One cultural parent makes no culture

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The ability to acquire knowledge and skills from others is widespread in animals and is commonly thought to be responsible for the behavioural traditions observed in many species. However, in spite of the extensive literature on theoretical analyses and empirical studies of social learning, little attention has been given to whether individuals acquire knowledge from a single individual or multiple models. Researchers commonly refer to instances of sons learning from fathers, or daughters from mothers, while theoreticians have constructed models of uniparental transmission, with little consideration of whether such restricted modes of transmission are actually feasible. We used mathematical models to demonstrate that the conditions under which learning from a single cultural parent can lead to stable culture are surprisingly restricted (the same reasoning applies to a single social-learning event). Conversely, we demonstrate how learning from more than one cultural parent can establish culture, and find that cultural traits will reach a nonzero equilibrium in the population provided the product of the fidelity of social learning and the number of cultural parents exceeds 1. We discuss the implications of the analysis for interpreting various findings in the animal social-learning literature, as well as the unique features of human culture.

The capacity to learn from others is a characteristic feature of human existence, and cultural transmission is widely thought to be responsible for the extraordinary demographic and ecological success of our species (Boyd & Richerson 1985). Humans acquire valuable skills and knowledge from others, and build on this reservoir of shared culture in a cumulative fashion (Cavalli-Sforza et al. 1982; Boyd & Richerson 1985; Ghirlanda & Enquist 2007). Other animals also benefit from social learning, which allows them to acquire solutions to survival problems such as 'what to eat?' or 'how to evade predators?' rapidly and efficiently (Galef & Laland 2005). The number of examples of animal social learning increases steadily, with interest fuelled by high-profile reports of inter- and intrapopulation variation in the behavioural repertoires of animal populations, and spawning claims of shared culture in apes (Whiten et al. 1999; van Schaik et al. 2003), monkeys (Perry et al. 2003) and cetaceans (Rendell & Whitehead 2001; Krützen et al. 2005). Other researchers have documented vocal dialects in the songs of numerous species of birds (Catchpole & Slater 2008) and traditional behaviour in fishes (Warner 1988, 1990). Such claims are reinforced by many reports of the spread of novel behaviour in natural animal populations, where previously unseen behaviour rapidly increases in frequency in a population, too rapidly to be plausibly attributed to population genetic or demographic factors (Lefebvre & Palameta 1988). Animal social learning appear to be widespread among vertebrates, and present in many invertebrates too (Leadbeater & Chittka 2007), and to underpin a broad variety of behavioural traditions in animals.

One feature of the now extensive literature on animal, including human, social learning is that little attention has been given to whether individuals acquire knowledge from a single individual or multiple models. Researchers commonly refer to instances of sons learning from fathers, or daughters from mothers, with little consideration of whether this is actually feasible. Particularly in the primatological and cetacean literatures, it is often assumed that social learning from mothers to offspring plays an important role in maintaining shared culture (Boesch 1991, 1993; Coussi-Korbel & Fragaszy 1995; Reader 1999; Mann & Sargeant 2003). In a meta-analysis of studies of primate social learning, Reader (1999) found that mother to offspring learning is overrepresented in the literature, given the null expectations for particular age classes. Reader observed more instances of social learning reported in nonadults,

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and fewer in adults, than would be expected by chance given the age distribution of individuals among the species tested. Similarly, adults are overrepresented as information transmitters. A large proportion of adult-to-nonadult cases (33/46) were reports of infants learning from their mothers, spanning 12 species. A well-known case is Boesch's (1993) claim that common chimpanzee, *Pan troglodytes*, infants learn to crack nuts from their mothers. Reader noted, however, that it is difficult to be certain that transmission from mother to infant or indeed any form of learning has genuinely occurred, on the basis of field observations alone. Other researchers (e.g. Coussi-Korbel & Fragaszy 1995) have suggested mother − offspring transmission is common in particular kinds (despotic) of primate society. In bottlenose dolphins, *Tursiops aduncus*, Mann & Sargeant (2003) noted that daughters acquire a repertoire of foraging behaviours that resembles their mother's, after spending long periods of time together. Birdsong is another case where people have reported males learning from fathers (e.g. bullfinches, *Pyrrhula pyrrhula*: Nicolai 1959; zebra finches, *Taeniopygia guttata*: Immelmann 1969; Darwin's finches, Geospizinae: Grant 1984; Millington & Price 1985; and marsh tits, *Poecile palustris*, Rost 1987). However, evidence that the father is the only cultural role model is frequently lacking. Far more commonly, young males copy their neighbours (Catchpole & Slater 1995). In summary, in the animal literature, reports of uniparental transmission exist but are comparatively rare, as they are in the human literature too (Shennan & Steele 1999), and far more commonly claims of biparental transmission or learning from multiple nonrelatives are reported (Boyd & Richerson 1985).

