periodically

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Abstract

Conformity is often observed in human social learning. Social learners preferentially imitate the majority or most common behavior in many situations, though the strength of conformity varies with the situation. Why has such a psychological tendency evolved? I investigate this problem by extending a standard model of social learning evolution with infinite environmental states (Feldman, M.W., Aoki, K., Kumm, J., 1996. Individual versus social learning: evolutionary analysis in a fluctuating environment. Anthropol. Sci. 104, 209–231) to include conformity bias. I mainly focus on the relationship between the strength of conformity bias that evolves and environmental stability, which is one of the most important factors in the evolution of social learning. Using the evolutionarily stable strategy (ESS) approach, I show that conformity always evolves when environmental stability and the cost of adopting a wrong behavior are small, though environmental stability and the cost of individual learning both negatively affect the strength of conformity.

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1. Introduction

It has often been argued that one of the most unique characteristics of the human is culture, which is brought about by the ability of social learning. Although sometimes other animals have been observed to learn socially (reviewed in Zentall, 2001; Brown and Laland, 2003; Byrne et al., 2004; Whiten et al., 2004; Galef and Laland, 2005), their learned behaviors are not as complex as those of the human. Hence, many anthropologists have researched why human social learning has evolved (reviewed in Flinn, 1997) and theoretically analyzed the conditions that facilitate the spread of social learning in a population (Cavalli-Sforza and Feldman, 1983; Boyd and Richerson, 1985, 1988; Rogers, 1988; Feldman et al., 1996; Henrich and Boyd, 1998; Wakano et al., 2004; Aoki et al., 2005; Wakano and Aoki, 2006).

Environmental stability is thought to be one of the most important factors of the evolution of social learning (Rogers, 1988; Feldman et al., 1996; Wakano et al., 2004; Aoki et al., 2005; Wakano and Aoki, 2006). It has been argued that individual learning is adaptive when environmental stability is low whereas innate behavior is adaptive when environmental stability is high, so that social learning can evolve only when environmental stability is intermediate (Wakano et al., 2004; Aoki et al., 2005). In these models, social learners simply imitate the previous generation’s behaviors according to their frequencies. But actually, human social learning strategy is more complex (reviewed in Laland, 2004).

For example, there is a powerful tendency of conformity in human social learning (reviewed in Boyd and Richerson, 1985). That is, social learners preferentially imitate the majority, or most common behavior (when there are three or more alternatives). This tendency is thought to cause the variation of culture between communities (Boyd and Richerson, 1985; Henrich and Boyd, 1998), to result in group selection (Boyd and Richerson, 1992), to affect adoption dynamics (Henrich, 2001), to stabilize cooperation and punishment (Henrich and Boyd, 2001) and to lead to selection in favor of more restrictive genes (genes that
allow a narrower range of signals to be recognized) (Lachlan and Feldman, 2003). Why do we have such a psychological mechanism? In what condition is it adaptive?

Conformity is obviously adaptive in some situations. For example, when learning a language, it may be advantageous to learn a language with more speakers because it is more useful to communicate with many people. A similar situation may apply to bird song. That is, song sharing among neighbors is thought to be beneficial to avoid aggressive interaction, and Lachlan et al. (2004) argued that conformity-enforcing behavior is successful in their model of bird song. Furthermore, conformity is argued to arise when status is important and seriously impaired by departures from the social norm (Bernheim, 1994).

Conformity is, however, often observed in situations where the merit of behaving as the majority is uncertain, as shown by some psychological experiments. For example, Coulta (2004) showed that individuals preferentially imitate the most common way when they write the date. Why even in such situation do we show a tendency of conformity? Why have we evolved to have such a psychological mechanism? This is the problem I investigate in this paper. As conformity is an attribute of human social learning, an evolutionary model of conformity should be formed as extension of social learning model. Then, the relevant question is whether environmental stability affects the strength of conformity bias.

Boyd and Richerson (1985) showed that natural selection favors conformist transmission relative to unbiased transmission in spatially varying environments, but their model did not include temporal environmental change. Henrich and Boyd (1998) analyzed a model of the evolution of conformist transmission in an environment that varies in both space and time. They assumed a haploid genetic system with 400 alleles that vary in both the degree of reliance on social learning and the strength of conformist transmission, and obtained the evolutionary equilibrium by way of numerical simulation. Then they showed that there is a synergistic relationship between the evolution of imitation and the evolution of conformism. That is, when environmental stability is high, social learning and conformist transmission evolve simultaneously. (Note that in this model innate behavior is not incorporated so that individual learning is adaptive when environmental stability is low and social learning is adaptive when environmental stability is high.) Moreover, they argued that conformist transmission is favored under a very broad range of conditions. However, Wakano and Aoki (submitted) found that some results of Henrich and Boyd (1998) are wrong. For example, they showed that the relationship between the strength of conformist transmission and environmental stability is not positive but negative. The reason why Henrich and Boyd (1998) obtained the wrong results is that they did not allow a sufficient number of iterations for true convergence to occur (Wakano and Aoki, submitted). Wakano and Aoki (submitted) checked this by replicating Henrich and Boyd (1998)'s simulations and showed that the stopping rule used by them is insufficient to obtain the true equilibrium values.

Moreover, Henrich and Boyd (1998)'s model considered two environmental states (two behaviors) so that when the environment changes twice, a behavior becomes adaptive again. Since the environment changes to various directions in the real world, the two environmental state model is somewhat unrealistic and the infinite environmental state model (Feldman et al., 1996) is preferable. Though comparative analysis of the two environmental state and the infinite environmental state models yielded qualitatively similar predictions about the evolution of social learning (Feldman et al., 1996), it is uncertain whether both models will yield similar results about the evolution of conformist transmission. In addition, the assumption of infinite environmental state entails that there will be many (more than two) alternative behaviors. In this paper, I develop a method to deal with the evolution of conformist transmission under these circumstances.

Kameda and Nakamichi (2002) extended Henrich and Boyd (1998)'s work by adding a cost to individual learning and argued that when individual learning is costly, conformity bias evolves to be small. This result is also supported by their laboratory experiment. However, the relationship between the strength of conformity bias and environmental stability is uncertain in their work.

