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Adaptive strategies for cumulative cultural learning

Micael Ehn [a,b], Kevin Laland [a,*]

[a] Centre for Social Learning and Cognitive Evolution School of Biology, University of St Andrews, United Kingdom
[b] The Centre for the Study of Cultural Evolution, Stockholm University, Sweden

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ABSTRACT

The demographic and ecological success of our species is frequently attributed to our capacity for cumulative culture. However, it is not yet known how humans combine social and asocial learning to generate effective strategies for learning in a cumulative cultural context. Here we explore how cumulative culture influences the relative merits of various pure and conditional learning strategies, including pure asocial and social learning, critical social learning, conditional social learning and individual refiner strategies. We replicate the Rogers' paradox in the cumulative setting. However, our analysis suggests that strategies that resolved Rogers' paradox in a non-cumulative setting may not necessarily evolve in a cumulative setting, thus different strategies will optimize cumulative and non-cumulative cultural learning.

1. Introduction

The success of humanity, in colonizing and thriving in virtually every terrestrial habitat, is widely attributed to our species' capacity for cumulative culture (Boyd and Richerson, 1985; Tomasello, 1999; Enquist and Ghirlanda, 2007). By "cumulative culture" we mean the capability to accumulate knowledge, and for iterative improvements in technology, over multiple generations. The capacity of human culture to amass ever more effective solutions through repeated bouts of innovation and social transmission, leading to the evolution of technology that no individual could alone invent, has been described as like a "ratchet" (Tomasello, 1994, 1999). However, it is not yet known how humans combine social and asocial learning so efficiently to generate cumulative learning.

Adaptive rules that govern use of social information are referred to as "social learning strategies" (Laland, 2004) or "transmission biases" (Boyd and Richerson, 1985; Henrich and McElreath, 2003). Formal theory suggests that individuals should be selective with respect to when they copy others, and from whom they learn (Boyd and Richerson, 1985, 1995; Henrich and McElreath, 2003; Laland, 2004), and a variety of social learning strategies have been proposed. In many instances, the relative merits of reliance on alternative social learning strategies have been examined through theoretical work using population genetic and game theory models (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Rogers, 1988; Henrich and Boyd, 1998; Enquist et al., 2007; Wakano and Aoki, 2007; Kendal et al., 2009). However, these analyses have not considered how best to learn in a cumulative cultural framework, and it is not clear that those strategies that work most effectively in a non-cumulative setting will necessarily be optimal in a cumulative setting. For instance, Henrich and Boyd (1998) found that conformist social learning is favoured by selection over a broad range of conditions, yet Eriksson et al. (2007) found that conformity hindered cumulative cultural evolution.

One feature of human success is extreme population growth, which is indicative of an increment in absolute fitness. However, anthropologist Rogers (1988) first pointed out the "paradox" inherent in the observation that the use of pure (unbiased) social learning did not increase average individual fitness in a population of asocial learners. Rogers found that when rare, the fitness of social learners exceeds that of asocial learners, but declines with frequency as there are fewer asocial learners producing adaptive information in a changing environment. The population evolves to a mixed evolutionarily stable state where, by definition, the fitness of social learners equals that of asocial learners. This finding is now commonly known as Rogers' paradox (Boyd and Richerson, 1995), so called because it contrasts with a commonly held assertion that culture enhances fitness, and that social learning increases human adaptability.

Previous theoretical studies have established that the average individual fitness at equilibrium can be enhanced if individuals switch strategically between reliance on asocial and social learning (Boyd and Richerson, 1995, 1996; Kameda and Nakanishi, 2003; Enquist et al., 2007). Rogers' paradox can be solved by learners that deploy an adaptive filter to evaluate a solution to a problem before it is accepted. The first such strategy was suggested by Boyd and Richerson (1996) and later named "critical social learning" by

* Corresponding author. Tel.: +44 1334 463568.
E-mail address: knl1@st-andrews.ac.uk (K. Laland).

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Enquist et al. (2007). A critical social learner is an agent that first tries social learning and if that does not yield a solution, the agent tries individual (or asocial) learning instead. Enquist et al. (2007) also suggested another strategy utilizing adaptive filtering of information: the "conditional social learner". Conditional social learning starts with individual learning and switches to social learning only if that failed. Enquist et al. based their model on that of Rogers (1988), but made changes to create a framework better suited for mathematical analysis. In the Enquist et al. model, individuals have to find a solution to a problem using either social, individual learning, or a combination of both. Having a correct (or "OK") solution yields a fitness of 1, whilst not having it gives no fitness gain (i.e. the "fitness" benefits associated with solving the problem must be considered as an increment to some unspecified baseline fitness). Learning is costly and this cost is subtracted from the fitnesses. There is also a probability that the environment changes, in which case the previous solution is no longer valid and a new one has to be found using individual learning. It was assumed that an old solution could never become valid again. Enquist et al. (2007) showed that both the critical and conditional social learner strategies outcompete pure asocial and social learning strategies. Moreover, they both increment mean individual fitness, to provide solutions to Rogers' paradox. Rendell et al. (2010) extended these findings to a spatially explicit context. While Enquist et al. (2007) report a clear superiority of the critical over the conditional social learner, Rendell et al. (2010) report a broad range of conditions under which the conditional social learner is the most effective strategy. However, it is not known whether these solutions apply in a cumulative cultural context, which is a distinctive feature of human social learning.

Here we extend the framework provided by Enquist et al. (2007) to analyze how cumulative culture influences the relative merits of their proposed learning strategies, as well as other closely related strategies. While the basics of the problem remain, a major difference is that here, in a cumulative context, having a solution is no longer a binary function (i.e. present/absent). Instead, cumulative culture can yield one or more better, more refined solutions to the problem at hand. Accordingly, the solution can be characterized by its level of refinement, with more refined solutions yielding higher fitness.

