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Success-biased social learning: Cultural and evolutionary dynamics

Ryan Baldini

Graduate Group in Ecology, UC Davis, One Shields Avenue, Davis, CA 95616, United States

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ABSTRACT

Success bias is a social learning strategy whereby learners tend to acquire the cultural variants of successful individuals. I develop a general model of success-biased social learning for discrete cultural traits with stochastic payoffs, and investigate its dynamics when only two variants are present. I find that success bias inherently favors rare variants, and consequently performs worse than unbiased imitation (i.e. random copying) when success payoffs are at least mildly stochastic and the optimal variant is common. Because of this weakness, success bias fails to replace unbiased imitation in an evolutionary model when selection is fairly weak or when the environment is relatively stable, and sometimes fails to invade at all. I briefly discuss the optimal strength of success bias, the complicated nature of defining success in social learning contexts, and the value of variant frequency as an important source of information to social learners. I conclude with predictions regarding the prevalence of success bias in different behavioral domains.

1. Introduction

Much human behavior is acquired by imitation of and teaching by others (Richerson and Boyd, 2005). Many consider our extensive reliance on this socially transmitted information, which can evolve quickly and accumulate large stores of knowledge over many generations, to be a major cause of our species' rapid colonization and eventual ecological dominance of virtually every ecosystem on the planet (Boyd and Richerson, 1995). This hypothesis has motivated a large body of theoretical research on adaptive social learning strategies—i.e. those that increase mean genetic fitness. Models suggest that for social learning to be adaptive, imitation of others should not be purely at random—or "unbiased" (Rogers, 1988; Boyd and Richerson, 1995; Enquist et al., 2007). Rather, social learners should be partly critical regarding what and from whom they copy. Experimental evidence shows that a wide variety of organisms can be quite savvy about whom they imitate (Laland, 2004; McElreath et al., 2008; Chudek et al., 2011; Laland et al., 2011).

Success bias is the name given to any social learning strategy that uses some measure of others' success to influence how learners adopt cultural traits. Success bias is a natural candidate for an adaptive learning strategy, since success-biased learners seem more likely than unbiased imitators – those who choose at random – to adopt successful cultural variants. Insofar as "success" resembles fitness, this strategy would be expected to confer higher fitness on social learners than unbiased imitation, on average. The logic of success bias is compelling; indeed, one could hardly imagine a more direct approach to the problem of adaptive social learning than by copying apparently successful traits directly. Other strategies, like conformity, by which individuals tend to adopt the most common behavior, seem indirect and potentially misleading in comparison.

Success bias can be considered a special case of "indirectly-biased" learning rules (Boyd and Richerson, 1985). In contrast to "directly-biased" learning rules, which evaluate the content of cultural variants themselves, indirectly-biased rules determine whom to imitate based instead on characteristics of potential social models. Specific indirectly-biased learning rules vary only in how they define the characteristics by which models are compared (e.g. a specific definition of success or prestige) and how these characteristics direct social learning (e.g. by some mathematical rule). My use of the term "success" is meant to imply that success-biased social learners ideally evaluate their models by some characteristic that is related to reproductive fitness or material well-being. As I discuss below, however, the definition of success for the social learner, and hence that of success bias for the theorist, has no strict definition. The results of this paper do not hinge on these definitional issues.

The purpose of this paper is two-fold. First, I present a new general model for studying the cultural and evolutionary dynamics that arise in success-biased learning populations. This is important because, though success bias is a logically appealing and probably widespread strategy in humans, no one has rigorously investigated its dynamics in a sufficiently realistic and mechanistic way. A few simple models exist, but these either lack explicit sampling behavior (Boyd and Richerson, 1985; Henrich, 2004, Chapter 7), ignore stochasticity in payoffs McElreath and Boyd, 2007; Kendal

E-mail addresses: ryanbaldini@gmail.com, rcbaldini@ucdavis.edu.

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et al., 2009; Nakahashi et al., in press, limit sample sizes to just two or three individuals (Schlag, 1998, 1999; McElreath et al., 2008; Kendal et al., 2009; McElreath et al., in press), or otherwise use evolutionarily irrelevant criteria to evaluate learning rules (Schlag, 1998, 1999). Including these attributes adds to the realism of social learning models and reveals a heretofore undiscovered feature of success-bias, described below.