McElreath et al. (2005) compared their laboratory experiments of social learning to theoretical expectations. Though they found in their theoretical expectations that conformity is always more advantageous than other candidate strategies in their experimental environment, conformity is observed in their laboratory experiments only when there is environmental fluctuation. This disagreement may be caused by the properties of the laboratory experiments. That is, in the laboratory experiments it is difficult for participants to find the best strategy (as defined by the theoretical expectations), so that participants may mainly behave according to their psychological tendency. So, humans may have a psychological tendency to increase the strength of conformity bias when they believe that environmental stability has decreased, though their theoretical expectations make the opposite prediction that more fluctuation means less reliance on conformity.

In this paper, I analyze the conditions for the evolution of positive conformity bias by extending the infinite environmental state mixed strategy model of Feldman et al. (1996). The evolutionarily stable strategy (ESS) method (Maynard Smith, 1982) is used to clarify the relationship between the strength of conformity bias and the environmental stability. The ESS approach is preferable to Monte Carlo or agent-based simulations when we want to obtain mathematically rigorous results. In Models 1 and 2, I use different expressions for conformist transmission by assuming that there are only two behaviors, correct and wrong. In these models, I numerically obtain the ESS values (of the strength of conformity bias and the
probability of adopting the individual learning strategy) and the condition for positive conformity bias to evolve under various conditions, and show that the results of both models are similar. Since the count of behaviors and count of environmental states is inconsistent in Models 1 and 2, I make both infinite in Model 3 by extending Model 2 and test whether the results of Models 1 and 2 are robust to infinite behavioral options.

2. Models

2.1. Overview

Consider a periodically changing 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 environmental state there is one optimal (correct) behavior (fitness: 1) and other behaviors are equally maladaptive (fitness: 1−s; i.e. the cost of maladaptive behavior is s). The environment changes every ℓ generations (ℓ≥1), so that one postchange generation experiences a different environmental state as the previous generation, and ℓ−1 subsequent generations experience the same state as that postchange generation. That is, larger values of ℓ imply more environmental stability.

Individual learners (IL) always achieve the optimal (correct) behavior, but suffer a fixed cost c. Social learners copy a behavior of the previous generation (oblique transmission). So, when the environment changes, social learners always copy a maladaptive (wrong) behavior and only IL behave correctly. The fitness of IL is 1−c, that of social learners behaving correctly (SLC) is 1, and that of social learners behaving wrongly (SLW) is 1−s (0<s<1). Of course, SLC also suffer some learning cost, but we set their relative fitness to 1 for simplicity. If c>s, IL are selected out and all organisms become SLW so that c<s is the necessary condition for the coexistence of SLC and IL.

Each organism can learn individually or socially and the probability of adopting the individual learning strategy is L (0≤L≤1). An organism cannot simultaneously use both strategies, so that once the learning mode is set the organism becomes an individual learner or a social learner.

Social learners may have a conformity bias. The strength of conformity bias is D (Model 1) or A (Models 2 and 3), and there is no conformity bias when D or A is 0.

I numerically investigate the ESS (Maynard Smith, 1982) of the probability of individual learning (L) and the strength of conformity bias (D or A) and analyze the condition for positive conformity bias to evolve.

2.2. Model 1

In this model, I assume for simplicity that there are only two behaviors, correct and wrong. This assumption is approximately valid when the frequency of organisms behaving correctly is almost 1 in the generation that precedes an environmental change. In such a situation, we can assume that there are two behaviors, one that is correct now and another that is wrong now but was correct in the previous environmental state. As shown later, this assumption holds approximately under many conditions so that the ESS values of L and D obtained with this model may be approximately correct. Otherwise, we have to assume that social learners regard all the maladaptive (wrong) behaviors as the same behavior. A more realistic model for the infinite environmental states, where social learners regard each wrong behavior as being different, is given by Model 3.

The probability that a social learner imitates a behavior with the frequency x in the previous generation is expressed as

\[ P(x, D) = x + Dx(1-x)(2x - 1), \]  

where D is the strength of conformity bias (0≤D≤1). This expression is commonly used to formulate conformist transmission (Boyd and Richerson, 1985; Henrich and Boyd, 1998, 2001; Henrich, 2001).

Let the frequency of organisms behaving correctly and wrongly be \( x^{(i)} \) and \( \bar{x}^{(i)} (\bar{x}^{(i)} = 1 - x^{(i)}) \), respectively, where i is the number of generations after the last environmental change (1≤i≤ℓ). Moreover, we write \( P(x^{(i)}, D) \) as \( P^{(i)}(D) \) and \( P(\bar{x}^{(i)}, D) \) as \( \bar{P}^{(i)}(D) = P^{(i)}(D) + \bar{P}^{(i)}(D) = 1 \). Then

\[ x^{(i)} = \frac{L(1-c) + (1-L)\bar{P}^{(i-1)}(D)}{T_{i-1}}, \]  
\[ \bar{x}^{(i)} = \frac{(1-L)(1-s)\bar{P}^{(i-1)}(D)}{T_{i-1}}, \]

where

\[ T_i = L(1-c) + (1-L)(1-s)\bar{P}^{(i)}(D) \]  
and \( \bar{x}^{(0)} = \bar{P}^{(0)}(D) = 1 \) (because all the previous generation’s behaviors are wrong after an environmental change).

Solving as Feldman et al. (1996), the condition that a mutant strategy (L+ΔL, D) cannot invade a population whose members all use the strategy (L, D) is

\[ F(L, D) \leq 0 \quad \text{(if } L = 0), \]
\[ F(L, D) = 0 \quad \text{(if } 0<L<1), \]
\[ F(L, D) \geq 0 \quad \text{(if } L = 1), \]

where

\[ F(L, D) = \sum_{i=0}^{\ell-1} \frac{f_i(L, D)}{T_i} \]

and

\[ f_i(L, D) = \frac{s\bar{P}^{(i)}(D) - c}{T_i}. \]
Fig. 1. The points that satisfy (5) (solid line) and (8) (dashed line) are shown in the parameter space of \( L \) (the probability of adopting the individual learning strategy) and \( D \) (the strength of conformity bias). Parameters are \( s = 0.5, c = 0.31 \) in all cases, and \( \ell = 4 \) in (a), 5 in (b), 6 in (c). The point of intersection (ESS) is \((0.261839, 1)\) in (a), \((0.169604, \ 0.324723)\) in (b), and \((0.105807, 0)\) in (c). Arrows indicate that to the left of solid line the successful \( L \)-mutant has a larger \( L \)-value than wild type, and above the dashed line the successful \( D \)-mutant has a smaller \( D \)-value than wild type. Directions of arrows are reversed to the right of the solid line and below the dashed line.