Our aim in this paper is to gain a theoretical understanding of how the number of cultural models affects the social learning and cultural transmission of knowledge and skills between generations. By definition cultural traits are learned, which means that they are not present at birth and may or may not be learned during an individual's lifetime. This means that every cultural trait can be described as absent or present in a given individual (i.e. has the individual learned how to fish for termites?). The same applies to humans, where the fact that individuals may vary in what vehicle they drive, which religion they follow or which food they cook does not preclude categorizing the traits as present or absent: that is, individuals may or may not acquire a religious belief, learn to drive a car or learn to cook yams, and one can quantify the numbers of religious people or car drivers in a population. This reasoning applies to all cultural traits. While there is extensive mathematical theory investigating the differential adoption of cultural variants (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985), there is comparatively little on how much culture will be present in a population, and which factors affect this. In this paper we explore how the mode of transmission impacts on the stability of a cultural trait. Using simple mathematical models, we consider whether uniparental transmission is actually feasible as an explanation for shared culture in animals. We also ask a related question about the number of learning trials necessary for shared culture, since another feature of the social-learning literature is the assumption that imitation can be extremely rapid (Laland et al. 1993; Hurley & Chater 2005), at the extreme allowing skills to be socially transmitted after a single learning trial. However, the plausibility of single-trial social learning as an explanation for behavioural tradition also remains unexplored. We then investigate whether transgenerational social learning, in various forms, can maintain a shared cultural trait starting from a situation where most individuals in the population possess the trait, and whether it can establish culture in a population starting from the situation where only a small number of individuals have the trait. We also consider the effects of finite population size, fitness differences between traits and additional individual learning of the transmitted trait. Our main theoretical result is that several cultural

models and repeated social learning is typically necessary to establish and maintain shared culture.

The paper has four sections: first we demonstrate that random copying of a single cultural parent cannot support culture; second, we establish that access to more than one cultural parent can maintain culture; third, we consider the effects of various kinds of transmission bias; and finally, we explore the circumstances under which cultural homogeneity, that is customary cultural traits shared by the majority of the population, can emerge.

ACCESS TO A SINGLE CULTURAL PARENT

Here we explore under which circumstances culture can be maintained in a population. We begin with the simple case of 'random' or 'unbiased' uniparental cultural transmission, by which we mean the copying of a single randomly chosen individual. This assumption is not as unreasonable as it might first appear. For instance, if we assume copying occurs in proportion to contact with the model, then one might a priori anticipate a large degree of copying from a single biological parent in species with uniparental care. We also consider how the probability of maintenance is affected if the trait has a significant fitness advantage, or if its prevalence in the population is bolstered by an additional individual.

In our model, two things determine whether an individual will learn a cultural trait socially. First, the cultural parent (who may or may not be the same as the biological parent) must possess the trait. Second, social learning must be successful. If q is the probability that the cultural parent has the trait (where $0 \leq q \leq 1$) and p the probability that a single social-learning trial is successful given that the cultural parent has the trait, the probability that the individual picks up the trait from a single social-learning trial is pq. We consider perfect social learning to be unrealistic (thus we assume that $p < 1$). Additional social-learning trials will increase the probability of the individual picking up the trait at some juncture. For simplicity, we assume that the probability of learning the trait is the same for each trial. Thus, after n learning trials with the same cultural parent the probability that the individual has picked up the trait is $(1 - (1 - p)^n)q$, which increases with n but is always less than q (since $p < 1$ by assumption).