Previous models of cumulative culture have studied the refinement of a cultural trait where the difficulty of acquiring a cultural trait is not reliant on its level of refinement (Boyd and Richerson, 1996; Henrich, 2004; McElreath, 2010). This models a situation where refining the solution to some problem does not increase the complexity of the solution. In this paper we assume that a more refined solution is also more complex and therefore harder to learn. One example of this is an axe. A rock will do as a simple axe. However, adding steps to the process of making an axe, such as sharpening the rock, drilling a hole and mounting a handle will increase the effectiveness of the tool, but at the same time make the process more complex and therefore harder to copy in full. This difference allows us to study the level of complexity that be maintained in a society, given a certain learning strategy. Our analysis suggests that different strategies will optimize cumulative and non-cumulative cultural learning.

2. Model

To extend Enquist et al.'s framework to allow for cumulative culture, we allow solutions to the problem to be proposed at different refinement levels. For simplicity, we assume that refinement of culture always takes place in simple discrete steps and follows a linear progression. Each level of refinement is directly dependent on the previous and is associated with an improvement in the efficiency of a solution to a problem and a corresponding increase in fitness of its user. Agents start without any solution and therefore accrue a fitness increment of 0 in addition to their baseline fitness. With some probability depending on their choice in learning strategy, they will find a basic solution, which we describe as refinement level 1. This solution is associated with a fitness increment. With some other probability, agents find a more refined solution, level 2, which confers higher fitness increment. Similarly, individuals can reach level 3 with some probability, and so on. We assume refinements can continue indefinitely and that the probability of reaching a certain level of refinement may depend on the distribution of knowledge in the population, as well as the probability of environmental change.

2.1. Environment

We assume that the environment can change with probability $1-p_{noCh}$, making p_{noCh} the probability of the environment staying the same between two generations. When the environment changes, it renders all previous solutions invalid (i.e. they return a fitness of 0).

2.2. Learning

We assume discrete generations. At the beginning of each generation, agents learn about their environment, in the process devising solutions to the problem. When learning, an agent is assumed to acquire a solution at a certain level of refinement, depending on the efficiency of that learning strategy, as well as chance. If, through learning, the probability of finding a solution with a refinement level equal to or greater than n is $p(n)$, then the probability of reaching exactly that level and nothing more is

$$p(n)\left(1-\frac{p(n+1)}{p(n)}\right). \tag{1}$$

Thus, learning within this framework is the same as sampling from the discrete probability distribution generated by $f(n)=p(n)(1-p(n+1)/p(n))$, which greatly simplifies the analysis. It then follows that the average level of refinement to a solution achieved by a given learning strategy is

$$\sum_{n=1}^{\infty} np(n)\left(1-\frac{p(n+1)}{p(n)}\right) = \sum_{n=1}^{\infty} p(n). \tag{2}$$

Previously, researchers have modeled learning in cumulative culture using a continuous (Gumbel) probability distribution (Powell et al., 2009; Henrich, 2004). In contrast, here we will derive the probability distributions that are associated with some social learning strategies common in the literature.

2.3. Fitness

We define a fitness function associated with cumulative learning, which increments by one "fitness unit" for every level of refinement, minus the cost (c) associated with the learning strategy deployed. This means that the fitness w of an agent is $w=w_0+n-c$, where w_0 is some baseline fitness, n is the level of refinement the agent has achieved and c is the cost incurred. While fitness normally only makes sense when it is positive, our model will only consider relative fitness, so we can set $w_0=0$ without loss of generality. The expected fitness of an individual is thus

$$\overline{w} = \sum_{n=1}^{\infty} p(n)-c. \tag{3}$$

Another possibility would be to have the cost be dependent on the amount of refinement, so that $w=n-nc$. However, this is equal to $w=(1-c)n$ so the cost would just change the slope of the fitness function compared to when the cost is constant. As this difference is unlikely to yield any interesting qualitative differences, we deploy the simpler solution of subtracting the cost, which has the additional advantage that it is consistent with Enquist et al. (2007). Another possibility is to assume that there is a diminishing return to more and more refined solutions, which can be captured by making the fitness a function of the logarithm of the refinement level

$$w = \mathrm{Log}(n) - c, \tag{4}$$

$$\overline{w} = \mathrm{Log}\left(\sum_{n=1}^{\infty} p(n)\right) - c. \tag{5}$$

We find that the choice in fitness function has some impact on which strategies that can evolve. We will begin our analysis with the simpler, linear fitness function and the strategies which can evolve in that setting. We will then move on to the more realistic logarithmic fitness function and the additional learning strategies that are made plausible by that change.

3. Linear fitness function

3.1. Pure individual learners

We begin by considering a pure individual (or asocial) learner, as considered by Rogers (1988) and Enquist et al. (2007). Individual learners are here denoted with a label *I*. Unlike the earlier treatments, our modeling structure allows the possibility of infinite refinement of any solution to the problem. This means that individual learning can no longer "always be successful", as in Rogers (1988), since this would imply that individual learners always manage to find an infinitely refined solution. Let p_I be the probability of successfully learning one refinement step through individual learning, then $p(n) = p_I^n$ is the probability distribution and $\sum_{n=1}^{\infty} p_I^n$ is the expected level of refinement across the population. We denote the cost of individual learning by c_I. The expected fitness $\overline{w}_I$ of individual learners is given by

$$\overline{w}_I = \sum_{n=1}^{\infty} p_I^n - c_I = \frac{1}{1-p_I} - 1 - c_I. \tag{6}$$