Fig. 2. In (a) and (b), the ESS values \((\hat{L}, \hat{D})\) and \( X \) (the frequency of organisms behaving correctly in the generation that precedes an environmental change) are plotted against \( \ell \) (the period of environmental change). \( \hat{D} \) on a reduced scale is also plotted against a certain range of \( \ell \) \((70 \leq \ell \leq 150)\) in (b). In (c), the ESS values \((\hat{L}, \hat{D})\) and \( X \) are plotted against \( c \) (the cost of individual learning). Parameters are \((s, c) = (0.5, 0.2)\) and \((0.05, 0.02)\) in (a), \((s, c) = (0.05, 0.028)\) in (b), \( s = 0.5 \) and \( \ell = 20 \) in (c). Note that when \( \hat{L} = 0 \) or 1, the value of \( \hat{D} \) becomes indefinite. In (a), \( X \) is always almost 1 in both parameter sets and \( \hat{L} \) and \( \hat{D} \) are monotonically decreasing as \( \ell \) increases, but in (b), \( X \) is not always almost 1 and \( \hat{D} \) is not monotonically decreasing. Though this tendency is very small so we cannot clearly recognize without the reduced scale, \( \hat{D} \) is slightly increasing in a certain range of \( \ell \). This apparently anomalous result was confirmed to be true by numerically iterating the recursions (not shown) in the frequencies of the strategies. Moreover, as shown in (c), \( \hat{L} \) and \( \hat{D} \) are monotonically decreasing as \( c \) increases.
Similarly, the condition that a mutant strategy \((L, D+\delta D)\) cannot invade is:

\[
H(L, D) \leq 0 \quad \text{(if } D = 0),
\]
\[
H(L, D) = 0 \quad \text{(if } 0 < D < 1),
\]
\[
H(L, D) > 0 \quad \text{(if } D = 1),
\]

where

\[
H(L, D) = \sum_{i=1}^{\ell} h_i(L, D)
\]

and

\[
h_i(L, D) = -\frac{\xi^{(i)}(1 - \xi^{(i)})(2\xi^{(i)} - 1)}{T_i}
\]

The details of calculation are shown in Appendix A.

ESS \((\bar{L}, \bar{D})\) is a point that satisfies both (5) and (8) (Fig. 1). Since \(E(L, D)\) and \(H(L, D)\) are too complicated to solve for the coordinates of the intersection analytically, I do so numerically by grid analysis. Fig. 2 shows that the strength of conformity bias \((\bar{D})\) and the probability of adopting the individual learning strategy \((\bar{L})\) both tend to decrease as the cost of individual learning \((c)\) or the period of environmental change \((\ell)\) increases. There is an exceptional case where \(\bar{D}\) is slightly increasing in \(\ell\) in a certain range of \(\ell\) (see Fig. 2b), but this increase is very small so that even in such a case \(\bar{D}\) tends to decrease in \(\ell\) on the whole. Moreover, such exceptional phenomena seem to occur when \(X\) (the frequency of organisms behaving correctly in the generation that precedes an environmental change) is substantially less than 1. That is, it seems that \(\bar{D}\) is monotonically decreasing as \(\ell\) increases as long as the assumption that there are two behaviors holds approximately. Extensive numerical work with various parameter sets reveals no exceptions. The summary of the results is shown in Table 1.

Next, we analyze the condition for positive conformity bias to evolve. The condition that \(\bar{D} > 0\) \((\bar{D} = 0\) is invadable, hence not an ESS) is expressed as

\[
H(L^*_i(0), 0) > 0,
\]

where \(L^*_i(0)\) is the value of \(L\) that satisfies (5) when \(D = 0\). The details of calculation are shown in Appendix B and the results are numerically obtained. Fig. 3 shows the regions in \((\ell, c)\)-parameter space where \(\bar{D} = 0\) or \(\bar{D} > 0\). The upper bound on \(c\) for \(\bar{D} > 0\) to evolve is monotonically decreasing in \(\ell\) when \(s\) is large (see Fig. 3a), but it is slightly increasing in a certain range of \(\ell\) when \(s\) is small (see Fig. 3b). This slight increase of upper bound on \(c\) corresponds to the slight increase of \(\bar{D}\) seen in Fig. 2b. For example, when \(s = 0.05\) and \(c = 0.028\), we can see from Fig. 3b that as \(\ell\) increases, \(\bar{D}\) goes from positive to 0, 0 to positive, and positive to 0, again, and this change is also seen in Fig. 2b.

However, in Model 3 where social learners can distinguish among the various wrong behaviors, the upper bound on \(c\) is monotonically decreasing in \(\ell\). So, this slight increase of the upper bound on \(c\) may be related to the assumption that there are only two behaviors (\(X\) is almost 1).

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Table 1

<table>
<thead>
<tr>
<th>The relationship between the ESS values and the parameters</th>
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<tbody>
<tr>
<td>When the period of environmental change ((\ell)) increases</td>
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<tr>
<td>------------------------------------------------------------</td>
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<tr>
<td>The probability of adopting the individual learning strategy ((\bar{L}))</td>
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<tr>
<td>The strength of conformity bias ((\bar{D}))</td>
</tr>
<tr>
<td>Monotonically decreases (see Fig. 2a)</td>
</tr>
</tbody>
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![Fig. 3.](image-url)
2.3. Model 2

In this model, we change the expression for conformist transmission (1) to
\[ P(x, a) = \frac{x^a}{x^a + (1 - x)^a}, \tag{12} \]
where \( a \) is the strength of conformity bias \((a > 0)\). There is no conformity bias when \( a = 1 \). This expression is not commonly used to formulate conformist transmission, but is mathematically simple and has been adopted by some researchers (Lachlan et al., 2004). The strength of conformity can also be written as
\[ A = \ln a. \tag{13} \]

Then, there is no conformity bias when \( A = 0 \), positive conformity bias when \( A > 0 \), and negative conformity bias when \( A < 0 \). (For simplicity, however, we use \( a \) in the following expressions.) Here, note that negative conformity bias \((A < 0)\) does not entail a negative correlation between the frequency of a behavior and the probability of imitating that behavior, but rather an increased randomness in the behavior chosen (when \( a \rightarrow 0 \) or \( A \rightarrow -\infty \) each of the two behaviors is imitated with probability \( \frac{1}{2} \) provided there are two behaviors, correct and wrong, in the previous generation). So, whether \( A \) is positive or negative, the probability of imitating a behavior is monotonically increasing in the frequency of that behavior. (But note that if we permit the range \( a < 0 \), we can consider “contrariness” social learner. For example, if we substitute \( a = -1 \) in (12), \( P(x, a) = 1 - x \). “Contrariness” is sometimes advantageous (Aoki, 1984), but it is obviously disadvantageous in infinite environmental state model because there are an infinite number of wrong behaviors of very low frequency. So, we consider only the range \( a > 0 \) in this model.)