Second, I argue that success bias in fact encounters difficulties that, despite its appealing logic, render it a poor strategy under some conditions. Specifically, a success bias that compares mean payoffs, all other things being equal, carries a greater-than-chance probability of adopting rare variants—a "rare variant bias". Consequently success bias performs poorly – worse than unbiased imitation – when the most successful variants are at high frequency. Insofar as selection and learning tend to keep adaptive variants common and maladaptive variants rare, this feature of success bias is a detriment to its effectiveness. I show in an evolutionary model that success bias fails to invade unbiased imitation when selection on cultural variants is fairly weak and when the environment is relatively stable. Conversely, success bias readily invades and may replace unbiased imitation when selection is relatively strong and when the environment is unstable.

The next section presents the mathematical implementation of success bias that I use throughout the paper. Section 3 describes the cultural dynamics that arise when a population uses this rule and reveals its rare variant bias. Section 4 investigates the evolution of success bias under natural selection by pitting it against unbiased imitation, and shows how various evolutionary parameters affect the equilibrium frequency of success-biased learning. Section 5 discusses the problem of the optimal strength of success bias, the difficulty that learners face in defining "success" in the first place, and the value of variant frequency as a source of information to social learners.

2. A success-biased learning rule

Models of learning rules in cultural evolution are generally ad hoc; lacking knowledge of any laws that govern the brain's learning processes, the best we can do is construct mathematical models that behave as desired. The rule given here provides a relatively simple way of assigning extra weight to variants with high mean payoffs. It allows us to continuously vary the strength of the bias from 0, such that all variants are weighted equally, to ∞, such that a learner always adopts the more successful variant in her sample.

Consider a large population of social learning individuals characterized by some socially learned trait. Suppose there are N variants for this trait in the population, whose frequencies are given by the vector $\vec{p}$; p_i gives the frequency of variant i. Every generation, the current crop of learners randomly sample n individuals (or models) from the previous generation and assess their success, S, according to some common, possibly arbitrary definition. I say arbitrary because the term "success" has no strict definition and is free to be defined in many ways. It can be any quantifiable property of an individual, e.g. number of offspring, number of cars owned, etc.. I assume that S is positive.

There are many ways that learners can make use of the information in S. One simple rule specifies that, for any individual, the probability of adopting variant i after sampling is

$$P(\text{adopt variant } i) = \frac{\bar{S}_i^\alpha}{\sum_{j=1}^{N} \bar{S}_j^\alpha}, \tag{1}$$

where $\bar{S}_j$ is the sample mean of variant j. $\bar{S}_j$ is defined as 0 if variant j is not sampled. Momentarily ignoring the α term, it is clear that the learner has a higher chance of adopting variant i if the average success of individuals with variant i in her sample is large. The parameter α adjusts the weight given to the more successful variants in one's sample. Notice that if $\alpha = 0$, the probability above always equals the reciprocal of the number of traits sampled. There is no tendency to pick the more successful variant in this case: each are weighted equally. On the other hand, as $\alpha \to \infty$, a learner will always adopt the variant with highest mean success in her sample.

I have chosen a rule whereby the learner compares the arithmetic mean payoffs for the sake of analytical ease. Also, arithmetic mean fitness is what matters within a single generation in the evolutionary model of Section 4, so it appears to be a natural choice. The results found in this paper are not unique to the exact form of the rule used here. For example, a success-biased rule that adopts variants with probability proportional to *differences* in mean payoffs (as suggested by Schlag (1998)), shows the same cultural dynamics analyzed below. In particular, that rule too contains a rare variant bias.

3. Cultural dynamics

3.1. A general recursion

For large populations, we can derive a recursion for any cultural variant using the following basic form:

$$p_{i,t+1} = \sum_{\text{all possible samples}} P(\text{sample a particular set of variants}) \, P(\text{adopt variant } i|\text{ sample}). \tag{2}$$