3.2. Pure social learners

We assume that a pure social learner observes a randomly chosen demonstrator agent and then tries to copy the solution exhibited by that demonstrator. Any error in the transmission of culture results in a lower level solution. This is similar to the model by McElreath (2010), where copying results in a solution that has a fraction of the fitness associated with the solution being exhibited by the cultural parent. The probability that they reach a certain level is thus also dependent on the proportion of the population with at least that level of refinement, as well as the environmental stability. Social learners are denoted with a label *S* and the probability of reaching level *n* through social learning, given that there is no environmental change, is given by

$$p_{S,n} = p_{noE}^n q_{n,t}, \tag{7}$$

where p_{noE} is the probability of successful social transmission (probability of *no error*) and $q_{n,t}$ is the proportion of the population with at least *n* steps of refinement at time *t*. It follows that the change in the distribution of knowledge over time resulting from social learning is given by

$$q_{n,t+1} = q_I p_I^n + q_S p_{noCh} p_{S,n}, \tag{8}$$

where q_I and q_S are the proportions of individual and social learners in the population and p_{noCh} is the probability that there was no environmental change since the last generational time-step. Assuming that genetic evolution is significantly slower than cultural evolution, then from (8) the stationary distribution $\hat{q}_n$ is given by

$$\hat{q}_n = \frac{q_I p_I^n}{1 - q_S p_{noCh} p_{noE}^n}. \tag{9}$$

The expected fitness of pure social learners is

$$\overline{w}_S = \sum_{n=1}^{\infty} \hat{q}_n p_{noCh} p_{noE}^n - c_S, \tag{10}$$

which, using (9), can be written as

$$\overline{w}_S = \sum_{n=1}^{\infty} \frac{q_I p_I^n p_{noE}^n p_{noCh}}{1 - q_S p_{noCh} p_{noE}^n} - c_S. \tag{11}$$

Using $q_I = 1 - q_S$ and (9) we consider what happens when the social learners go to fixation

$$\lim_{q_S \to 1} \hat{q}_n = 0, \tag{12}$$

which, together with (11) gives

$$\lim_{q_S \to 1} \overline{w}_S = -c_S. \tag{13}$$

Thus, where the proportion of social learners in the population to increase to 1, there would be no models with a solution of any refinement level and social learning would become useless. This means that we have replicated the original Rogers' paradox in this cumulative setting, which is illustrated by Fig. 1. While this result is not at all unexpected considering previous studies have shown that Rogers' paradox is stable across many different conditions (e.g. Boyd and Richerson, 1995; Rendell et al., 2010), Rogers' paradox has previously not been explored in cumulative culture.

3.3. Conditional social learner

The conditional social learner is one of the strategies that have been found to perform better than both pure social learning or pure individual learning in a non-cumulative setting (Enquist et al., 2007; Rendell et al., 2010). This strategy involves first trying individual learning and then switching to social learning if that fails to provide an OK solution. To implement this strategy in the cumulative

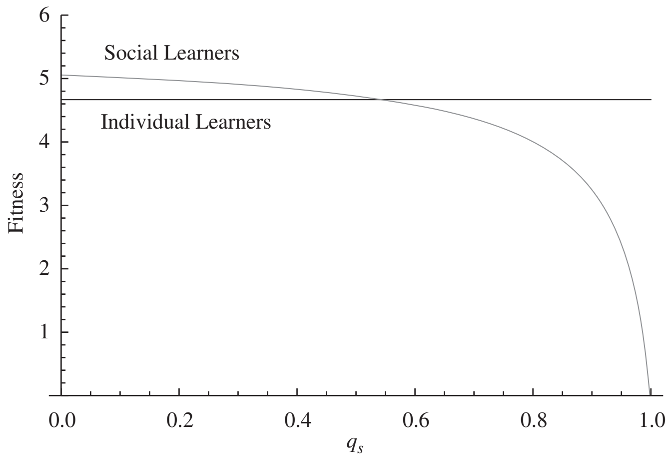

Fig. 1. The Rogers paradox in the cumulative setting. Here too, the social learners fitness decreases to a level below that of individual learners as they take over the population. Plotted with $p_I = 0.85$, $p_{noE} = 0.99$, $p_{noCh} = 0.99$, $c_I = 1$, $c_S = 0.2$.

setting, we have to define what substitutes for “an OK solution”. Since the cutoff point for an OK solution will influence the fitness of conditional social learners, we use a parameter, k to represent the cutoff point. This implementation is also similar to the selective learners in Boyd and Richerson (1995), where individuals learn individually and evaluate the quality of the result. If the signal from the environment has a high enough quality, they adopt the solution acquired from individual learning, otherwise they copy another individual. We have chosen not to implement an extra cost for the cognitive machinery needed to evaluate the solution acquired and decide whether to invest in more learning. Such costs have been implemented in previous models and will create a threshold at which the conditional strategy is better than the unconditional and will not provide any additional insights (see Boyd and Richerson, 1996; McElreath, 2010).

Here, the conditional social learner will be denoted *IS* (Individual first, then Social) and it has an expected fitness of

$$w_{IS} = \begin{cases} \overline{w}_I + (1-p_I)\sum_{j=0}^{k-1}\left(p_I^j \sum_{n=j+1}^{\infty} \hat{q}_n p_{noE}^{n-j} p_{noCh}\right) - (1-p_I^k)c_S & \text{if } k>1, \\ \overline{w}_I + (1-p_I)\sum_{n=1}^{\infty}\hat{q}_n p_{noE}^{n} p_{noCh} - (1-p_I)c_S & \text{else} \end{cases}, \tag{14}$$

when k levels of refinement is required for an OK solution. In competition with the pure individual learner this yields

$$q_{n,t+1} = q_I p_I^n + q_{IS}\left(p_I^n + (1-p_I)q_{n,t}p_{noCh}\sum_{j=0}^{\min(k,n)-1} p_I^j p_{noE}^{n-j}\right), \tag{15}$$

which gives (using $q_I = 1-q_{IS}$)

$$\hat{q}_n = \frac{p_I^n}{1-(1-p_I)p_{noCh}q_{IS}\sum_{j=0}^{\min(k,n)-1} p_I^j p_{noE}^{n-j}}. \tag{16}$$

It is apparent that $\hat{q}_n$ increases with q_{IS}, which means that $\overline{w}_{IS}$ will also increase with q_{IS}. Thus the conditional social learner strategy always has a higher fitness than the individual learner strategy, provided $\overline{w}_S > 0$. This means that the conditional social learner provides a solution to Rogers' Paradox in the cumulative setting. Fig. 2 shows the distribution of culture in a population of conditional social learners. We can see a small drop at $k+1$, due to this being the first level of refinement which the individuals have just one chance to learn. The right hand graph shows that the conditional social learner is fairly efficient at solving the problem. The probability mass of $n \geq k$ is significantly larger than that for $n < k$.