As in Model 1, the condition for a mutant strategy \((L + dL, a)\) not to invade a population whose members all use the strategy \((L, a)\) is
\[
\begin{align*}
F(L, a) &\leq 0 \quad \text{(if } L = 0), \\
F(L, a) &= 0 \quad \text{(if } 0 < L < 1), \\
F(L, a) &\geq 0 \quad \text{(if } L = 1),
\end{align*}
\tag{14}
\]
where
\[ F(L, a) = \sum_{i=0}^{\ell-1} f_i(L, a) = \sum_{i=0}^{\ell-1} \frac{s \bar{P}(i)(a) - c}{T_i} \tag{15} \]
and \( T_i = L(1-c) + (1-L)(1-s \bar{P}(i)(a)) \). Similarly, the condition that a mutant strategy \((L, a + da)\) cannot

![Fig. 4. In (a) and (b), the ESS values \( \hat{L}, \hat{A} \) and \( X \) (the frequency of organisms behaving correctly in the generation that precedes an environmental change) are plotted against \( \ell \) (the period of environmental change). \( \hat{A} \) on a reduced scale is also plotted against a certain range of \( \ell \) (30 \( \leq \ell \leq 100 \)) in (b). In (c), the ESS values \( \hat{L}, \hat{A} \) and \( X \) are plotted against \( c \) (the cost of individual learning). Parameters are \((s, c) = (0.5, 0.2)\) and \((0.05, 0.02)\) in (a), \((s, c) = (0.05, 0.0273)\) in (b), \( s = 0.5 \) and \( \ell = 20 \) in (c). As described in the main text, \( A \rightarrow \infty \) when \( \frac{s}{c} < \ell < \left(\frac{s(1-s)}{2}\right)/(2(1-s)) \) and \( \hat{L} = 1 \) and \( \hat{A} \) is indefinite when \( \ell \leq \frac{s}{c} \). In (a), \( X \) is always almost 1 in both parameter sets and \( \hat{L} \) and \( \hat{A} \) are monotonically decreasing as \( \ell \) increases, but in (b), \( X \) is not always almost 1 and \( \hat{A} \) is not monotonically decreasing. Though this tendency is very small so we cannot clearly recognize without the reduced scale, \( \hat{A} \) is slightly increasing in a certain range of \( \ell \). This apparently anomalous result was confirmed to be true by numerically iterating the recursions (not shown) in the frequencies of the strategies. Moreover, as shown in (d), \( \hat{L} \) and \( \hat{A} \) are monotonically decreasing as \( c \) increases, and from the transformation of inequality (24), \( A \rightarrow \infty \) when \( \frac{s}{c} < c < \left(\frac{s(2-s)}{2}\right)/(2(1-s)) \) and \( \hat{L} = 1 \) and \( \hat{A} \) is indefinite when \( c \leq \frac{s}{c} \).]
In invade is
\[
H(L, a) \leq 0 \quad (\text{if } a \to 0),
\]
\[
H(L, a) = 0 \quad (\text{if } a \neq 0, \infty),
\]
\[
H(L, a) \geq 0 \quad (\text{if } a \to \infty),
\]
where
\[
H(L, a) = \sum_{i=1}^{\ell-1} h_i(L, a)
\]
\[
= \sum_{i=1}^{\ell-1} \frac{x^{(i)} - (\ln x^{(i)} - \ln(1 - x^{(i)}))}{[x^{(i)} + (1 - x^{(i)})^n]^2 T_i}.
\]

ESS \((\hat{L}, \hat{A})\) is a point that satisfies both (14) and (16). As in Model 1, these values can be numerically obtained (Fig. 4) and turn out to be similar to Model 1. That is, the strength of conformity bias \((\hat{A})\) and the probability of adopting the individual learning strategy \((\hat{L})\) tend to decrease when the cost of individual learning \((c)\) or the period of environmental change \((\ell)\) increases. Sometimes \(A\) is slightly increasing in \(\ell\) in a certain range of \(\ell\), but such phenomena seem to occur when \(X\) does not approach 1 (see Fig. 4b). That is, it seems that \(A\) is monotonically decreasing as \(c\) or \(\ell\) increases as long as the assumption that there are two behaviors holds approximately.

![Graph](image)

Fig. 5. The sign of \(\hat{A}\) is shown in parameter space of \(\ell\) (the period of environmental change) and \(c\) (the cost of individual learning). \(\hat{A} > 0\) below the solid line. Since \(\hat{L} = 1\) and \(\hat{A}\) is indefinite when \(\ell = 1\), the upper bound on \(c\) for \(A > 0\) to evolve is plotted against the range \(\ell \geq 2\). Parameter is \(s = 0.5\) in (a) and \(s = 0.05\) in (b).

Next, the condition that \(\hat{a} > 1(\hat{A} > 0)\) (positive conformity bias evolves) is
\[
H(L^*_c(1), 1) > 0,
\]
where \(L^*_c(1)\) is the value of \(L\) that satisfies (14) when \(a = 1\). The results are numerically obtained (Fig. 5) and also turn out to be similar to Model 1 (compare Figs. 3 and 5). As in Model 1, the upper bound on \(c\) for \(A > 0\) to evolve is not monotonic in \(\ell\) when \(s\) is small. The slight increase in the upper bound on \(c\) corresponds to the slight increase of \(A\) seen in Fig. 4. The similarity between the results of Models 1 and 2 means that the two expressions for conformist transmission (1) and (12) have similar properties. So, we can use (12) instead of (1) in the studies of conformist transmission, and the difference between two expressions may not greatly affect the results.