To begin with, we assume that cultural parents are drawn independently at random from the parent population. In this case the probability that the cultural parent has the trait (q) is equal to the proportion of individuals that possess the trait in the parental generation. We want to know how this proportion changes over time. First, consider an infinite population. If the proportion with the trait is x in the parental population and individuals are allowed only one social-learning trial, then the proportion possessing the trait in the next generation is exactly px. It follows that the proportion will always decrease from generation to generation, according to the exponential form

$$x_t = x_0 p^t,$$

where x_0 is the proportion at time $t = 0$ and x_t the proportion at time t.

Qualitatively, this result holds also for repeated trials of social learning with the same cultural parent, although the decline becomes less steep when the number n of trials increases. With the above assumptions, the proportion of individuals with the trait will decline towards zero according to the exponential form

$$x_t = x_0 (1 - (1 - p)^n)^t. \tag{1}$$

In a finite population, expression (1) describes the behaviour of the expected value of the proportion. It follows that social learning

from a single randomly chosen cultural parent alone can neither establish nor maintain culture in a population. The reason for this is that only those individuals who happen to have a cultural parent carrying the trait will have the opportunity to learn the trait socially; since social learning sometimes fails, the proportion of individuals with the trait will always tend to decrease. While in some instances perseverant individuals may engage in repeated bouts of learning, and not stop until they have learned a trait, unless all individuals did the same such that everybody always copied with perfect fidelity (which we view to be implausible) the same issue arises: social learning from a single cultural parent is insufficient to support a stable culture.

We now discuss how the conclusion stands up to scrutiny of two pathways through which the decline of the trait could be compensated: (1) fitness benefits and (2) asocial learning.

Compensation Through Fitness Benefits

Up to now we have been assuming that there is no fitness benefit to acquiring the cultural trait. However, our overall conclusion is not sensitive to inclusion of fitness benefits in the model, because they would have to be unrealistically high to compensate for imperfect social learning unless the efficiency of social learning (p) is close to one. To see this let αT and T be the individual's survival time (i.e. the time that it can serve as a cultural model) if the individual possesses or does not possess the trait, respectively. Thus α describes the strength of natural selection on the cultural trait. In an infinite population this would change the population frequency x according to

$$x_{t+1} = \frac{\alpha p x_t}{\alpha p x_t + (1 - p x_t)}, \quad x_\infty = \frac{\alpha p - 1}{p(\alpha - 1)}. \quad (2)$$

It follows that the condition $\alpha p > 1$ must be satisfied for a nonzero equilibrium frequency (x_∞) to be possible. For instance, if $p = 0.9$ then the trait must increase the survival time by more than 11% to maintain any culture; to maintain a population frequency of 90% the trait must increase survival time by 111%. Fitness differences of this magnitude are extremely unlikely (Kingsolver et al. 2001) while, judging from demonstrator − observer correlations, cultural transmission with a fidelity as high as 0.9 is rare in humans (see Cavalli-Sforza et al. 1982; Boyd & Richerson 1985, pp. 50−51; Shennan & Steele 1999) and rarer still in nonhuman animals (Laland et al. 1993). Even birdsong, which is generally thought to be among the highest fidelity cultural transmission systems observed in animals, has an error rate of 15−25% per generation, and this is the product of multiple learning episodes from multiple tutors (Catchpole & Slater 2008). While whether or not the fidelity of social learning is ever sufficiently high to allow for stable uniparental transmission is an empirical question, the current evidence suggests that, at best, this level of compensation may happen in rare circumstances, and it is unlikely to be a general pattern.

Compensation Through Asocial Learning

Thus far we have assumed that there is no asocial (individual) learning. Our conclusion could potentially change if asocial learning of the cultural trait is sufficiently common that it reinforces trait frequency: that is, a combination of uniparental transmission and asocial learning might lead to trait maintenance. This double option of social and asocial learning has been explored in a number of models (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; McElreath & Strimling 2008), sometimes with imperfect asocial learning (Boyd & Richerson 1985), or with asocial learning tried

only when social learning fails (Boyd & Richerson 1996; Enquist et al. 2007, 2008; Strimling et al. 2009).

