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Critical Social Learning: A Solution to Rogers's Paradox of Nonadaptive Culture

ABSTRACT   Alan Rogers (1988) presented a game theory model of the evolution of social learning, yielding the paradoxical conclusion that social learning does not increase the fitness of a population. We expand on this model, allowing for imperfections in individual and social learning as well as incorporating a "critical social learning" strategy that tries to solve an adaptive problem first by social learning, and then by individual learning if socially acquired behavior proves unsatisfactory. This strategy always proves superior to pure social learning and typically has higher fitness than pure individual learning, providing a solution to Rogers's paradox of nonadaptive culture. Critical social learning is an evolutionarily stable strategy (ESS) unless cultural transmission is highly unfaithful, the environment is highly variable, or social learning is much more costly than individual learning. We compare the model to empirical data on social learning and on spatial variation in primate cultures and list three requirements for adaptive culture. [Keywords: social learning, origin of culture, culture, biology, mathematical modeling]

O NE OF THE MOST debated questions about culture is its relationship to biological fitness. Given that genetic evolution has endowed humans with extensive capacities for culture, we may expect culture to be genetically adaptive—that is, beneficial to survival and reproduction, at least on average (Richerson and Boyd 2005). The impressive ecological success of humans, who have colonized almost every terrestrial habitat with densities unprecedented for animals of similar size, seems to confirm this expectation (McEvedy and Jones 1978). In 1988, however, Alan Rogers published a mathematical analysis of the evolution of social learning, according to which culture is not adaptive in the genetic sense (Rogers 1988).

Rogers studied an evolutionary game with two genetically determined strategies—individual learners and social learners—and analyzed how they contributed to culture (defined as traits influenced by social learning). Assuming a moderately variable environment, he showed that if individual learning is more costly than social learning, then genetic evolution leads to an equilibrium in which individual and social learners coexist. At this equilibrium both strategies have the same fitness of individual learners in the absence of social learners. Thus, in Rogers's model, the ability for social learning is of no advantage to the individual or the population. On the contrary, the spread of social learning decreases the number of individual learners and thus impairs a population's ability to create culture and react to environmental change (Figure 1a).

The fundamental reason for Rogers's surprising result is that, in his model, only individual learners create information. Social learners have a fitness advantage when they are few, because they can imitate individual learners without paying the cost of individual learning (Figure 1b). When they are many, however, social learners will mostly imitate other social learners and may acquire information that has been outdated by environmental change. Thus, genetic evolution initially favors the spread of social learners in a population of individual learners, but as they increase in frequency their fitness advantage decreases. Ultimately an equilibrium is reached at which social learners have become so common that their initial fitness advantage is wholly lost (Figure 1b). Robert Boyd and Peter J. Richerson (1995) have considered several variations of Rogers's model, showing that his results are likely to apply to any evolutionary game in which social and individual learners play against each other, and the value of information is frequency independent.
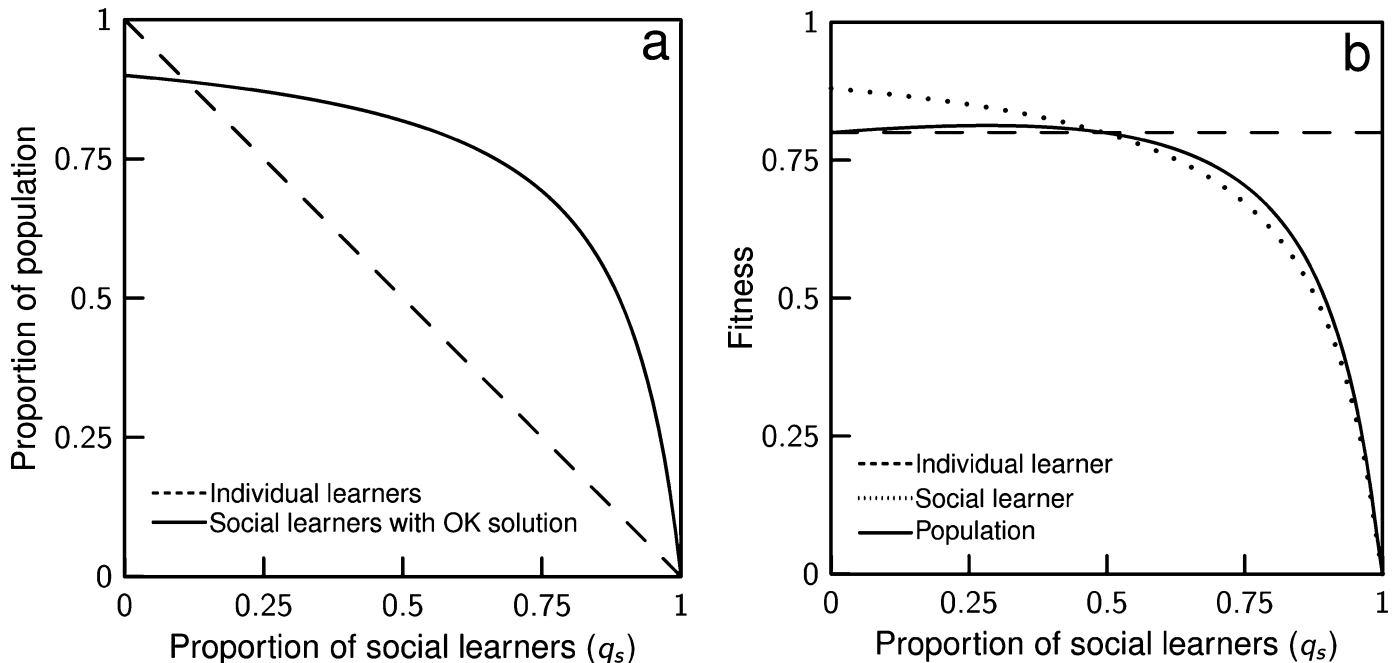
FIGURE 1. Some results from Rogers's (1988) model. a: The proportion of social learners with an OK solution decreases as social learners increase in frequency (and individual learners decrease). b: Fitness of individual learners, social learners, and population fitness as a function of the proportion of social learners in the population. The equilibrium proportions are where lines intersect. Both panels are based on our formulation of Rogers's model (see text), with $c_i = 0.2$, $c_s = 0.02$, $p_i^{OK} = 1$ and $p_s^{OK \to OK} = 0.9$.