Evolution will drive k to the point where the availability of information on higher level solutions is scarce enough in the population to make social learning ineffective

$$\min_k \sum_{n=k}^{\infty} \hat{q}_n p_{noE}^{n+1-k} p_{noCh} - c_S \geq 0. \tag{17}$$

3.4. Social learning and individual refinement

With a linear fitness function, the relation between the cost and the benefit of learning another step using individual learning is constant. This means that it is never useful to evaluate a solution in order to decide whether to use individual learning to refine that solution or not. Therefore, critical social learning is not a stable strategy in this setting. Whereas k for the conditional social learner will evolve to a specific value, evolution of a corresponding parameter for the critical social learner would cause the parameter to increase indefinitely ($k \to \infty$). This would effectively remove the critical component of the critical social learner. Accordingly, we propose another strategy, which we call the *individual refiner*. An individual refiner first uses social learning and then always uses individual learning to refine any solution found by social learning, i.e. it acts exactly like a critical social learner with $k = \infty$ (Fig. 3). Previous models have also considered strategies incorporating social and individual learning in an unconditional fashion (Boyd and Richerson, 1996; McElreath, 2010). The average fitness of individual refiners, which we denote *IR*, is simply the fitness of a social learner plus that of

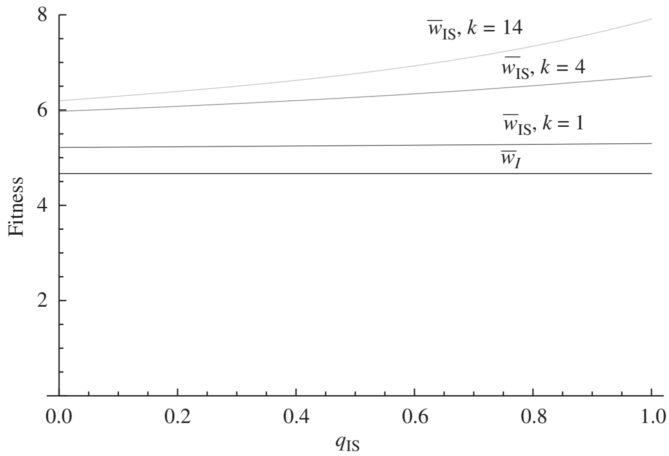

Fig. 3. Fitness of the conditional social learner with different values for k. With these parameters, the fitness is maximized when $k=14$. Plotted with $p_{noE} = 0.95$, $p_{noCh} = 0.99$, $p_I = 0.85$.

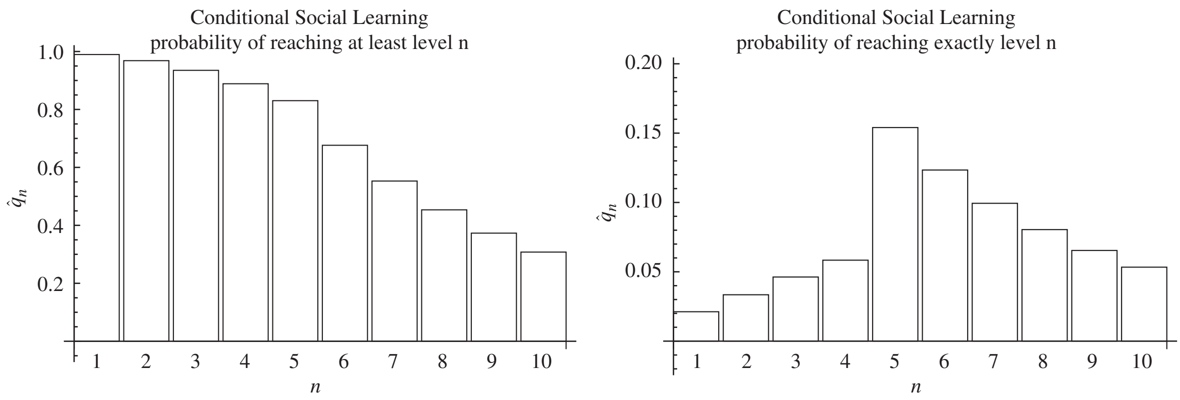

Fig. 2. The proportion of the population with at least refinement level n (left) and the proportion of the population with exactly level n (right) for $n \leq 10$ in a population consisting of conditional social learners. Plotted with $p_{noE} = 0.95$, $p_{noCh} = 0.99$, $p_I = 0.85$, $k=5$.

an individual learner

$$\overline{w}_{IR} = \overline{w}_S + \overline{w}_I. \tag{18}$$

The proportion of the population with a refinement level of at least n is given by

$$q_{n,t+1} = q_I p_I^n + q_{SI}\left[p_{noCh}p_{S,n} + (1-p_{noCh}p_{S,1})p_I^n + \sum_{j=1}^{n-1} p_{noCh}p_{S,j}(1-q_{j+1,t}p_{noE})p_I^{n-j}\right], \tag{19}$$

where the first two terms within the brackets are the probability of reaching level n by only social learning and the probability of reaching level n in the case of an environmental change, in which case only individual learning can be used. The last term between the brackets is the probability of reaching level n by a combination of social and individual learning. The sum gives the probability of reaching exactly level j using social learning and then learning the remaining $n-j$ levels using individual learning.

The individual refiners always perform better than the conditional social learners when social learning is beneficial. This is easy to see from the fact that individual learning has the same fitness benefit regardless of when it is performed (before or after social learning), while social learning is more efficient at lower levels of refinement (due to them being more wide-spread in the population). Further, this order allows the individual refiners always use both social learning and individual learning, which also increases fitness, as well as makes sure that they perform well even when making up the entire population.

The decrease in the proportion of the population (Fig. 4) with refinement level n does not exhibit any sudden drop, but rather it decreases very slowly compared to all other strategies presented in this paper.