In this model, we can determine the condition for \(\hat{a} \to \infty(\hat{A} \to \infty)\). When \(\hat{a} \to \infty\), social learners always imitate the majority, so the condition that social learners can imitate correct behavior is \(\hat{x}_{(i)} > \frac{1}{2}\). From (2) (we obtain after rewriting \(P^{(i)}(D)\) as \(P^{(i)}(a)\)),
\[
1 - s - s + 1 - c.
\]

When (19) is satisfied, social learners only behave wrongly after an environmental change and otherwise behave correctly. That is, \(P^{(i)}(\infty) = 1\) and \(P^{(i)}(\infty) = 0(1 \leq i \leq \ell - 1)\). Substituting in (15) gives
\[
F(L, \infty) = \sum_{i=1}^{\ell-1} \frac{sP^{(i)}(\infty) - c}{L(1 - c) + (1 - L)(1 - sP^{(i)}(\infty))}
\]
\[
= \frac{s - c}{L(1 - c) + (1 - L)(1 - s)} + (\ell - 1)
\]
\[
\times \frac{(-c)}{L(1 - c) + (1 - L)}
\]
\[
= s(1 - c) - cL(1 - s) - cL(s - c)L.
\]

Then, (14) is satisfied when
\[
\hat{L} = 1 \quad (\text{if } \ell \leq \frac{1}{c}),
\]
\[
\hat{L} = \frac{s(1 - c) - cL(1 - s)}{cL(s - c)} \quad (\text{if } \frac{1}{c} < \ell < \frac{s(1 - c)}{cL(s - c)}),
\]
\[
\hat{L} = 0 \quad (\text{if } \ell \geq \frac{s(1 - c)}{cL(s - c)}).
\]

Hence,
\[
\frac{s(1 - c) - cL(1 - s)}{cL(s - c)} > \frac{1 - s}{1 - s + 1 - c}
\]
is necessary for \(\hat{a} \to \infty\). Solving (22) for \(\ell\) yields
\[
\ell < \frac{s(1 - s + 1 - c)}{2c(1 - s)}.
\]

Moreover, when \(\ell \leq s/c\), we have \(\hat{L} = 1\) (social learner cannot invade), and all \(a\) are neutrally stable. (When \(\hat{L} = 1\), there are no social learners so that the value of \(a\) is
As described in the legend of Fig. 4, the behavior of the model is consistent with the assumption of infinite environmental states because both the count of behaviors and count of environmental states are infinite in this expression.

As (1) and (12) have similar property described above, this expression may also have similar property so that it is appropriate to use it as an expression for conformist transmission.

In this model, we cannot obtain the ESS values because there is no general expression for \( h(L, a) \), but we can obtain the condition for \( \hat{A} > 1 (A > 0) \) to hold (positive conformity bias evolves). As in Model 2, the condition is

\[
\begin{align*}
H(L^*_i(1), 1) &= \sum_{i=1}^{\ell-1} h(L^*_i(1), 1) > 0, \\
\end{align*}
\]

where \( L^*_i(1) \) is the same as in Model 2 because when \( a = 1 \), \( P(x_j, 1) = x_j \) in both models, so that \( f(L, 1) \) is the same as in Model 2.

As mentioned above, there is no general expression for \( h(L, a) \), but we can obtain \( h(L, 1) \) as follows. Assume that the population has reached equilibrium in the infinite states environment. Let \( X \) be the frequency of the correct behavior in the generation that precedes an environmental change, which we call generation 0 (equivalent to generation \( \ell \) of the previous environment). Also set \( \bar{X} = 1 - X \), which is the sum of the frequencies of the various incorrect behaviors in the same generation; i.e., \( \bar{X} = \hat{x}^{(i)} + \bar{X} = \hat{x}^{(i)} + X \), where \( \hat{x}^{(i)} \) is the frequency of organisms behaving correctly in generation \( i \) (\( 1 \leq i \leq \ell \)).

All preexisting behaviors become incorrect when the environment changes (between generations 0 and 1). Then, when there is no conformity bias (\( a = 1 \)), the frequency of currently incorrect behavior that was correct in the previous environment is \((1 - \hat{x}^{(i)})X\) in generation \( i \), which becomes \( \bar{X}X \) in generation \( \ell \) (generation 0). Similarly, the frequency of currently incorrect behavior that was correct two environments ago is \((1 - \hat{x}^{(i)})X \bar{X} \) because this frequency is \( \bar{X}X \) in generation 0. In general, since the relative abundances of the various incorrect behaviors remains constant, the frequency of currently incorrect behavior that was correct \( n \) environments ago is \((1 - \hat{x}^{(i)})X \bar{X}^{n-1} \).

So at \( a = 1 \),

\[
\begin{align*}
P(x, a) &= \frac{x^a}{x^a + [(1 - x)X]^a + [(1 - x)\bar{X}]^a + \cdots} \\
&= \frac{x^a}{x^a + (1 - x)^a/(1 - \bar{X})^a}, \\
\end{align*}
\]

where \( x \) is the frequency of organisms behaving correctly. Therefore, in the \( i \)th generation

\[
\begin{align*}
h_i(L, 1) &= \frac{\hat{x}^{(i)}(1 - \hat{X})\ln \hat{x}^{(i)} - \ln(1 - \hat{x}^{(i)}) + \ln(1 - \hat{X}) + ((\bar{X} \ln \bar{X})/(1 - \bar{X}))}{T_i}, \\
\end{align*}
\]

where \( T_i = L(1 - c) + (1 - L)(1 - s\hat{x}^{(i)}) \).

\[
\hat{x}^{(i)} = \frac{s(1 - L) + L(1 - c)}{s(1 - L) + L(1 - c)((1 - cL)/(1 - L)(1 - s))} \\
\]
the upper bound on $\bar{c}$ and of $A$ reveals no exceptions. That is, the slight increase of the upper bound on $c$ for $A > 0$ to evolve is plotted against the range $\ell \geq 2$. Parameter is (a) $s = 0.5$ (b) $s = 0.05$.