The idea that asocial learning can compensate for losses is of direct interest to the topic of this paper. Could it be that, say, common chimpanzee culture is maintained through a combination of asocial and social learning with only the mother as cultural parent? In fact, evidence exists, from experiments on Norway rats, *Rattus norvegicus*, conducted with a single cultural parent (Laland & Plotkin 1992), that additional individual learning can indeed reinforce socially transmitted information to bolster the stability of foraging traditions.

We explore this possibility by assuming that an individual who fails in social learning has a probability a of discovering the same trait through asocial learning (as in Enquist et al. 2007). Under this assumption the probability of successful learning of the cultural trait is

$$px + (1 - px)a,$$

given one social-learning trial. In an infinite population this gives the dynamics

$$x_{t+1} = p x_t + (1 - p x_t)a,$$

so that the equilibrium frequency of the cultural trait in an infinite population is

$$x_\infty = \frac{a}{1 - p(1 - a)} \Leftrightarrow a = \frac{(1 - p)x_\infty}{1 - p x_\infty}. \quad (3)$$

It follows, as illustrated in Fig. 1, that to maintain high population frequencies (high values of x_∞) the trait must be easy to obtain through asocial learning (high value of a). For instance, to maintain a trait frequency in the population of 90% when the efficiency of social learning is $p = 0.9$ requires the success of individual learning to be as high as $a = 0.474$. This implies that in the complete absence of social learning ($p = 0$), 47.4% of the population would have the trait anyway. This leads to the paradoxical conclusion that uniparental social learning could only account for highly prevalent or universal traits in cases where the trait concerned is so easy to acquire asocially that asocial learning, rather than social learning, will be the main driving force. Conversely, traits that are difficult to
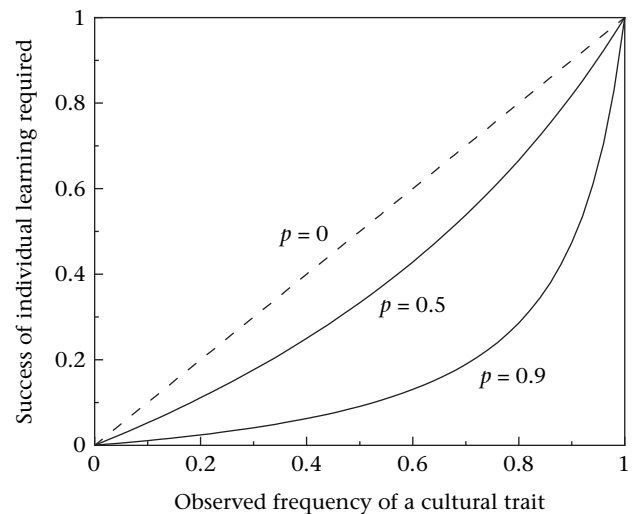
Figure 1. The figure shows how successful asocial learning (variable a) must be to maintain an observed frequency of a trait when each individual has only one cultural parent. Information is provided for three different values of p, the efficiency of social learning.

acquire asocially cannot be brought to high frequency in a population through learning from a single cultural parent. Thus even combined with asocial learning, uniparental social learning has little explanatory power for the prevalence of cultural traits.

In conclusion, it is surprisingly difficult for uniparental cultural transmission to maintain culture, even when an advantageous trait is transmitted or asocial learning compensates for transmission losses.