4. Logarithmic fitness function

With a logarithmic fitness function the difference between the benefit and the cost of individual learning will vary, depending on the individuals previous knowledge when engaging in individual learning. An individual will therefore have to evaluate whether a solution needs to be refined further also in the case when social learning is performed first. This leads us to the critical social learner as defined by Enquist et al. (2007): "[An agent] 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.".

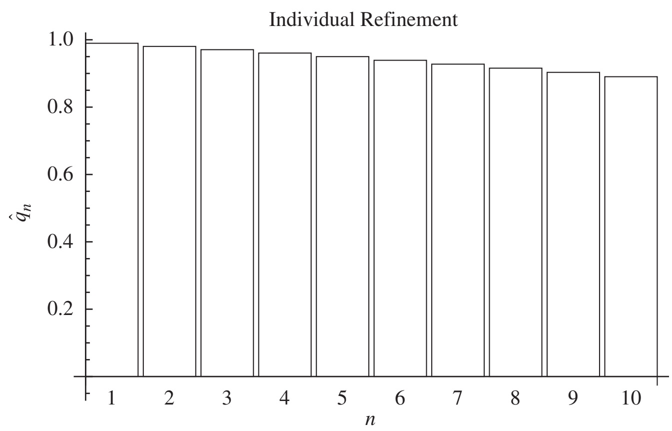

Fig. 4. The proportion of the population with at least refinement level n for $n \leq 10$ in a population consisting of individual refiners. Plotted with $p_{noE} = 0.95$, $p_{noCh} = 0.99$, $p_I = 0.85$.

4.1. Critical social learner

The critical social learner starts by utilizing social learning and if that does not provide an acceptable solution, uses individual learning to refine that solution further. The critical social learner is very similar to the conditional social learner in that it has a parameter, k, that defines which level of refinement is considered OK. Critical social learning will be denoted as SI. The expected fitness of SI is simply the logarithm of the expected level of refinement found by social learning plus the expected level of refinement found by individual learning multiplied by the probability that social learning failed to reach at least refinement level k minus the associated costs

$$\overline{w}_{SI} = \mathrm{Log}\left(\sum_{n=1}^{\infty} p_{S,n}p_{noCh} + p_{S<k}\left(\frac{1}{1-p_I}-1\right)\right) - c_S - p_{S<k}c_I, \tag{20}$$

where $p_{S<k}$ is the probability of social learning rendering a solution with a refinement level less than k

$$p_{S<k} = \sum_{j=1}^{k-1} \hat{q}_j p_{noE}^j p_{noCh}(1-\hat{q}_{j+1}p_{noE}) + (1-\hat{q}_1 p_{noCh}p_{noE}). \tag{21}$$

From this definition, we can see that critical social learning will always perform at least as well as pure social learning, assuming individual learning has a positive payoff and k is not set too high. We can assume that pure social learners would be replaced by critical social learners. Adding the critical social learner changes the proportion of the population with a solution of level n at time t, $q_{n,t}$

$$q_{n,t+1} = q_I p_I^n + q_{SI}\left(p_{noCh}p_{S,n} + (1-p_{noCh}p_{S,1})p_I^n + \sum_{j=1}^{\min(k-1,n-1)} p_{noCh}p_{S,j}(1-q_{j+1,t}p_{noE})p_I^{n-j}\right). \tag{22}$$

The equations for the stationary distribution are given in Appendix A.

The probability of a critical social learner reaching level $m \leq k$ has to be at least $p_I^m + x$ where x is the increased probability because of the capability of social learning. Thus the probability of a critical social learner reaching level m is always higher than that of a pure individual learner. Because of this $\hat{q}_m$ increase with q_{SI} for all $m \leq k$.

For levels $m > k$ we have three possibilities. First, there is some probability not to reach that level at all. Second, that level might be reached through pure social learning. Third, the level might be reached by first using social learning and then individual learning. After a critical social learner reaches refinement level k, the learning strategy for the rest of the refinement steps is set. If social learning worked all the way up to this point, the agent will not fall back on individual learning and thus is acting like a pure social learner. This happens with probability

$$p_{noE}^k p_{noCh}\hat{q}_k. \tag{23}$$

Alternatively, the social learning failed at some point during the learning process and individual learning was used for part of the way. We have already established that $\hat{q}_m$ increases with q_{SI} for $m \leq k$, so when the proportion of critical social learners increases the probability of reaching level k through just social learning (Eq. (23)) also increases. This implies that fewer critical social learners engage in individual learning when q_{SI} increases and therefore the probability of discovering better solutions, or rediscovering lost information decreases. Thus a large proportion of the critical social learners will tend to "get stuck" on level k and only a smaller part of the

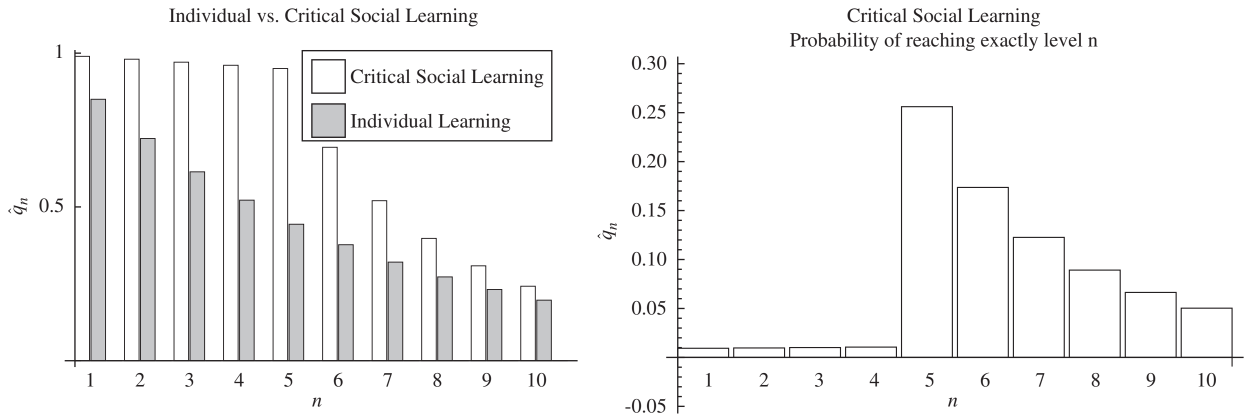

Fig. 5. The graph on the left is a comparison of the proportion of the population with at least refinement level n for $n \le 10$ in a population consisting of pure individual learners and one consisting of critical social learners. On the right is the proportion of the critical social learners that reach exactly level n. Plotted with $p_{noE} = 0.95$, $p_{noCh} = 0.99$, $p_I = 0.85$, $k=5$.