Rogers's result is a theoretical one that follows from his assumptions, but it seems to be at odds with empirical observations. Several attempts have been made to escape this paradox. Bennett Galef (1992, 1995) observed that animals do not use social learning indiscriminately, as in Rogers's model. Boyd and Richerson (1995; see also Richerson and Boyd 2005:111 ff.) mathematically analyze two strategies that combine individual and social learning. In the first model, the strategy is to try social learning when individual learning fails to provide good evidence about which behavior to adopt (see Kameda and Nakanishi 2003 for a computer simulation of a similar scenario). In the second model, the strategy is to use individual learning to improve a behavior obtained by social learning. Boyd and Richerson show that both strategies can be evolutionarily stable and can yield higher fitness than individual learning alone. These models, however, analyze somewhat different problems than Roger's model. In the first model, for instance, individual learning is cost free, and in neither model is a pure social learning strategy considered (i.e., a strategy in which individual learning plays no role).

In this article we reexamine Rogers's paradox in its original formulation. We think Rogers should be credited not only for pointing out the paradox but also for introducing a modeling framework that allows studying important issues without excessive complexity. Below we first summarize and slightly reformulate Rogers's model. Then we introduce an additional strategy, the "critical social learner," that allows culture to be adaptive under most circumstances. Individuals adopting this strategy first try social learning and then resort to individual learning if the solution obtained

by social learning proves unsatisfactory. We show that this simple extension of the model has important consequences:

1. Critical social learners always do better than pure social learners.
2. Given that learning pays, either critical social learners or individual learners, and sometimes both, are evolutionary equilibria (evolutionarily stable strategies, or ESSs; see Maynard Smith 1982). Pure social learning is never an ESS, and there are no stable polymorphisms (coexistence of different strategies).
3. A population of critical social learners has higher fitness than a population of individual learners: culture can be both adaptive and creative.
4. The same conclusions hold also when individual learning is difficult or the environment is stable.
5. Errors in cultural transmission and environmental variability have the same influence on cultural evolution.

ROGERS'S MODEL

We reformulate Rogers's model with a more generalizable notation and setting. Rogers (1988) considers gene-culture coevolution in the imaginary Snerdwumps. These creatures face a survival problem (e.g., where to find food) whose solution can be looked for either through individual learning (e.g., by trial and error) or social learning (imitating other individuals). Which strategy is used is genetically determined for each individual.

Rogers supposes that the environment sometimes change, so that a solution that works for one generation

TABLE 1. Symbol legend.