That is, the frequency of any variant in the next time period is equal to the probability of sampling a particular combination of variants times the probability of adopting variant i given that sample, summed over all possible combinations of variants. Eq. (2) can be written more formally by using the multinomial distribution to describe sampling frequencies and the learning rule developed above, which produces

$$p_{i,t+1} = \sum_{\vec{n}} \left(\frac{n!}{\prod_{j}^{N} n_j!} \prod_{j=1}^{N} p_{j,t}^{n_j} \right) \mathrm{E}_{\vec{n}} \left(\frac{\bar{S}_i^\alpha}{\sum_{j}^{N} \bar{S}_j^\alpha} \right), \tag{3}$$

where

$$\mathrm{E}_{\vec{n}} \left(\frac{\bar{S}_i^\alpha}{\sum_{j}^{N} \bar{S}_j^\alpha} \right) = \int \frac{x_i^\alpha}{\sum_{j}^{N} x_j^\alpha} f_{\bar{S}|\vec{n}}(\vec{x}) \, \mathrm{d}\vec{x}.$$

Here, $\vec{n}$ is the vector of sample sizes for each variant, 1 through N; n_j gives the number of times the variant j is sampled. $f_{\bar{S}|\vec{n}}$ is the probability density function of $\vec{\bar{S}}$, the vector of mean successes to variants 1 through N, when the sample sizes of the traits are $\vec{n}$. Eq. (3) is easily extended to give a vector of recursions for all cultural variants.

Analysis of this recursion in its most general form is very difficult. I will proceed in this paper by only treating cases where just two cultural variants, called A and B, exist. In this case, the state of any population is specified by just one quantity, $p = p_A$, the frequency of the variant A. The recursion then reduces to

$$p_{t+1} = \sum_{i=0}^{n} \binom{n}{i} p_t^i (1-p_t)^{n-i} \times \iint \frac{x^\alpha}{x^\alpha + y^\alpha} f_{\bar{S}_A|i}(x) f_{\bar{S}_B|n-i}(y) \, \mathrm{d}x\mathrm{d}y, \tag{4}$$

where $f_{\bar{S}_A|i}$ is the probability density function for $\bar{S}_A$ given that the learner has sampled i individuals with variant A, and similarly for $f_{\bar{S}_B|n-i}$. Notice that the multinomial probabilities associated with each possible sample have been simplified to the binomial case.

I proceed with analysis by specifying the probability distributions that underlie the success payoffs to variants A and B. Even with common probability distributions (e.g. normal, exponential, gamma, etc.), however, the sums and integrals above appear to be impossible to solve in elementary terms. In the following Section 1 make some analytical progress by assuming normal distributions for S_A and S_B and using graphical analysis techniques.

3.2. Under normally distributed payoffs

Suppose that the successes associated with traits A and B are independently and normally distributed. That is,

$$S_A \sim \mathcal{N}(\mu_A, \sigma_A^2) \quad \text{and} \quad S_B \sim \mathcal{N}(\mu_B, \sigma_B^2).$$

This assumption is not altogether unreasonable given the ubiquity of normal distributions in nature (Frank, 2009). Suppose further that α is essentially infinite, so that social learners always adopt the more successful variant in their samples. I will briefly discuss the fairness of this assumption later. For now, it will suffice to say that I have found no instance where increasing α does not result in a uniform increase in the probability of adopting the more successful variant if payoffs are normally distributed. Hence, the first assumption appears to justify the second.

With these assumptions, it follows that the probability of adopting variant A is

$$P(A) = P(\bar{S}_A - \bar{S}_B > 0).$$

The difference between the means of two normal random variables is itself normally distributed. Specifically,

$$\bar{S}_A - \bar{S}_B \sim \mathcal{N}\left(\mu_A - \mu_B, \frac{\sigma_A^2}{n_A} + \frac{\sigma_B^2}{n_B}\right).$$

Using this fact, we find that recursion (4) reduces to

$$p_{t+1} = p_t^n + \sum_{i=1}^{n-1} \binom{n}{i} \times p_t^i (1-p_t)^{n-i}\, \Phi\left(\frac{\sqrt{i(n-i)}(\mu_A - \mu_B)}{\sqrt{i\sigma_B^2 + (n-i)\sigma_A^2}}\right), \quad (5)$$

where Φ is the cumulative distribution function of a standard normal (i.e. $\mathcal{N}(0, 1)$) variable. If we let $\sigma_A = \sigma_B = \sigma$, so that the variances in payoffs to A and B are equal, then recursion (5) further reduces to

$$p_{t+1} = p_t^n + \sum_{i=1}^{n-1} \binom{n}{i} p_t^i (1-p_t)^{n-i}\, \Phi\left(\frac{\sqrt{i(n-i)}}{\sqrt{n}C}\right), \quad (6)$$

where

$$C = \frac{\sigma}{\mu_A - \mu_B}.$$

C is the ratio of the standard deviation in success for both variants to the difference between their means. It is a dimensionless measure of the difficulty of distinguishing the expected returns to A and B. Under these conditions the cultural recursion depends on only two parameters, n and C, which allows for relatively easy graphical and asymptotic analysis of cultural dynamics.