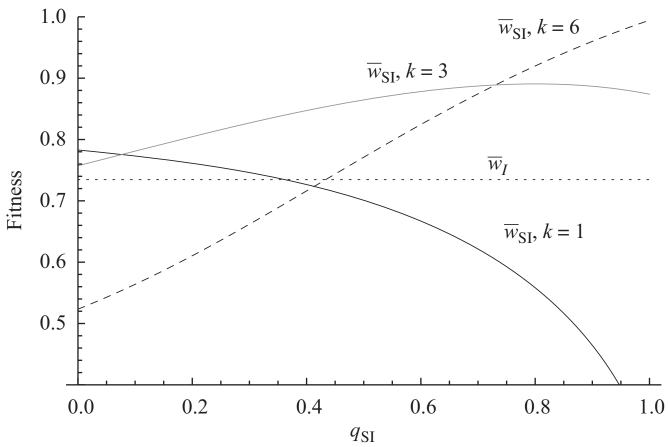

Fig. 6. Fitness for the pure individual learner (dotted) and the critical social learner when an OK solution consists of at least k steps of refinement. When $k=1$, the critical social learner does not solve the Rogers' paradox. At the individual level $k=3$ is the optimal, while at the group level $k=6$ maximizes fitness. Plotted with $p_{noE} = 0.9$,$p_{noCh} = 0.99$, $p_I = 0.85$, $c_S = 0.5$, $c_I = 1$, note that the y-axis does not start at 0.

individuals advance past that level. This means that there will be fewer individuals with a level of refinement significantly above k for critical social learners than individual learners. It follows that critical social learners will have a higher average fitness than pure individual learners only if k is set high enough. However, pure individual learners will still often have a higher proportion of the population with refinement levels over k (Fig. 5). If k is set too low, the fitness of the critical social learners will decrease when they take over the population (Fig. 6), thus not solving Rogers' paradox.

In a population consisting entirely of critical social learners, evolution will drive k to the level of refinement after which the cost of individual learning is higher than the benefit of the increased refinement. That is the value that best satisfies

$$\min_k \operatorname{Log}\left(k + \frac{1}{1-p_I} - 1\right) - c_I - \operatorname{Log}(k) \ge 0, \tag{24}$$

which gives

$$k = \left\lfloor \frac{p_I}{(e^{c_I}-1)(1-p_I)} \right\rfloor. \tag{25}$$

This value is however different from the optimum at a group level. If an individual decides to refine a solution further even though it is not individually beneficial to do so, others that learn socially from this individual will benefit from the higher level of refinement, yielding a higher average fitness in the group (Fig. 6).

4.2. Evolutionary stability

In the logarithmic setting, the critical social learner and the conditional social learner will have a higher fitness than any of the other strategies presented in this paper. By calculating which strategies are evolutionary stable for a large number of combinations[1] of parameters, we can, just as Enquist et al. (2007) did, establish that the critical social learner is the only ESS for most of the parameter space. The conditional social learner is an ESS only when individual learning is very cheap and/or efficient compared to social learning.

5. Amount of socially transmitted behavior

Culture is reliant on information that is transmitted socially between individuals. Because we have concentrated on strategies that combine individual and social learning, not all information acquired through deployment of such conditional strategies will actually be socially transmitted.

We plotted the amount of socially transmitted information for a wide range of parameter values and found that a surprisingly small proportion of the information is transmitted socially, even when the environment is very stable. Fig. 7 shows how various parameters affect the proportion of socially transmitted information associated with particular strategies. We can see that, across all of the strategies, typically a minority of the information is socially transmitted, only when social learning is significantly more efficient than individual learning will we see more than half of the information being transmitted socially. Conditional social learning never reaches a proportion of socially transmitted information that is over 70%. The critical social learner strategy achieves 90% socially transmitted information in the best case. The individual refiner is the only strategy that approaches having 100% of the behaviour socially transmitted.

One result that holds across all the strategies is that the proportion of socially transmitted information is at its largest when social learning has high fidelity (p_{noE} high) and individual learning is not

[1] The calculations were done with k set to the optimum for each strategy.