ACCESS TO MORE THAN ONE CULTURAL PARENT

We now explore the effect on the maintenance of a cultural trait of learners having more than one cultural parent. Any animal species with biparental care, alloparenting, or that lives or forages in social groups would have the opportunity for multiple cultural parents. Here we assume that each social-learning trial occurs with a new cultural parent randomly drawn from the parent population (i.e. oblique inheritance, Cavalli-Sforza & Feldman 1981). This is consistent with observations of social learning in animals, which suggest that transmission is more frequently oblique or horizontal than vertical (Laland et al. 1993). In such circumstances, the probability of successful learning after n social-learning trials, each from a different cultural parent, is

$$1 - (1 - pq)^n. \tag{4}$$

As before, q denotes the probability that a cultural parent has the trait and p is the fidelity of social learning. Note that this expression reduces to pq in the special instance where there is only one social-learning trial ($n = 1$), and hence a single cultural parent. In contrast with the previous case, however, here it is possible that the probability of picking up the trait is greater than q so that culture can be maintained in a population. We now develop the details of this argument.

In an infinite population, with the same reasoning as earlier, the proportion of individuals with the trait in the next generation is exactly

$$x_{t+1} = 1 - (1 - px_t)^n. \tag{5}$$

As we prove in the Appendix (Proposition 1), the frequency x_t of trait-bearers will evolve towards a nonzero equilibrium given by the fixed-point equation

$$x = 1 - (1 - px)^n \tag{6}$$

whenever the product of the fidelity of social learning and the number of cultural parents satisfies

$$pn > 1. \tag{7}$$

For instance, in order for a population to maintain a cultural trait when individuals have $n = 2$ learning trials, each with a different cultural parent, it is necessary and sufficient to have a social-learning fidelity of $p > 0.5$. If the transmission fidelity is below this threshold, then social learning alone cannot maintain culture in a population. A single learning trial, like a single cultural parent, can never maintain culture.

Equation (6) can be rewritten as

$$p = \frac{1 - (1 - x)^{1/n}}{x}. \tag{8}$$

For instance, in order for a population to maintain an equilibrium frequency of at least 90% trait-bearers when the number of learning trials per individual is $n = 10$, equation (8) says it is sufficient that the fidelity of social learning satisfies $p \geq (1 - 0.1^{1/10})/0.9 \approx 0.23$.
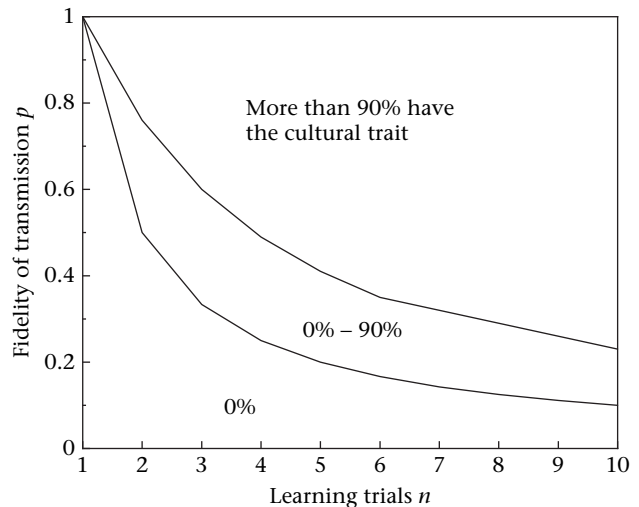
Figure 2. The diagram shows how combinations of the number (n) of learning trials and the fidelity of social learning (p) promote different equilibrium frequencies (x_∞). Each learning trial uses a new cultural parent drawn at random from the parent population (see text).

Figure 2 shows the equilibrium frequencies obtained by various parameter combinations.

In a population of finite size cultural drift will influence the dynamics. Two phenomena are worth pointing out. First, new innovations are likely to be lost immediately, and this applies to populations of any finite size. Second, any cultural trait will eventually disappear from the population even if it has become established in the population. However, this event rapidly becomes very rare as population size grows. This is illustrated in Fig. 3, which provides both example trajectories and expected lifetimes for cultural traits under varying parameter values, including size of the population. For reasonably large populations, it follows that once a trait has become established in the population it will typically be maintained for a very long time. The frequency will fluctuate around the equilibrium value of the 'infinite population case' given by equation (6). Figure 3b shows that a significant proportion of innovations, although initially carried only by a single individual, can become established in the population.