Fig. 7. The signs of $\hat{A}$ in Models 2 and 3 are compared in parameter space of $\ell$ (the period of environmental change) and $c$ (the cost of individual learning). $\hat{A} > 0$ in the regions below the dashed line and the solid line in Models 2 and 3, respectively. Since $L = 1$ and $\hat{A}$ is indefinite when $\ell = 1$, the upper bound on $c$ for $A > 0$ to evolve is plotted against the range $\ell \geq 2$. Parameter is (a) $s = 0.5$ (b) $s = 0.05$.

and

$$
\bar{X} = \frac{s(1 - L) + L(1 - c)}{s(1 - L) + L(1 - c)((1 - c)L/(1 - L)(1 - s))^\ell}. 
$$

(30)

As in previous models, condition (26) can be evaluated numerically and is shown in Fig. 7. Compared with Model 2, the upper bound on $c$ for $\hat{A} > 1(\hat{A} > 0)$ to hold is monotonically decreasing in $\ell$ in this model, though it is not in Model 2 when $s$ is small (see Fig. 5b). Extensive numerical work with various parameter sets reveals no exceptions. That is, the slight increase of the upper bound on $c$ in Model 2 is apparently caused by failure of the assumption that there are only two behaviors ($X$ is almost 1). Since the slight increase of the upper bound on $c$ corresponds to the slight increase of $\hat{A}$ in Model 2, the slight increase of $\hat{A}$ may disappear in Model 3.

Furthermore, Fig. 7b suggests that when $s$ and $\ell$ are small, conformity bias $A$ always evolves to be positive under the condition that $c < s$. That is, positive conformity bias necessarily evolves as long as individual learner and social learner coexist. Let us solve for the condition that positive conformity bias necessarily evolves under the condition that $c < s$. Note $L^*_\ell(0)$ decreases from 1 to 0 as $c$ increases from $s/\ell$ to $s$ (see $L^*_\ell(0)$ in Fig. 10; $L^*_\ell(0)$ in Model 1 is same as $L^*_\ell(1)$ in Models 2 and 3 because $D = 0$ is equivalent to $a = 1$). Hence, only when $H(L, 1) > 0$ is satisfied for all internal values of $L$ ($0 < L < 1$) does (26) always hold and conformity bias $A$ always evolves to be positive. Since $H(0, 1) = 0$, $H(1, 1) = 0$, and $dH(1, 1)/dL < 0$, it is necessary that $dH(0, 1)/dL > 0$, i.e.

$$
\sum_{i=1}^{\ell - 1} (1 - s)^{-i} - 1 \left\{ 1 - \ln \frac{(1 - s)^{-\ell} - 1}{(1 - s)^{-\ell} - 1} \right\} > 0. 
$$

(31)
Extensive numerical work suggests that when (31) is satisfied, \( H(L,1) > 0 \) is also satisfied. I show condition (31) in Fig. 8. The upper bound on \( s \) such that \( \hat{A} \) is positive for all \( c \) is monotonically decreasing as \( \ell \) increases.

The condition that \( \hat{a} \to \infty (\hat{A} \to \infty) \) is same as in Model 2, because when \( \hat{a} \to \infty \) all social learners imitate the same behavior so that there are two behaviors at most in any generation. Fig. 9 shows the relationship between \( s, c \) and \( \hat{A} \). In contrast to Model 2 (Fig. 6), the borderline between \( \hat{A} < 0 \) and \( \hat{A} > 0 \) intersects the line \( c = s \) and this point of intersection corresponds to (31). Though (31) is inequality of \( s \) and \( \ell \), Fig. 9 suggests that \( \ell \) is always positive when \( c \) is smaller than the value of \( s \) that is obtained by (31).

3. Discussion

In this paper, I mainly analyzed the condition for positive conformity bias to evolve and the relationship between the strength of conformity bias and the cycle of environmental change. As a result, I found that the strength of conformity bias tends to be larger when the cycle of environmental change is shorter. That is, environmental stability negatively affects the strength of conformity bias.

This result can be explained as follows. As shown in above models, when the cycle of environmental change is short, the benefit of individual learning is large so that \( \hat{L} \) (the probability of adopting the individual learning strategy) is large. This tendency corresponds to other papers (Feldman et al., 1996; Henrich and Boyd, 1998; Wakano et al., 2004; Aoki et al., 2005; Wakano and Aoki, 2006). Since IL always achieve the correct behavior in these models, social learners easily imitate correct behavior if the proportion of IL is large. Then correct behavior is the majority in many generations and social learners with positive conformity bias have an advantage. That is, there is a positive correlation between the strength of conformity bias and the probability of adopting the individual learning strategy. So, when the cycle of environmental change is short, \( \hat{L} \) becomes large and as a result the strength of conformity bias also becomes large.

I should justify the assumption of “periodically changing environment”. Readers may surmise that the most advantageous strategy in such an environment is to change the learning strategy periodically. Of course so, but such a strategy may not be advantageous in a randomly changing environment. The reason why I considered “periodically changing environment” is mathematical convenience to analyze the relationship between the strength of conformity bias and environmental stability. Studies of social learning evolution (Feldman et al., 1996; Wakano et al., 2004; Aoki et al., 2005; Wakano and Aoki, 2006) of which my model is an extension have shown that the effect of environmental stability on the frequency of individual learning is similar in a randomly changing environment and a periodically changing environment. Since there is a positive correlation between the frequency of individual learning and the
are better to select different strategies in different situations. If we can recognize parameter values of a situation, we may select the ESS corresponding to the parameter values because the condition-dependent strategy corresponding to the ESS may evolve to be stable provided the other entire members in the same situation select the same condition-dependent strategy. That is, we would evolve to have a condition-dependent strategy of conformity that is corresponding to the ESS. Of course we cannot recognize the parameter values of a situation all the time so that we may estimate them from the past experiences and the circumstances to select the strategy. Provided the situation we face is similar to the situation considered in my models, the tendency of condition dependency might be similar to my models’ result. That is, the strength of conformity bias and the probability of adopting the individual learning strategy might be larger when we think that the cost of individual learning or the environmental stability is small in the situation we face. In the laboratory studies, Kameda and Nakanishi (2002) found that conformity is less common when the cost of individual learning is high and McElreath et al. (2005) found that conformity is observed only when there is environmental fluctuation. These results may suggest that we have a psychological tendency to strengthen conformity when we feel the cost of individual learning or the environmental stability is small. This tendency corresponds to my models’ prediction.