First, note that as $C \to 0$, the argument of Φ approaches ∞. Since $\lim_{x\to\infty} \Phi(x) = 1$, we conclude that this strong success bias leads very quickly to fixation for the more successful variant if there is little variation in success and the difference between the expected payoffs to A and B is large. This makes sense, because under these conditions the learners always recognize the more successful variant whenever they sample it. Conversely, as $C \to \pm\infty$, the argument of Φ approaches 0. Since $\Phi(0) = 0.5$, we conclude that if the variation in payoffs to variants A and B are very large compared to the difference between their means, then on average the learner fails to distinguish the two. In this case, a success-biased learner might as well choose a variant by coin flip.

Fig. 1a graphs the recursions numerically for various C when $n = 10$. The dashed line shows the recursion $p_{t+1} = p_t$, which would describe cultural evolution in a population with no learning biases (i.e. traits are copied at random). The equilibria points $\hat{p}$ occur where the curved recursion lines intersect the diagonal dashed line (these are stable under most conditions). The patterns shown appeal to intuition. When C is low, learners can quickly recognize a rare successful trait and bring it to a high frequency. When C is high, the process is slower and the equilibrium value $\hat{p}$ is lower, since the uncertainty in payoffs cause many to adopt the less successful variant.

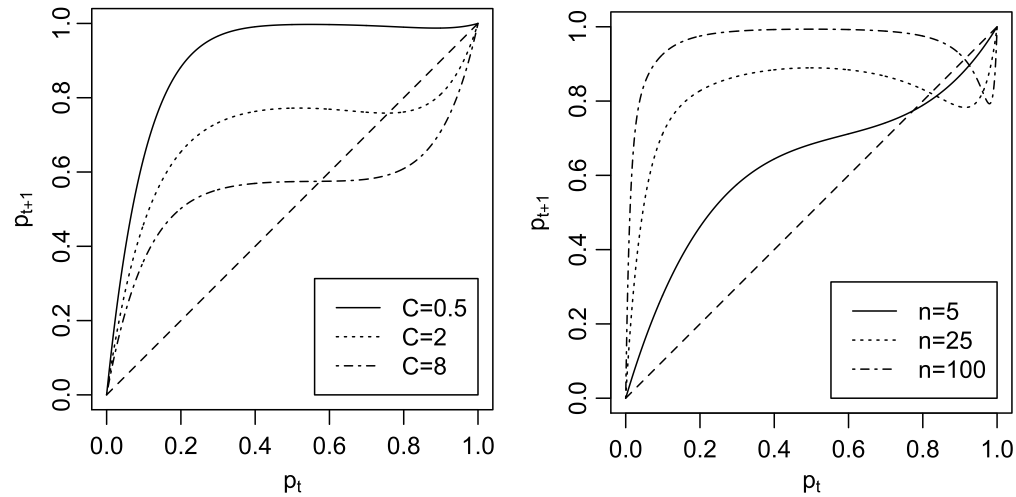
Fig. 1b graphs the recursion for various n when $C = 2$. Here, $\hat{p}$ generally rises with n because learners can more accurately assess the expected payoffs to each variant when sample size is large.

3.3. Success bias is biased toward rare variants

An important and novel result, made apparent in Fig. 1, is that when there is sufficient stochasticity in the payoffs to different variants, even a population composed entirely of strongly success-biased social learners fails to bring the more successful variant to fixation. This surprising outcome results from an unexpected feature of success bias: any learning rule that only evaluates variants by mean payoffs carries an inherent bias toward rare variants. By definition, a learning rule is biased toward rare variants if, given two variants with the same payoff distribution, the rule adopts the rarer variant with probability greater than the rare variant's frequency in the population. Clearly unbiased imitation does not have a rare variant bias: traits are chosen at random and therefore adopted in exact proportion to their commonness.