Strategies	
i	Individual learning
s	Social learning
si	"Critical social learner": tries s first, then i
is	"Conditional social learner": tries i first then s
w_x	Fitness of strategy x
Costs	
c_s	Cost of social learning
c_i	Cost of individual learning
Proportions	
q^{OK}	Proportion of individuals with an OK solution
q_x	Proportion of population adopting strategy x
Probabilities	
p_i	Probability of acquiring an OK solution by individual learning
$p_s^{OK \to OK}$	Probability of acquiring an OK solution given that one observes an individual who has an OK solution (probability of functional transmission)
p_s^{OK}	Probability of acquiring an OK solution by social learning ($p_s^{OK} = q^{OK} p_s^{OK \to OK}$)

may not work for the next. In his model the environment switches between two possible states, but here we drop this assumption both for mathematical simplicity and because it is rare for an environmental change to undo previous changes (Feldman and Laland 1996). Instead, we assume that change results in a new state, in which there is a new unique solution to the survival problem. We call the latter an OK solution, and we calibrate the fitness scale so that the fitness of having an OK solution is 1, whereas the fitness of not having it is 0.

The core of the model is the interplay between various costs, proportions (of certain subsets of the population), and probabilities (of certain events). Table 1 lists all symbols. We denote costs by the symbol c, proportions by q, and probabilities by p. Some parameters are the same for all states of the environment: the cost of individual learning, c_i, and of social learning, c_s, as well as the probability of individual learners obtaining an OK solution, p_i^{OK}. Rogers assumed $p_i^{OK} = 1$, but we shall see that the conclusions do not depend on this assumption.

The probability that a social learner obtains an OK solution, p_s^{OK}, depends on the variability of the environment and other parameters:

$$p_s^{OK} = q^{OK} p^{noChange} p_s^{noError} \tag{1}$$

where q^{OK} is the proportion of individuals who have an OK solution in the population (which depends on cultural evolution, see below), $p^{noChange}$ is the probability of the same solution being correct in the next generation (i.e., a measure of the constancy of the environment), and $p_s^{noError}$ is the probability of copying a solution without error (i.e., a measure of the fidelity of social learning). The factors $p^{noChange}$ and $p_s^{noError}$ always appear together in the analysis; to avoid cumbersome formulas we introduce $p_s^{OK \to OK} = p^{noChange} p_s^{noError}$, which is the probability that, given that an

OK solution is observed, a social learner will successfully imitate it and thereby have a solution that is still OK in the new generation. We call $p_s^{OK \to OK}$ the *probability of functional transmission*.

Fitness Functions

The fitness of an individual learner is the probability of finding an OK solution minus the cost of individual learning:

$$w_i = p_i^{OK} - c_i. \tag{2}$$

Similarly, the fitness of a social learner is

$$w_s = p_s^{OK} - c_s = q^{OK} p_s^{OK \to OK} - c_s. \tag{3}$$

Cultural Evolution

Let q_t^{OK} denote the expected proportion of the population having the OK solution at generation t. Assuming that the genetically determined proportions of individual and social learners are q_i and q_s, respectively, the expected proportion of an OK solution in the next generation is

$$q_{t+1}^{OK} = q_i p_i^{OK} + q_s p_{s,t+1}^{OK} \tag{4}$$

where $p_{s,t+1}^{OK}$ is the probability of socially learning an OK solution in generation $t+1$:

$$p_{s,t+1}^{OK} = q_t^{OK} p_s^{OK \to OK}. \tag{5}$$

This cultural dynamics yields an equilibrium value of q^{OK} that can be calculated by the equation

$$q_{t+1}^{OK} = q_t^{OK} \tag{6}$$

which has the unique solution

$$q^{OK} = \frac{p_i^{OK}(1 - q_s)}{1 - p_s^{OK \to OK} q_s} \tag{7}$$

having used $q_i = 1 - q_s$.

Genetic Evolution

Assuming that cultural evolution is much faster than genetic evolution, we can calculate the fitness of the social learning strategy in equation 3 using the value of at cultural equilibrium, equation 7:

$$w_s = \frac{p_s^{OK \to OK} p_i^{OK}(1 - q_s)}{1 - p_s^{OK \to OK} q_s}. \tag{8}$$

Thus, the fitness is expressed as a function of the proportion of social learners in the population. Rogers depicted the situation in a graph similar to Figure 1b. When social learners are few, they have a fitness advantage compared to individual learners, but this advantage decreases as social learners become more common. Thus, genetic evolution will increase the number of social learners until an equilibrium is reached where the fitness of the two strategies is equal:

$$w_s = w_i. \tag{9}$$

The equilibrium value of q_s and $q_i = 1 - q_s$ can be computed from equations 2 and 8 (see Figure 1). The key observation is that at equilibrium the fitness of social learners is the same as the fitness of individual learners—which is always the same. Hence the paradoxical conclusion of Rogers's model is that culture, in the sense of culturally acquired solutions to survival problems, does not increase the fitness of Snerdwumps.