In this paper, I assumed that the only factor that causes a previously adaptive behavior to become maladaptive is a temporal change in the natural environment. But other factors can be considered. For example, when we migrate to other places, the environment we face may change so that migration induces environmental instability. Since environmental stability negatively affects the strength of conformity bias, migration rate may positively affect the strength of conformity bias. This indication corresponds to Henrich and Boyd (1998). Moreover, invention of better technique causes a previous adaptive technique to be maladaptive. So, the frequency of new invention, i.e. the speed of technological advance, may also positively affect the strength of conformity bias. In short, the factors that change the fitness of behaviors may have similar property to environmental change. So, my result may be applicable to the situation that environmental change does not occur but another factor changes the fitness of behaviors. Moreover, we might have a condition-dependent strategy of conformity that we strengthen conformity when we feel the fitness of behaviors frequently changes.

In Model 3, I showed that conformity bias always evolves to be positive when environmental stability and the cost of doing wrong behaviors are small (see Fig. 8). That is, (positive) conformity always evolves when wrong behaviors are not so maladaptive compared with the correct behavior. In other words, we always evolve to conform when the decision of a behavior has little importance for our life.

This result can be explained as follows. When the cost of doing wrong behaviors is small, the frequency of wrong behaviors decreases slowly and as a result $\dot{X}$ becomes large (note that from (30) $dX/ds < 0$ when there is no conformity bias). It means that there are several wrong behaviors that have low but not ignorable frequency. Since social learners regard each wrong behavior as being different in Model 3, (positive) conformity is advantageous to avoid imitating such wrong behaviors of low frequency. This has very important suggestion to consider the evolution of conformist transmission. That is, though many previous studies of conformity focused on the reason why conformity increases the probability of imitating correct behaviors, this result suggests that what is important is why conformity decreases the probability of imitating wrong behaviors. Readers may think that this result is caused by the assumption of infinite environmental state model, which supposes that there are one correct behavior and an infinite number of wrong behaviors. But I think such a situation is not so unrealistic because a “correct behavior” may consist of many factors and a change of a factor may make the behavior incorrect so that the number of correct behaviors is far fewer than that of wrong behaviors in many realistic situations.

Moreover, as the above discussion of the condition-dependent strategy, the result of Model 3 implies that we would conform when we feel a task to be unimportant for our life. This indication has very interesting suggestion for psychological experiments of conformity. Psychological experiments obviously have little influence for participants’ life so that participants may feel the task unimportant and show conformity. This may possibly be a reason that many psychological experiments have reported the universal tendency of conformity. Furthermore, even in real life, not so many behaviors might have large influence for our fitness so that the tendency of conformity is thought to be reasonable. As shown in Fig. 9, even when the cost of doing wrong behaviors ($s$) is large, conformity bias always evolves to be positive as long as the cost of individual learning ($c$) is sufficiently small. Note that the fitness of IL is relative to that of SLC. That is, if there is little difference between the cost of individual learning and the intrinsic cost of social learning ($d$, as defined in Aoki et al., 2005), positive conformity bias always evolves. It is reasonable to suppose that what is difficult to learn individually is also difficult to learn socially, so that the difference between the fitness of IL and that of SLC may be small. Therefore, in many situations, parameter $c$ may be sufficiently small for positive conformity bias to evolve.

In conclusion, conformity may evolve in the broad range of the realistic situations though environmental stability negatively affects the strength of conformity bias. Of course my model is too simple to express the situations of the real world, but it may be sufficient to overview the relationships of factors. My model, however, does not consider “innate” behavior that many models of social learning have adopted (Cavalli-Sforza and Feldman, 1983;
Appendix A

Assume that a mutant strategy \((L + dL, D)\), i.e. an L-mutant, is introduced at low frequency into a population whose members all use the strategy \((L, D)\). Define the frequency of wild type behaving correctly and wrongly as \(x^{(i)}\) and \(\bar{y}^{(i)}\), and that of L-mutant as \(y^{(i)}\) and \(\bar{y}^{(i)}\), respectively, where \(i\) is the number of generations after the last environmental change \((1 \leq i \leq t)\). Then

\[
x^{(i)} = (x^{(i-1)} + \bar{y}^{(i-1)}) \frac{L(1-c) + (1-L)P(x^{(i-1)} + y^{(i-1)}, D)}{T_{i-1}},
\]

\[
\bar{x}^{(i)} = (x^{(i-1)} + \bar{y}^{(i-1)}) \frac{(1-L)(1-s)P(\bar{x}^{(i-1)} + \bar{y}^{(i-1)}, D)}{T_{i-1}},
\]

\[
y^{(i)} = (y^{(i-1)} + \bar{y}^{(i-1)}) \frac{(L + dL)(1-c) + (1-L - dL)P(x^{(i-1)} + y^{(i-1)}, D)}{T_{i-1}},
\]

\[
\bar{y}^{(i)} = (y^{(i-1)} + \bar{y}^{(i-1)}) \frac{(1-L - dL)(1-s)P(x^{(i-1)} + \bar{y}^{(i-1)}, D)}{T_{i-1}},
\]

where

\[
T_i = (x^{(i)} + \bar{y}^{(i)})[L(1-c) + (1-L)(1-sP(\bar{x}^{(i)} + \bar{y}^{(i)}, D))] + (y^{(i)} + \bar{y}^{(i)})[(L + dL)(1-c) + (1-L - dL)(1-sP(\bar{x}^{(i)} + \bar{y}^{(i)}, D))]
\]

and

\[
\bar{x}^{(0)} = \bar{y}^{(0)} = P(\bar{x}^{(0)} + \bar{y}^{(0)}, D) = 1.
\]

Hence, the frequency of L-mutant is

\[
y^{(i)} + \bar{y}^{(i)} = (y^{(i-1)} + \bar{y}^{(i-1)}) \frac{(L + dL)(1-c) + (1-L - dL)(1-sP(\bar{x}^{(i-1)} + \bar{y}^{(i-1)}, D))}{T_{i-1}}.
\]

Obviously, the frequency of L-mutant increases if

\[
\lambda = \prod_{i=0}^{t-1} \frac{(L + dL)(1-c) + (1-L - dL)(1-sP(\bar{x}^{(i)} + \bar{y}^{(i)}, D))}{T_i} > 1.
\]

Since the frequency of L-mutant is small \((y^{(i)}, \bar{y}^{(i)} \ll 1)\), this can be rewritten as

\[
\lambda = \prod_{i=0}^{t-1} \left(1 + dL \frac{s\bar{P}^{(i)}(D) - c}{L(1-c) + (1-L)(1-s\bar{P}^{(i)}(D))} \right).
\]