That success bias carries a rare variant bias is not obvious by inspection of the learning rule—after all, the rule itself completely disregards variant sample frequency. Fig. 2 shows a recursion for a population of success biased learners when the two variants have the same payoff distribution. It is clear from this figure that the bias exists: a stable cultural equilibrium occurs only at $p = 0.5$, meaning the rare variant is favored despite having the exact same payoff distribution as the common variant. The bias arises because the learning rule treats the mean payoff to each variant as a *single observation*. It does not matter how many times each variant is sampled; only their means are compared. As a result, success bias naturally produces a "handicap" for a rare variants that are unlikely to be imitated at random.

For a simple demonstration of this, imagine the case where a population contains two variants with identical payoff distributions that are symmetrical about the mean. Let the initial frequency of variant A be 0.1. Supposing that learners sample $n = 10$ individuals, one can easily calculate the frequency of variant A in the next generation. With probability $0.9^{10} \approx 0.35$, a learner samples only variant B. None of these learners adopt variant A. We can also safely ignore the negligible proportion of learners who sample only variant A. The rest obtain some mixed sample containing A and B. Since A and B are identically and symmetrically distributed, the probability of adopting A given a mixed sample is exactly 0.5, regardless of how many variants are sampled. Hence p_{t+1}, the frequency of A in the next generation, is $0.5(1 - 0.9^{10}) \approx 0.326$. A has increased in frequency simply because it was less common than B. The reason, again, is that success bias does not "care" how many times A is



(a) $n = 10$. (b) $C = 2$.

Fig. 1. Success-biased cultural recursions.

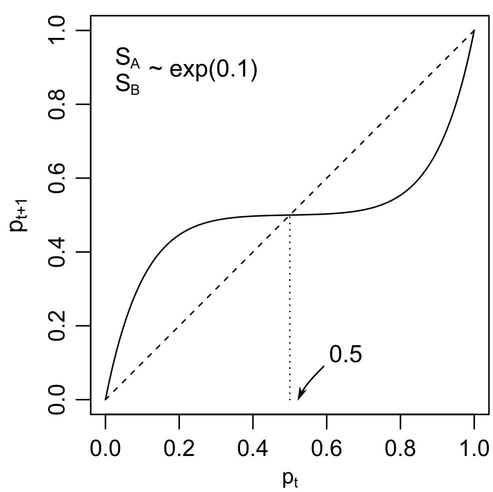


Fig. 2. The recursion for two variants with identically distributed payoffs. Both variants have payoffs distributed exponentially with mean $= 10$. Parameters: $n = 10$, $\alpha = 20$.

sampled compared to B; ironically, by ignoring variant frequency it actually creates a bias for rare variants.

Eq. (6) demonstrates this property for normally distributed success payoffs, which are symmetrical about the mean. If $\mu_A = \mu_B$, then the argument of Φ goes to zero, so

$$p_{t+1} = p_t^n + \frac{1}{2}(1 - p_t^n - (1 - p_t)^n).$$

Simple calculations and stability analysis verify that $\hat{p} = 0.5$ is the unique stable cultural equilibrium when $n > 2$.[1]

The story is more complicated when the payoff distributions are not symmetrical about the mean. Suppose variants A and B are identically, exponentially distributed. These payoffs are not symmetrical about the mean: a learner is more likely to get a payoff below the mean than above. Nonetheless, if B is common, then the sampled mean of B approaches a normal distribution as per the central limit theorem because it is frequently sampled. This approach to normality changes the distribution's shape, and in particular makes the payoff to B more symmetrical. Individuals who sample 9 of variant B but only 1 of variant A will usually find the mean of S_B to be greater than S_A because of this effect: $\bar{S}_B$, having a more symmetrical distribution, is now usually near the expected payoff, while S_A, having the original exponential distribution, is usually below it. Hence, learners with mixed samples have a probability greater than 0.5 of adopting the common variant. Still, I have not found any case where this probability actually exceeds the frequency of the common trait in the population, despite my best efforts to create such an effect (e.g. by producing extremely right-skewed distributions). Hence it appears that the rare variant bias exists for all payoff distributions, though I have not been able to prove this rigorously. An example is Fig. 2, where S_A and $S_B \sim \exp(0.1)$.