EXTENDING THE MODEL

We now introduce another genetically determined strategy, the critical social learner, who starts by socially learning a solution and then critically evaluates whether this seems to be an OK solution; if it is not OK, individual learning is tried. We assume that the evaluation itself is cost free (see the Discussion). We write this strategy as "si" because social learning is tried first, then is sometimes followed by individual learning. A strategy of this kind has been considered, in a different context, by Boyd and Richerson (1996).

Fitness Functions

The expected fitness of a critical social learner is the same as the expected fitness of a social learner plus the expected fitness of an individual learner weighted with the probability that the solution acquired by social learning is not OK:

$$
\begin{aligned}
w_{si} &= w_s + \left(1 - p_s^{OK}\right)w_i \\
&= q^{OK}p_s^{OK \to OK} - c_s + \left(1 - q^{OK}p_s^{OK \to OK}\right)\left(p_i^{OK} - c_i\right).
\end{aligned}
$$
(10)

Cultural Evolution

By definition, the probability that a critical social learner acquires an OK solution is $p_s^{OK} + (1 - p_s^{OK})p_i^{OK}$. Let q_{si} denote the proportion of critical social learners in the population. Then equation 4 for the expected proportion of an OK solution in generation $t + 1$ is augmented by one term:

$$
q_{t+1}^{OK} = q_i p_i^{OK} + q_s p_{s,t+1}^{OK} + q_{si}\left(p_{s,t+1}^{OK} + \left(1 - p_{s,t+1}^{OK}\right)p_i^{OK}\right).
$$
(11)

The equilibrium equation 6 now yields the following expected proportion of an OK solution in the population

$$
q^{OK} = \frac{p_i^{OK}(1 - q_s)}{1 - p_s^{OK \to OK}(q_s + (1 - p_i^{OK})q_{si})}
$$
(12)

where q_i has been eliminated using $q_i = 1 - q_s - q_{si}$.

Genetic Evolution

If individual learning is adaptive (i.e., $w_i > 0$), then critical social learners will always be better off than social learners (except in the uninteresting special case where social learners always obtain an OK solution). Hence the genetic evolutionary dynamics must have $q_s = 0$ at equilibrium, in

which case equation 12 simplifies to

$$
q^{OK} = \frac{p_i^{OK}}{1 - p_s^{OK \to OK}(1 - p_i^{OK})q_{si}}.
$$
(13)

The critical social learner strategy is an ESS if $w_{si} > w_i$ when almost all individuals adopt this strategy. With $q_{si} = 1$ and $q_i = 0$ equation 13 reduces to

$$
q^{OK} = \frac{p_i^{OK}}{1 - p_s^{OK \to OK}(1 - p_i^{OK})}.
$$
(14)

The condition $w_{si} > w_i$ writes

$$
q^{OK}p_s^{OK \to OK} - c_s + \left(1 - q^{OK}p_s^{OK \to OK}\right)\left(p_i^{OK} - c_i\right) > p_i^{OK} - c_i
$$
(15)

which together with equation 14 gives the ESS condition:

$$
c_i > p_i^{OK} - 1 + \frac{1 - (1 - p_i^{OK})p_s^{OK \to OK}}{p_i^{OK}p_s^{OK \to OK}}c_s.
$$
(16)

According to this condition, critical social learning is favored by lower cost of social learning, c_s, and higher cost of individual learning, c_i (Boyd 1988; Boyd and Richerson 1985; Feldman et al. 1996), as well as less environmental changes and more faithful cultural transmission (both increasing $p_s^{OK \to OK}$, the probability of functional transmission). Increasing the probability of finding an OK solution through individual learning (p_i^{OK}) from 0 to 1 first favors and then slightly disfavors critical social learning. Some of these dependences on parameters are illustrated in Figure 2. Note in particular that critical social learning is an ESS even when the cost of individual learning is 0 (unless p_i^{OK} is close to 1). Overall, the effect of the cost of individual learning is very weak for $p_i^{OK} < 1$.