Next, supposing \(dL\) small, we can approximate

\[
\lambda = 1 + dL \sum_{i=0}^{t-1} \frac{s\bar{P}^{(i)}(D) - c}{T_i} + (dL)^2 \sum_{i=1}^{t-1} \sum_{j=0}^{i-1} \frac{s\bar{P}^{(i)}(D) - c}{T_i} \cdot \frac{s\bar{P}^{(j)}(D) - c}{T_j},
\]
where
\[ T_i = L(1 - c) + (1 - L)(1 - s\bar{P}^{(i)}(D)). \] (4)

Therefore, for an internal value of \( L \) to be stable, it is necessary that
\[ F(L, D) = 0, \] (5)
where
\[ F(L, D) = \sum_{i=0}^{t-1} f_i(L, D) = \sum_{i=0}^{t-1} \frac{s\bar{P}^{(i)}(D) - c}{T_i}. \] (6, 7)

Then, \( \lambda < 1 \) is satisfied because
\[
\sum_{i=1}^{t-1} \sum_{j=0}^{t-1} \frac{s\bar{P}^{(i)}(D) - c}{T_i}, \frac{s\bar{P}^{(j)}(D) - c}{T_j} = \frac{1}{2}\left[ \left( \sum_{i=0}^{t-1} \frac{s\bar{P}^{(i)}(D) - c}{T_i} \right)^2 - \sum_{i=0}^{t-1} \left( \frac{s\bar{P}^{(i)}(D) - c}{T_i} \right)^2 \right] = -\frac{1}{2} \sum_{i=0}^{t-1} \left( \frac{s\bar{P}^{(i)}(D) - c}{T_i} \right)^2 < 0. \] (A.11)

So, \( F(L, D) = 0 \) is the necessary and sufficient condition for an internal value of \( L \) to be evolutionarily stable. Moreover, (A.10) implies that when \( F(L, D) > 0 \), the successful \( L \)-mutant has a larger \( L \)-value than wild type, and vice versa. Therefore, \( F(L, D) \leq 0 \) is the necessary and sufficient condition for \( L = 0 \) to be evolutionarily stable and \( F(L, D) \geq 0 \) is that for \( L = 1 \).

Similarly, when a mutant with strategy \((L, D + dD)\), i.e. a \( D \)-mutant, is introduced at low frequency into a population whose members all use the strategy \((L, D)\), the frequency of \( D \)-mutant is
\[
y^{(i)} + p^{(i)} = (y^{(i-1)} + p^{(i-1)}) \frac{L(1 - c) + (1 - L)(1 - s\bar{P}^{(i-1)}(D + dD))}{T_{i-1}}
= (y^{(i-1)} + p^{(i-1)}) \left\{ 1 - \frac{(1 - L)s(\bar{P}^{(i-1)}(D + dD) - \bar{P}^{(i-1)}(D))}{T_{i-1}} \right\}. \] (A.12)

So, if \( L < 1 \), \( D \) is evolutionarily stable when
\[
H(L, D) \leq 0 \quad \text{(if } D = 0),
H(L, D) = 0 \quad \text{(if } 0 < D < 1),
H(L, D) \geq 0 \quad \text{(if } D = 1), \] (8)
where
\[ H(L, D) = \sum_{i=1}^{t-1} h_i(L, D) = \sum_{i=1}^{t-1} \frac{\bar{x}^{(i)}(1 - \bar{x}^{(i)})(2\bar{x}^{(i)} - 1)}{T_i}. \] (9, 10)

If \( L = 1 \), all values of \( D \) are clearly neutrally stable with regard to \( D \)-mutants.

**Appendix B**

When \( D = 0 \), \( \bar{x}^{(i)} \) is generally expressed as
\[ \bar{x}^{(i)} = \frac{s(1 - L) + L(1 - c)}{s(1 - L) + L(1 - c)((1 - c)l/(1 - L)(1 - s))^i}. \] (29)

Then, we can analytically prove that \( dF(L, 0)/dL < 0 \). So, when \( D = 0 \), there is only one value of \( L \) that satisfies (5) and we write it as \( L^*_1(0) \).

Let us consider the condition for the strategy \((L^*_1(0), 0)\) to be stable. As mentioned in Appendix A, when \( F(L, D) > 0 \) the successful \( L \)-mutant has a larger \( L \)-value than wild type and when \( H(L, D) > 0 \) the successful \( D \)-mutant has a larger \( D \)-value than wild type and vice versa. As shown in Appendix A, the strategy \((L^*_1(0), 0)\) is evolutionarily stable against \( L \)-mutants (and also convergent stable because \( dF(L, 0)/dL < 0 \)). Then, when \( H(L^*_1(0), 0) \leq 0 \), the strategy \((L^*_1(0), 0)\) is not invaded by
D-mutants. So, the condition $\hat{D}>0$ can be expressed as

$$H(L(0,0),0)>0.$$

Note $H(0,0)=0$, $H(1,0)=0$, $dH(0,0)/dL<0$, and $dH(1,0)/dL<0$. Hence, provided there is only one internal value of $L$ that satisfies $H(L,0)=0$, which we write as $L^*_f(0)$, we have $H(L,0)<0$ when $0<L<L^*_f(0)$ and $H(L,0)>0$ when $L^*_f(0)<L<1$. Then (11) can be rewritten as

$$L^*_f(0)>L^*_h(0).$$

Fig. 10 shows the relationship between $c$ and $L^*_f(0)$ and $L^*_h(0)$. With the parameter set of Fig. 10, $L^*_f(0)$ is monotone in $c$, so only one internal value of $L$ satisfies $H(L,0)=0$ for all $c$ ($0<c<s$) and therefore (B.1) is the condition $\hat{D}>0$. Moreover, as shown in Fig. 10, (B.1) is obviously satisfied to the left of the intersection of $L^*_f(0)$ and $L^*_h(0)$. So, this point of intersection represents the threshold of $c$, which is shown in Fig. 3. When $c$ is smaller than this threshold, $\hat{D}>0$. For all parameter sets considered, $L^*_f(0)$ and $L^*_h(0)$ are similarly expressed as Fig. 10 so that (B.1) is the condition for $\hat{D}>0$ and the intersection of $L^*_f(0)$ and $L^*_h(0)$ represents the threshold of $c$.

References