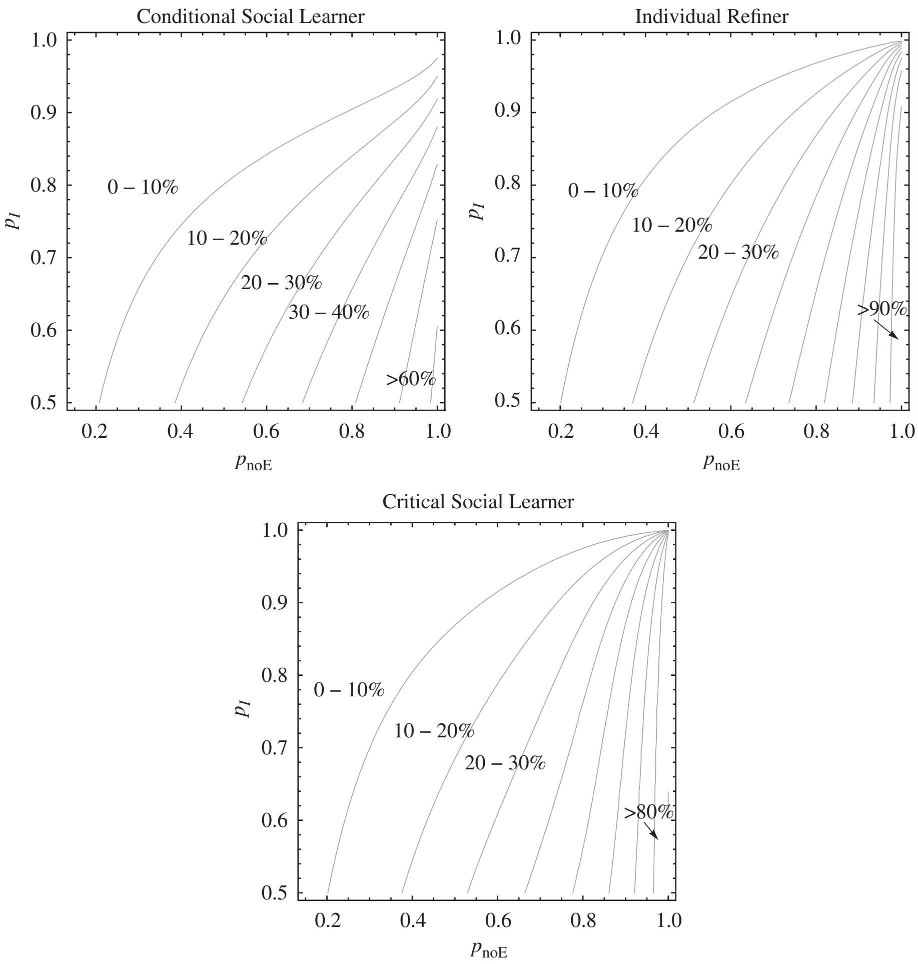

Fig. 7. Proportion of information that is socially transmitted. Plotted with $p_{noCh}=0.9$ and $k=5$ for the critical- and the conditional social learners.

effective (p_I low). This is quite intuitive, since if individual learning is efficient compared to social learning a lot of behavior would be learned by trial and error. Conversely, when individual learning is inefficient and social learning is accurate, the rare innovations have a high probability of spreading through the population.

6. Accumulating culture over several generations

Human culture accumulates innovations and refinements over long periods of time (Boyd and Richerson, 1985; Enquist and Ghirlanda, 2007). Hence, it is also interesting to explore which of the aforementioned strategies have the capacity to accumulate cultural knowledge over several generations. For culture to be accumulated over several generations there obviously needs to be a way to transfer culture from one generation to the next, but for all strategies except the pure individual learner this is satisfied by social learning. However, secondly, for cumulative culture the next generation needs to be able to build on this transmitted knowledge, since merely copying it would just be keeping the same information level within the population, rather than allowing knowledge to accumulate. As, within this framework, errors in copying can not lead to discovery of new innovations, the pure learners can not accumulate culture over generations. The conditional social learner starts by using individual learning so it is also unable to build on something generated by a previous generation.

If we define culture accumulated over generations as any refinement of information copied from a previous generation, then critical social learners would occasionally generate culture that is accumulated over generations, when they are not satisfied with just one refinement step ($k>1$). However, individual refiners would always generate culture accumulated over generations, assuming they got at least one level of refinement through social learning.

Another definition of cumulative culture might be as occurring when populations reach a level of refinement that is higher than that which is possible within just one generation. Of course, because of how the individual learning works within this framework, any level is possible to reach, but with a very low probability for high levels. We can, however, look at the expected level of refinement instead.

Generating more culture than one round of individual learning would easily be achieved by the strategies that utilize both social and individual learning at the same time. A suitable benchmark is the amount learned behavior that, on average, is generated by two attempts of individual learning. This could be achieved by individual refiners or critical social learners with a threshold for an OK solution that is high in relation to the expected level of refinement found by individual learning. The requirement for individual refiners to reach this level is that social learning is more efficient than individual learning,

$$\sum_{n=1}^{\infty} p_{S,n} > \sum_{n=1}^{\infty} p_I^n, \tag{26}$$

which requires a high level of current information in the population, as well as a fairly stable environment and efficient copying.

7. Discussion

We have explored how cumulative culture influences the relative merits of various pure and conditional learning strategies, including pure asocial and social learning, critical social learning, conditional social learning and individual refiner strategies. Our analyses reveal several results that are noteworthy.

First, we show, using pure social and individual learning strategies, that Rogers' Paradox is replicated in a cumulative culture setting. That is, pure social learning does not increase mean individual fitness, even when culture is cumulative. This means that there is nothing inherent about the cumulative culture context that renders Rogers (1988) result irrelevant, and strategic solutions are required if we are to explain the demographic and ecological success of our species.

Second, we find that one strategy known to resolve Rogers' paradox in a non-cumulative setting, namely the critical social learner (Enquist et al., 2007), will not evolve in a cumulative setting if fitness increases linearly with increased refinement of the solution. When fitness increase as the logarithm, whether the critical social learner does increase mean fitness hangs critically on to what extent the agents are willing to satisfy with a particular level of solution to the problem. We find that, with the critical social learner, where we set the refinement level that is deemed an OK solution determines whether the critical social learner will increase mean fitness, and that high level solutions (high k) are required for this strategy to prove a solution to Rogers' paradox. This has important implications that go beyond the merits of this particular strategy. Nearly all of the research into cultural evolution has explored social learning strategies in a non-cumulative cultural learning context, yet cumulative culture with increasing complexity would seem to be a characteristic feature of human culture. Our analysis suggests that researchers cannot assume that strategies that are effective in a non-cumulative context will prove effective in a cumulative setting, and that further cumulative culture analyses are required to determine which strategies are most effective strategies, under which conditions.