When critical social learning is an ESS, average fitness is higher than in a population of individual learners (otherwise the population could be invaded by individual learners, violating the ESS condition). The crucial factor behind this result is that critical social learners are able to maintain a higher proportion of individuals with an OK solution, which translates in a higher probability of successful social learning. That is, although in Rogers's model q^{OK} decreases as social learners increase in frequency (equation 7), the reverse holds for critical social learners, as equation 13 is an increasing function of q_{si}. The right panels of Figure 2 show the proportion of individuals with an OK solution in populations consisting either of individual or critical social learners. When individuals learners always find an OK solution, $p_i^{OK} = 1$, there is no difference between the two populations. However, when $p_i^{OK} < 1$, a population of critical social learners maintains a higher proportion of individuals with an OK solution than a population of individual learners. The difference is particularly striking when the environment is stable and transmission is faithful, in which case almost all critical social learners have an OK solution even when the probability of finding one through individual learning is low.
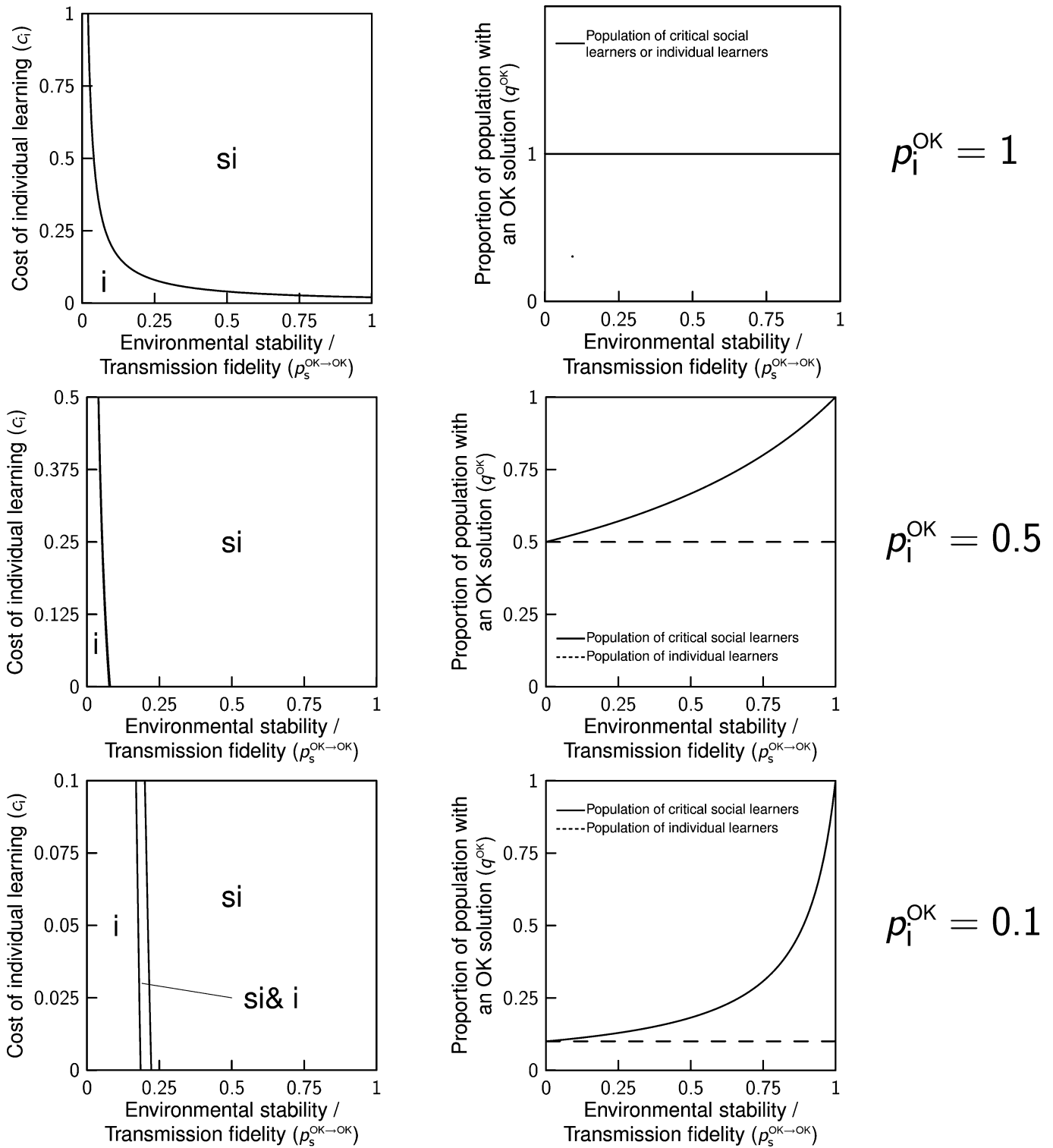
FIGURE 2. Left: Evolutionary stability of strategies in the extended Rogers' model. The vertical scales differ because of the requirement that individual learning be adaptive ($c_i < p_i^{OK}$). The cost of social learning is $c_s = 0.02$. The lower panel shows a region where both i and si are ESSs (cf. the first model in Boyd and Richerson 1996). The condition for i to be an ESS, determined in the same way as equation 16, is $c_i < p_i^{OK} - 1 + c_s/p_s^{OK \to OK} p_i^{OK}$. This is compatible with equation 16 so that for some parameter values both i and si are ESSs. Unless c_s is large or p_i^{OK} very small, however, this region is extremely small (the two lines coincide in the upper panel and are indistinguishable in the middle one). Right: proportion of individuals with an OK solution in populations of critical social learners or individual learners.
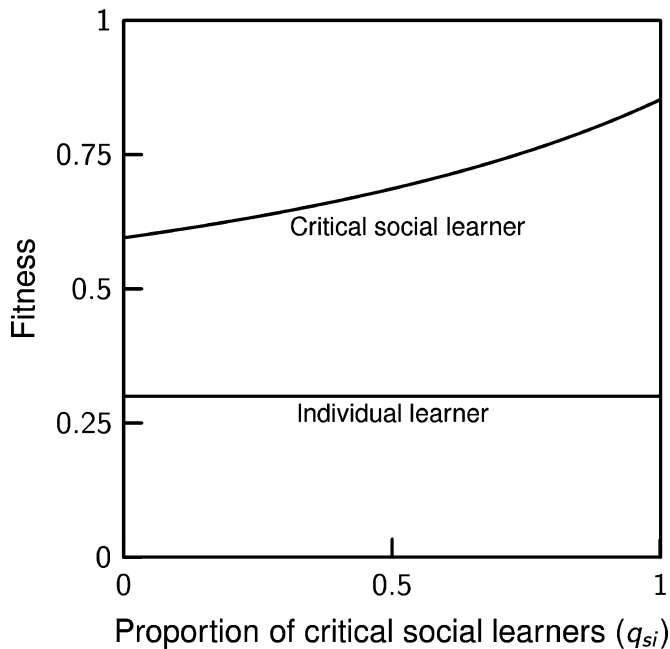
FIGURE 3. The fitness of critical social learners always increases as their frequency increases in a population consisting of critical social learners and individual learners (cf. Figure 1b). In this figure, we have $c_i = 0.2, c_s = 0.02, p_i^{OK} = 0.5$, and $p_s^{OK \to OK} = 0.9$, but the result is true for all parameter values (q^{OK} always increases with q_{si} equation 1).