The interaction between the unintended rare variant bias and the intended payoff-oriented bias determines the shape of the cultural recursions. When payoff expectations differ greatly and stochasticity is small, the payoff-oriented bias dominates for all p such that the better variant is brought to fixation. When there is much overlap between variant payoffs, however, the rare variant bias becomes strong as the optimal variant approaches fixation, resulting in a polymorphic equilibrium for cultural variants. When the cultural variant is more common than this equilibrium, success bias performs *worse* than unbiased imitation. This fact has important evolutionary implications, as analyzed below.

4. Evolutionary dynamics: success bias vs. unbiased imitation

When payoffs are stochastic and the optimal variant is common, success bias is less likely to adopt the optimal variant than is unbiased imitation. Insofar as adaptive processes, such as selection and individual learning, tend to keep adaptive variants common and maladaptive variants rare, this feature of success bias implies that it may prove a poor strategy under many conditions. In this Section I present an evolutionary model to investigate how temporal environmental variation and payoff stochasticity affect the prevalence of success bias as opposed to unbiased imitation and individual learning.

Consider a large, asexual population faced again with the task of acquiring the optimal of two cultural variants. By optimal I mean that it confers the highest expected fertility at that point in time, although one's actual fertility is only stochastically related to the cultural trait of interest (due to chance events and the effects of other traits). Specifically, fertility is Poisson distributed,

[1] When $n = 2$, it is impossible to have a mixed sample where one variant outnumbers the other, so a rare variant bias cannot exist. In this case, all points in [0, 1] are neutrally stable.

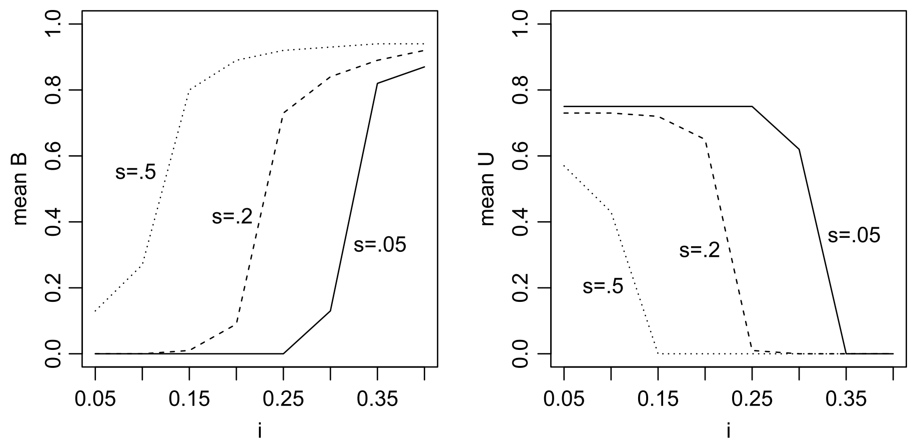


Fig. 3. Mean simulated values for prevalence of success bias, B, and unbiased imitation, U, across 35,000 generations, per environmental instability, i, and strength of selection, s. Baseline fertility, f_0, is set at 1. $n = 10$. $\alpha = 20$; this is a very strong success bias. c, the cost of learning, is set such that a population containing only individual learners and unbiased social learners would have a mean U of approximately .75. The formula for this is $c = 1 - \frac{1+s\frac{(1-.75)(1-i)}{1-.75(1-i)}}{1+s}$. Simulations were run in R programming language.

and individuals with the optimal behaviors have expected fertility of $f_0(1+s)$ (momentarily ignoring learning costs), while those with the non-optimal behavior have just f_0. Hence the parameter s determines the strength of selection for the optimal variant. Every generation the environment shifts with probability i, such that a novel variant becomes optimal.[2]

There are three genetically inherited learning strategies: individual learning, unbiased imitation, and success bias. Individual learners always acquire the optimal variant, but the costs of trial-and-error learning result in an expected fertility $f_0(1+s)(1-c)$. Unbiased imitators simply select one individual at random from the previous generation and adopt her behavior, at no cost. Success-biased social learners sample n individuals from the previous generation and use the learning rule developed in this paper, at no cost. An important assumption here is that the measure of success that social learners use is exactly that which natural selection acts on (i.e. fertility, in this case). In reality, this probably never holds; the common definition of success may diverge strongly from fitness. This complication implies that this model will actually *overestimate* the optimal reliance on success bias. See the discussion for clarification of this matter.