Third, we find that the conditional social learner, another strategy known to resolve Rogers' paradox in a non-cumulative setting, also does so in a cumulative setting. This gives us two possible hypotheses as to the kind of strategies that may underly human success. Humans may have adopted a critical social learner strategy, and copied first then refined asocially, but did so showing ambition to achieve high levels of success, without satisficing at lower levels of refinement. Alternatively, humans may have pursued a conditional social learning strategy, and learned asocially first, and only copied when this was not successful. We find that the conditional social learner excels where asocial learning is effective and social transmission leads to transmission error, and the critical social learner excels where asocial learning is unlikely to be successful, but high fidelity social transmission takes place.

It is interesting to speculate as to the possible role of high-fidelity information transmission processes, such as teaching through direct instruction, facilitated by verbal language, which (by increasing p_{noE}) might plausibly have tipped the balance from pursuing a conditional to a critical social learning strategy, amongst our ancestors. There is little hard data on this issue, however, researchers have suggested that nonhuman animals frequently appear to rely first on asocial learning and to copy only when this is not effective (Kendal et al., 2005). It is therefore conceivable that a switch to the social-learning-first strategies occurred in the hominins.

This paper introduces a new method of adjusting learning effort. In our model, natural selection acts upon the threshold level at which critical and conditional social learners are content with a solution and decides not to invest additional effort in learning using another learning strategy. This implementation is similar, but distinct from that in previous models on cumulative cultural evolution such as McElreath (2010). In McElreath (2010) natural selection acts directly upon the amount of effort put into social and individual learning, influencing the efficiency of the two different methods of acquiring information, rather than the cutoff point between them. Future research can combine these two implementations, creating a new set of strategies. These strategies can for example put a large amount of effort into social learning and only if this fails to yield an acceptable solution, use individual learning. While it seems unlikely that such a change would challenge the general findings in this paper, together with learning from multiple cultural parents (see Enquist et al., 2010), it may help explain the huge amount of social learning we can observe in the human society.

Fourth, we introduce another strategy, which we call the individual refiner, which might plausibly constitute a compelling learning mechanism capable of explaining recent human history. The individual refiner first uses social learning, and then refines through individual learning, and continues to do so irrespective of the level achieved. This strategy not only provides a solution to Rogers' paradox in the cumulative setting, but does so in a manner that generates high fitness across a broad range of conditions, that leads to high amounts of socially transmitted behaviour in the population, and accumulates significantly more innovations over the generations than any other strategy considered here (Fig. 8). In contrast, it is striking how the other strategies do not accumulate large amounts of socially transmitted behaviour (Fig. 7). Given the well-recognized reliance of children on imitation (Boyd and Richerson, 1985; Harris and Corriveau, 2011), it is not implausible that something like an individual refiner strategy, or indeed a critical social learner strategy, could be implemented in humans through a switch from a heavy reliance on social learning at a young age to greater reliance on asocial learning with experience. More generally, there is some evidence that both nonhuman animals and humans frequently pursue a copy when uncertain strategy (van Bergen et al., 2004; Kendal et al., 2005; Harris and Corriveau, 2011), which is consistent with their relying on social learning as a first measure, but decreasing such reliance with experience.

In practice, while we have considered each of these strategies in isolation, we expect some combination of these, and probably other, strategies to be deployed by humans. Recent studies of social learning suggest that animals and humans are capable of combining strategies in an adaptive fashion, and we see no reason why that should be different in a cumulative setting.

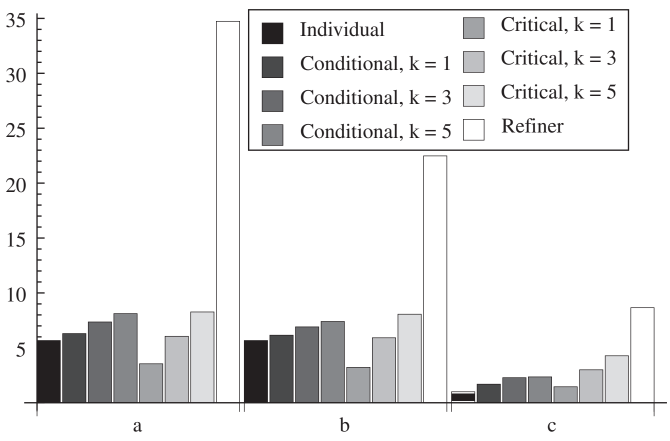

Fig. 8. Total amount of learned behavior accumulated by populations of individual learners, conditional social learners, critical social learners and individual refiners. Plotted with: (a) $p_I = 0.85$, $p_{noE} = 0.95$, (b) $p_I = 0.85$, $p_{noE} = 0.9$, $p_{noCh} = 0.9$, (c) $p_I = 0.5$, $p_{noE} = 0.95$, $p_{noCh} = 0.9$.

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Appendix A

The stationary distribution of culture in a population critical social learners is given by

$$\hat{q}_1 = \frac{p_I}{1 - p_{noCh} p_{noE} q_{SI} + p_I p_{noCh} p_{noE} q_{SI}} \tag{27}$$

and

$$\hat{q}_n = \frac{p_I^n + p_{noCh} q_{SI} (p_I p_{noE}^{n-1} \hat{q}_{n-1} - p_I^n p_{noE}^{n-1} \hat{q}_1 + \sum_{j=1}^{n-2} p_I^{n-j} p_{noE}^j \hat{q}_j (1 - p_{noE} \hat{q}_{j+1})}{1 + p_{noCh} p_{noE}^n q_{SI} (p_I \hat{q}_{n-1} - 1)}, \tag{28}$$

when $n \le k$ and

$$\hat{q}_n = \frac{1}{(1 + (p_I - 1) p_{noCh} p_{noE} q_{SI})(p_{noCh} p_{noE}^n q_{SI} - 1)} \Bigg(p_I^n (p_{noCh} p_{noE} q_{SI} - 1) + q_{SI} (-1 - p_{noCh} p_{noE} q_{SI} (p_I - 1)) \sum_{j=1}^{k-1} \hat{q}_j p_{noCh} p_{noE}^j (1 - \hat{q}_{j+1} p_{noE}) p_I^{n-j} \Bigg), \tag{29}$$

when $n > k$.

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