DISCUSSION

Critical social learning offers a solution to Rogers's paradox because, under most circumstances, it allows culture to be adaptive and preserves individual creativity. The main reason for this is that the spread of critical social learning does not depress fitness. Figure 3 shows that the fitness of the critical social learner increases as a function of the proportion of critical social learners in the population. This stands in contrast with Rogers's original model, in which the fitness of social learners decreases when the latter become abundant (see Figure 1b). We now discuss whether critical social learning is a plausible strategy and how it modifies our understanding of the evolution of culture.

Is Social Learning Critical?

The critical social learning solution to Rogers's paradox depends on two main assumptions. The first is that critical social learning is possible. We do not think this is controversial. Although many theoretical models consider social and individual learning alternative strategies (Boyd and Richerson 1985; Rogers 1988), actually any species capable of social learning is also capable of individual learning. Likewise, the common assumption that social learners be uncritical toward socially acquired behavior (Boyd and Richerson 1985; Rogers 1988) is probably not true of actual social learning (Galef 1995; Laland 1996, 2004). For instance, any species capable of trial-and-error learning has mechanisms to evaluate the consequences of actions, and it seems unrealistic that these mechanisms do not operate at all on behavior acquired by social learning (Galef 1995).

The second assumption is that critical social learners do not pay a cost when they evaluate socially acquired behavior. We made this assumption partly for mathematical simplicity but also because it is not crucial: considering a cost of critical evaluation does not introduce any new qualitative features in the model, provided this cost is not so large that critical social learning becomes inferior to pure social learning. Our main result is equation 16, the condition for critical social learning being an ESS against individual learning. If a cost of critical evaluation, c_e, is considered, this condition is modified simply by adding c_e to the cost of social learning—that is, by replacing c_s with $c_s + c_e$. Thus, the form of equation 16 is unchanged, meaning that the dependency on p_i^{OK} and $p_s^{OK \to OK}$ is as discussed above: critical social learning is favored when individual learning is difficult and when the environment is stable and cultural transmission is faithful. Of course, the exact form of the boundary between the regions where individual or critical social learning are ESSs (see Figure 2) depends now on c_e as well. When c_e is similar in magnitude to c_s, the boundary is only slightly displaced. To significantly expand the region where individual learning is an ESS, c_e must be roughly as large as c_i. We believe this is an unlikely case, because checking whether a solution is OK should generally be easier than actually coming up with the OK solution.

Adaptive Filtering Makes Culture Adaptive

Critical social learners do well because rather than blindly sticking with unsatisfactory solutions acquired through social learning, they abandon them. This is an example of "adaptive filtering"—that is, a process whereby adaptive traits are more likely to be retained in a population than are maladaptive traits. In previous work (Enquist and Ghirlanda 2007), we have suggested that adaptive filtering is necessary for adaptive culture: simple social learning is not enough. This remark also explains the findings by Boyd and Richerson (1995) and Tatsuya Kameda and Daisuke Nakanishi (2003): both studies considered strategies that made informed decisions about what to do and what potential solutions to use, thus acting as adaptive filters. For instance, in Boyd and Richerson (1995, model 3), individuals rely on culture when an informed decision is not possible or uncertain. According to our results, it should be the informed decision that makes culture adaptive, not the uncritical use of culture when such a decision is not possible. Therefore, the adaptive value of culture should decrease when uncritical reliance on culture increases and when the ability to discriminate between OK and non-OK solutions decreases. The latter is obvious as decreasing the ability to discriminate between behaviors increases the chance of selecting the wrong one. As for the former, individual strategies are described in this model by a parameter d, such that with increasing values of d individuals rely more and more on imitation rather than on their own experience. Boyd and Richerson (1995) prove that there is an optimal level of d, greater than zero. On the one hand, this means that individual learners fare worse than those who rely on both individual and social learning (this is the point emphasized in
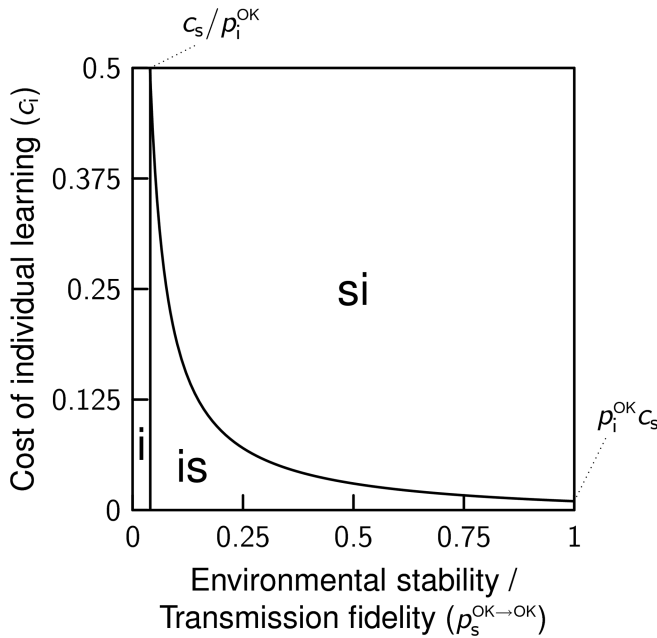
FIGURE 4. Evolutionary stability of strategies as a function of model parameters when the "conditional social learner" strategy is included as a further extension of Rogers's model (cf. Figure 3). Parameter values: $p_i^{OK} = 0.5$, $c_s = 0.02$.

the article). On the other hand, the same result implies that individuals should not rely too much on social learning, which would deprive them of adaptive filtering capacities.

Social Learning Should Usually Be Tried First

Kevin N. Laland (personal communication, July 1, 2006) suggested to us yet another strategy, which we call "conditional social learning," that tries individual learning before social learning. Such a strategy is often discussed in the literature, for instance in suggestions that social learning is tried when individual learning proves unproductive or too costly (reviewed in Laland 2004). Conditional social learning should be able to generate adaptive culture because, as critical social learning, it has adaptive filtering abilities (adaptive behavior is preserved in the population because individual learning is always tried). The fitness of this strategy is:

$$w_{is} = w_i + \left(1 - p_i^{OK}\right)w_s \qquad (17)$$

where the subscript ^{is} indicates that individual learning is tried before social learning. This strategy is clearly superior to an individual learner (given that $w_s > 0$); the question is how it fares against the critical social learner. Repeating the same kind of analysis as above shows that the conditional social learner cannot be invaded by critical social learners if the cost of individual learning is sufficiently small:

$$c_i < \frac{p_s^{OK \to OK}(1 - p_i^{OK})}{p_s^{OK \to OK}}c_s. \qquad (18)$$

If the opposite holds, a conditional social learner cannot invade a population of critical social learners. Thus, if

the cost of social learning is zero, then the conditional social learner strategy is never an ESS. In fact, the cost of social learning must be roughly of the same magnitude as the cost of individual learning for the conditional strategy to beat the critical strategy, which contradicts the common assumption about social learning being considerably cheaper. Hence, under most circumstances, the critical social learner is the superior strategy. Figure 4 shows which strategy is an ESS depending on parameter values. Note that in cases when the conditional social learner is an ESS, social learning is often of little use because of high environmental variability or inaccurate transmission. Considering a cost of critical evaluation does not modify these results because both the critical and the conditional social learner would pay such a cost.

It has often been suggested that social learning should be tried first when a behavior is either too costly or too complex to be invented by a single individual (Boyd and Richerson 1985, 1996; Henrich and McElreath 2003). Equation 18, however, depends only weakly on p_i^{OK}, which means that it is profitable to try social learning first, under most conditions, irrespective of whether it is easy or difficult to find an OK solution.

Are Inventions Rare?

In our model, individual learning has a cost, c_i, and a probability of success, p_i^{OK}. Most models, on the other hand, assume that individual learning always produces optimal behavior and only consider its cost (Aoki et al. 2005; Boyd and Richerson 1995; Rogers 1988). In such models, the main advantage of social learning is its smaller cost. Our results show that the probability that individual learning is successful, p_i^{OK}, can be an equally important factor in the evolution of social learning (see also Boyd and Richerson 1996). For instance, when p_i^{OK} is small, critical social learning can be an ESS even when the cost of individual learning is small (incl. zero), given that the probability of functional transmission, $p_s^{OK \to OK}$, is high enough and social learning is not too costly (equations 16 and 18). The reason is that critical social learning pays more and more as an OK solution becomes harder to find (see Figure 2).

It is difficult to know whether the probability of success or the cost of individual learning has been a more important factor in the evolution of social learning, but two recent extensive surveys suggest that invention is indeed difficult for chimpanzees and orangutans. Andrew Whiten and colleagues (2001) chart chimpanzee behavior patterns whose geographical distribution among study sites suggests a cultural origin (see also Whiten et al. 1999). The authors conclude that 12 behaviors have most likely been invented at a single site, later diffusing to other sites; eight behaviors appear to derive from single inventions followed by significant transformation in the course of diffusion; four behaviors are recorded at only one site, and thus seem to have been invented only once; and 11 behaviors appear to have been invented more than once. The latter, the authors note, comprise the simplest behaviors (e.g., using a stick as a club), whereas complex behaviors like cracking

nuts with stone anvils have almost certainly been invented at one site only. Carel P. van Schaik and colleagues (2003) reach similar conclusions regarding orangutan culture, noting also that, for both chimpanzees and orangutans, groups that live closer together have more similar culture.

CONCLUSION: THREE REQUIREMENTS FOR ADAPTIVE CULTURE

Work on the evolution of culture seems to converge on three basic requirements for the origin of adaptive culture. First, social transmission must be faithful enough. This is an obvious requirement and a major focus of research on animal and human imitation (e.g., Laland 2004; Tomasello et al. 1993). Second, for culture to be adaptive, the rise of social learning should not depress individual creativity. This is the lesson of the original model by Rogers (1988). We have seen above that using individual creativity when social learning fails seems to be the best strategy under most conditions. Third, there must be ways to limit the spread of maladaptive culture (adaptive filtering). Here, suggestions vary and are often not mutually exclusive (Mameli in press). Summarizing many years of work, Richerson and Boyd (2005) suggest that, in addition to the mechanisms reviewed above, genetic evolution has equipped humans with psychological mechanisms that indirectly favor the acquisition of adaptive cultural variants, such as the preferential imitation of common behavior or the behavior of successful individuals. We have suggested that individuals can also play a direct role in weeding out maladaptive culture by evaluating their own behavior (see also Enquist and Ghirlanda 2007). The precise mix of factors that has allowed adaptive culture to arise in humans, as well as an understanding of how pervasive maladaptive culture actually is, remain open to investigation.

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