In conclusion, changing the model so that individuals have more than one cultural parent has a dramatic effect on the possibility of longstanding culture. In this case, if innovations made by a single individual are lucky enough to spread in the first few generations, then they can be maintained in the population for a long time by social learning alone.

Another potentially important observation, based on the shape of the curves in Fig. 3, is that for a given population size there is a threshold effect, where a small increase in social-learning efficiency (p) will change cultural traits from being short lived to virtually immortal. This may help to explain the difference in the sheer amount of culture observed in humans compared to other animals. We develop this point further in the Discussion.

PREFERENCES FOR CULTURAL PARENTS

In the previous sections we assumed that the individual could not choose its cultural parents. This assumption is likely to apply in many circumstances, for instance among territorial species of animals or species that do not aggregate into social groups. However, in social species individuals may have the option of selecting a cultural parent other than its biological parents, giving
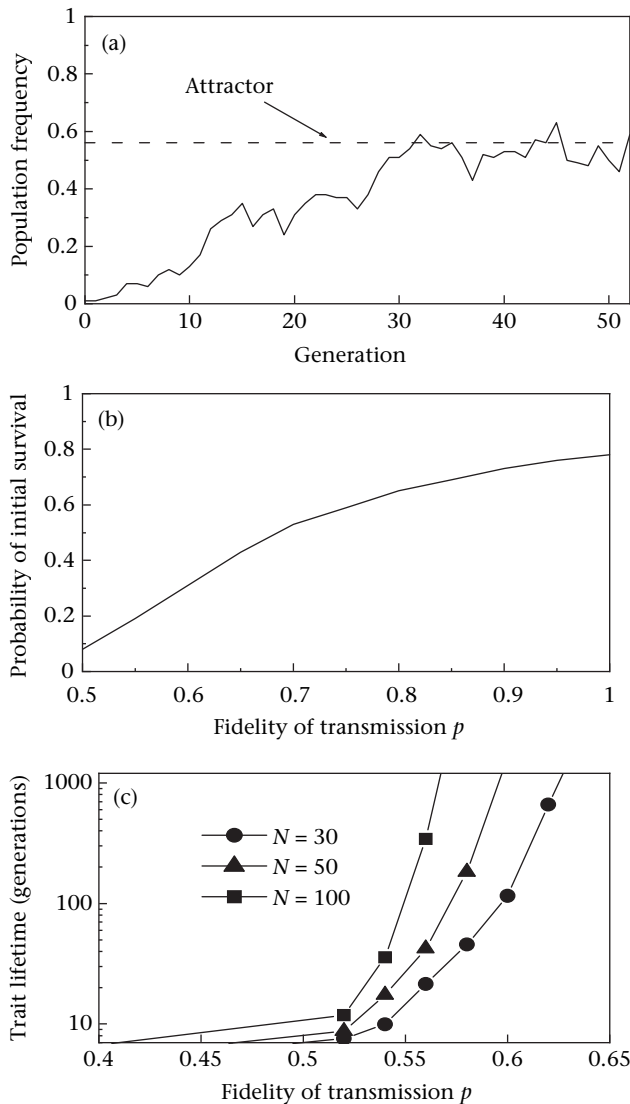
Figure 3. Cultural evolution in finite populations. (a) A random walk of the population frequency starting from a low frequency. The attractor is the equilibrium value of the infinite case. Parameters: $N = 100$, $n = 2$ and $p = 0.6$. (b) The likelihood that an innovation will succeed in spreading (to at least 10% of the population) as a function of the efficiency of social learning (p). Parameter values: $N = 100$ and $n = 2$. (c) The expected lifetime, measured in generations, of a cultural trait as a function of the efficiency of social learning (p). Each learning trial uses a new cultural parent drawn from the parent population (see text). Parameter value: $n = 2$.

rise to more oblique transmission and allowing for the possibility of more complicated social-learning strategies. If the frequency of the cultural trait is higher among such chosen parents, this could potentially promote the maintenance of culture. In practice, this requires that some cue is available that allows the individuals to find cultural parents that are more likely to have the trait. Note that it is not automatic that individuals of a social species always have such options of choosing a cultural parent. Furthermore, such a choice is possible only if multiple individuals are sampled, which in many respects is similar to individuals having multiple demonstrators. Thus, the results in this section do not change our previous conclusions about the difficulty of maintaining culture when individuals attend solely to a single cultural parent.