Let the frequency of success-biased learners be given by B (for Biased) and that of unbiased social learners by U. The aim of this analysis is to track how natural selection affects these frequencies over a long period of time at various parameters. Although far from being comprehensive, Fig. 3 shows the effect of two important parameters, s and i, on the mean frequency of B and U.

Note the apparent monotonic effects of both s, the strength of selection, and i, the instability of the environment, under both simulations. At least for the range of parameters shown, an increase in the strength of selection favors a greater reliance on success bias. This is because success-biased learners can more accurately identify the optimal variant as the difference between the expected payoffs increases.

The effect of i reflects the central finding that success bias performs poorly when the optimal variant is common. At low i, the environment is relatively stable. Learners have plenty of time to bring the optimal variant to high frequency between environmental shifts, so the optimal variant is usually common. Unbiased learning performs better than success bias under these conditions, hence the prevalence of unbiased imitation at low i. The increase in environmental instability with i causes the frequency of the optimal variant to be lower on average, since learners have fewer generations bring it to high frequency. Success-biased learners perform better than unbiased imitators in such conditions, hence the prevalence of success-biased learners at high i.

When both s and i are high, success bias completely replaces unbiased imitation. Thus we predict success bias to be common when the best variants frequently change and when selection is strong (or stochasticity in payoffs is weak). At intermediate levels, three learning strategies coexist in a stable polymorphism in both simulations (individual learning, whose frequency is not shown but can be deduced from Fig. 3, is always present, since a population without individual learners is doomed to remain outdated after an environmental switch). And, finally, when the environment is relatively stable (i is low) and selection is fairly weak (s is small), success bias is selected to low frequency or extinction.

The effects of remaining parameters can be inferred by the same logic. Increasing n, the number of individuals sampled by success-biased learners, has a similar effect to increasing s: it causes success-biased learning to be more accurate and therefore increases the mean value of B. Since increasing n apparently always increases the effectiveness of success bias, one might suppose that n should always evolve upward. But sampling is inherently costly; time spent gathering data cannot be used to forage, compete for mates, care for offspring, etc.. Local population size also places an upper bound on n. Increasing c, the cost of individual learning, discourages individual learning and consequently lowers the frequency of the optimal variant on average. As with increasing i, this tends to favor success bias over unbiased imitation. Simulations (not shown) confirm these inferences.

5. Discussion

5.1. The optimal strength of success bias

The models analyzed above assume large or infinite α, such that learners essentially always adopt the variant with the highest payoff their samples. The evolution of the strength of success bias is a complicated and interesting problem in its own right that I

[2] Because the probability of adopting the optimal variant via success bias depends on the number of variants in the population, I require that only two variants remain present in the population at any given time. This means that, after an environmental change, a new optimal variant is introduced while one of the resident variants is removed. Although this is an admittedly contrived scenario, it is unlikely that it will strongly affect the conclusions below. Future investigations should allow for more than two variants.

do not investigate rigorously here. There is reason, however, to suspect that α may not always evolve toward infinity. Consider the case where payoffs to the optimal variant are highly skewed, so that most payoffs to this variant are well below the expectation. A strongly biased learner with a small sample size would often conclude that the suboptimal variant is best because it confers a higher payoff most of the time. A more weakly biased learner would "take the bait" less often, and so we might expect selection to favor a relatively low α.

Schlag (1998) rigorously investigated this problem under arbitrary success payoff distributions when $n = 2$. He concluded via sophisticated mathematical analysis that optimal learning rules would adopt the more successful variant in one's sample with probability proportional to the difference between their payoffs. This finding implies that always adopting the best variant in one's sample, i.e. $\alpha \rightarrow \infty$, is not optimal. Schlag's criterion for optimality, however, is irrelevant for evolutionary problems. Schlag limited his search for rules that always performed at least as well as unbiased imitation ("Always Improving" rules), regardless of underlying payoff distributions. But selection does not "care" how well rules perform under all hypothetical instances. What matters is how well strategies perform on average under the conditions actually faced by the population. The fact that the strongly biased learning rule depicted in Fig. 1 sometimes performs worse than unbiased imitation is irrelevant if the optimal variant never reaches high frequency. This fact is well demonstrated by the evolutionary model of Section 4: a strong, but not Always Improving, success bias can replace unbiased imitation if the population usually faces conditions under which success bias does best. For the moment, then, the evolution of strength of success bias remains an open problem.