We consider three cases of preferential choice and compare these cases with our previous analysis of social learning from random individuals (equation 6).

First, we consider the case in which individuals endeavour to imitate models that have the trait. This can be interpreted as a situation where the learner has prior knowledge that the trait exists, and actively tries to acquire it. If there are no search costs associated with locating an individual with the trait, then the equilibrium is established in one generation and equals the probability of learning the trait after n learning trails.

$$x_{t+1} = x_\infty = (1 - (1 - p)^n).$$ (9)

Figure 4 shows how learning from random encounters is clearly inferior to learning only from individuals who have the trait. This case, where individuals can without cost choose to learn only from individuals that have the trait, may be unrealistic but sets an upper limit to what preferences can contribute to the maintenance of culture. In reality, it is likely to take some time or effort for individuals to find a cultural model with the trait. One way of thinking about this is that such costs reduce the number of social-learning trials, thus right shifting the blue line in Fig. 4.

That individuals use the trait itself as a cue when selecting cultural parents is probably rare in animals (although possibly more common in humans). An alternative is to use an indirect cue that is associated with an increased probability that the bearer possesses the cultural traits. For instance, it has been suggested that individuals associate and learn preferentially from individuals that are successful (Boyd & Richerson 1985). Plausibly, particularly skilful or successful individuals may have acquired better cultural variants or more cultural traits. The latter possibility suggests that successful individuals are more likely to possess any particular cultural trait than other individuals, so that young individuals who preferentially associate with such skilful individuals would be more likely to learn the trait. In humans there is experimental evidence of preferential copying of the most successful individual (Mesoudi & O'Brien 2008).

To model this case, we assume that individuals are either successful or unsuccessful, and that the probability of becoming a successful individual if one is a trait-bearer is a factor $\alpha > 1$ higher than if one is not a trait-bearer. In a generation with a proportion x of trait-bearers, the probability that a given successful individual has the trait is then $\alpha x/(\alpha x + (1 - x))$. Thus, if each individual in the
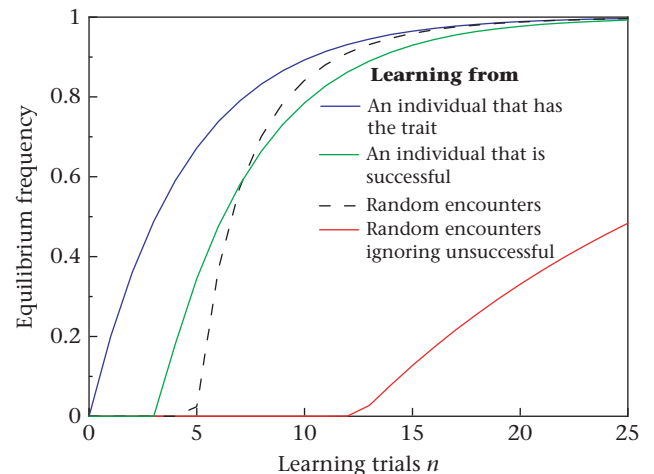
Figure 4. Equilibrium frequencies for the cultural trait for different cases of selective solution learning compared with learning from random encounters of cultural parents (hatched black curve). Blue curve: learning from an individual with the trait. Green curve: learning from a successful individual. Red curve: learning from random encounters ignoring unsuccessful individuals. Note that in the blue and green curves there are no search costs included. Such costs would shift the curves to the right (see text). Values used in these examples: $p = 0.2$, $q = 0.2$ (proportion of successful), $\alpha = 2$.

next generation copies a randomly drawn successful individual in n learning trials with the same model, the dynamics is given by

$$x_{t+1} = (1 - (1 - p)^n)\alpha x_t / (\alpha x_t + 1 - x_t), \tag{10}$$

for which the unique equilibrium value is

$$x_\infty = \max\left(\frac{\alpha(1 - (1 - p)^n) - 1}{\alpha - 1}, 0\right). \tag{11}$$

We now compare this result with our previous results about learning from random encounters (equation 6). As illustrated in Fig. 4, unless the number n of learning trials is very small, the equilibrium number of trait-bearers is higher with a strategy of 'copy different random individuals' than with one of 'copy one random successful individual'.