5.2. Success is not fitness

In the evolutionary model developed here, success was assumed to be equal to fitness. In any social learning population where success is largely culturally-defined, however, it is unreasonable to assume that the common definition of success used by learners will exactly equal that which natural selection maximizes, i.e. fitness, if anything. If the fitness concept is to be used, it is probably best defined as the expected long-term (asymptotic) growth rate of a lineage (Roff, 2008). An individual's actions can have important long-term effects on the growth of her lineage that may be undetectable within her lifetime (e.g. the effect of biased sex ratios only become visible in the grand-offspring generation). Unless social learners have access to long-term genealogical data, they can only use imperfect, contemporary information to guide their decisions. Hence I suspect it is actually *impossible* to use fitness to guide social learning; fitness is simply not accessible to learners in real populations.[3]

This complication implies that some imperfect definition of success must be "constructed" by the population—be it culturally, genetically, or individually. The equilibrium reliance on success bias depends on how closely this definition corresponds to actual fitness. If correspondence is weak, then the reliance on success bias will be quite low—lower than found in the models above. Of course, we expect natural selection to act on this definition so as to increase its correspondence to real fitness. But environmental stochasticity and the rapid dynamics of cultural evolution would probably ensure that this correspondence will fluctuate over time, often leading to many generations where the common definition of success is far removed from fitness.

Empirical findings appear to support the hypothesis that cultural success can diverge widely from reproductive success. People in most modern nations today appear to be more concerned with the acquisition of wealth and prestige than with reproduction (Hill, 1984). Such wealth- and prestige-seeking apparently does little to improve reproductive success in modern societies, and probably interferes in many cases. Kaplan et al. (1995) found that income correlated negatively with number of grand-offspring among New Mexican men. More recent research suggests a more complicated relationship between wealth and reproductive success; Hopcroft (2006) found that wealthier US men tend to have more biological offspring than less wealthy men, while the opposite is true for women. Education, another potential measure of success, appears to consistently correlate negatively with offspring number, especially for women (Vining, 1986; Hopcroft, 2006). The question arises whether this apparently negative relationship between cultural and reproductive success is an evolutionary novelty in human history, or if maladaptive prestige-seeking behaviors are also common in smaller-scale, traditional human populations. I know of no study that has explicitly investigated this question as stated, though numerous examples of costly and conspicuous consumption in various small-scale societies (e.g. Rappaport (2000) and Boyd and Richerson (1985, Chapter 7)) suggests that maladaptive culture may not be unique to modern societies. Most studies investigating the tie between cultural and reproductive success have hypothesized positive correlations between them. That positive relationships are usually found suggests that cultural success may have corresponded well to genetic fitness throughout most, but not all, of human history.

6. Predictions for human social learning

A success bias that compares mean payoffs is not a universally effective strategy: it performs very well under specific conditions, and poorly otherwise. If human social learning strategies are domain-specific, then a reasonable prediction of this analysis is that success-bias will be important in behavioral domains characterized by rapid turnover of optimal variants, but relatively unimportant in domains where the optimal behavior shows little variation over time. I know of no study investigating how quickly optimal variants change in differing behavioral domains, but it seems likely that such variation exists (e.g. do the best foraging practices change faster than the best farming practices?).

Adaptive, domain-sensitive social learning seems more likely if learning strategies are themselves culturally transmitted, since culture can more rapidly evolve to changing conditions and may be more flexible across domains. Unsurprisingly, the development of social learning strategies themselves is an unstudied problem. Still, it seems likely that social learning strategies are at least partly socially and individually learned. If so, then perhaps the rapid rate of innovation in modern societies in recent centuries has encouraged success-oriented learning to a greater extent than would be the case in traditional societies, where innovations are probably less frequent. One might test this by experimentally comparing social learning strategies across human groups that vary in the extent to which they are economically and socially "modern".

If human social learning is instead general-purpose, such that we tend to use a few universally effective learning heuristics in all behavioral domains, then the analysis in this paper suggests that success bias should be relatively weak. Humans have probably evolved to use a variety of information sources to guide social learning processes, with payoffs being only partly influential. A combination of weakly biased learning rules, with the conservative

[3] This complication did not arise in the model developed above, by design, because I supposed an extremely simple selective pressure that acted only on fertility in non-overlapping generations.

tendency to "follow the crowd", would probably provide the most robust strategy in the long term.

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