Furthermore, we can envision a learning strategy that is a mix between copying a successful individual and copying a number of different random individuals. Let the individual that is learning split his n learning trials between the two strategies. If he spends i trials looking at random individuals and $n - i$ trials looking at one successful individual the probability that he picks up the trait P is

$$P = 1 - \left(1 - \frac{\alpha x}{\alpha x + (1 - x)}\left(1 - (1 - p)^{n-i}\right)\right)(1 - px)^i. \tag{12}$$

As this function P is unimodal in i we can find the optimal i by solving $P(i) = P(i + 1)$ and rounding up. The optimal $i = [n - 1 + (\ln(\alpha))/(\ln(1 - p))]$ which is positive when $\alpha < 1/(1 - p)^{(n-1)}$. This quickly leads to unreasonably high vales of α; for instance when $n = 10$ and $p = 0.5$ α needs to be higher than 512 for it to be better to look only at the successful individual.

If we introduce a cost of searching for a successful individual, then the green curve in Fig. 4 will be shifted to the right, increasing the advantage of the 'copy different random individuals' strategy. In conclusion, our analysis shows that although a single successful individual is more likely to possess the trait, it is typically better to learn from more than one individual.

Another way of showing the importance of learning from many individuals is to consider what happens if learners ignore unsuccessful individuals as cultural parents. We do this by modifying equation (5) for learning from random encounters in the previous section so that learners only learn when encountering successful individuals. The recursion for this is

$$x_{t+1} = 1 - \left(1 - \frac{1 - pq\alpha x_t}{\alpha x_t + 1 - x_t}\right)^n,$$

where q denotes the proportion of successful individuals in the population (which for simplicity we assume to be fixed). Note that x_{t+1} is smaller than in equation (5). It follows that the equilibrium frequency is smaller. The red line in Fig. 4 shows that the effect of ignoring unsuccessful individuals can have dramatic consequences.

Note that the problem we study here is the likelihood of obtaining a trait, whereas most discussions of success bias have dealt with variants of a given trait (see e.g. Boyd & Richerson 1985; Henrich & McElreath 2003), which is a different issue. Several conclusions can be drawn from the above analysis of preferences among potential cultural parents.

First, learning from a single cultural parent can potentially maintain culture if multiple potential parents are sampled. This is possible if learners choose among the potential partners according to some preferences that give a sufficient increase in the probability of copying someone who is a trait-bearer to compensate for the loss in trait frequency caused by imperfect social learning ($p < 1$). However, even here, multiple individuals must be processed in some way for individuals to acquire knowledge that could preserve culture.

Second, our results also show that learning from a single successful individual is typically not the best strategy for maintaining culture. This finding is reminiscent of the game-theoretical observation of Schlag (1998) that copying the most successful individual is not an optimal learning strategy. In addition, learning just from a single successful individual seems unrealistic: In most social species the young first spend time with their parent or parents, and only later have the option of learning from other individuals such as successful ones.

HOMOGENEITY INDICES AND CUSTOMARY CULTURAL TRAITS

In this section we explore under which circumstances we would expect cultural homogeneity or customary cultural traits possessed by most of the population (Whiten et al. 1999). The presence of a customary variant, in which a single belief or behaviour dominates, can be contrasted with a situation where there are a number of cultural variants present but none reaches a high frequency in the population. Here we show that single cultural parents cannot produce customary cultural variants, regardless of innovation rates.

We use a cultural homogeneity index as a measure of the presence of customary variants. The index we use, known in biology as the Simpson similarity index, is the probability that two randomly drawn individuals carry the same variant. This index has been used in cultural evolution studies as a measure of similarity/diversity (Kandler & Laland 2009). If we denote the frequency of variant i by $x^{(i)}$, then the cultural homogeneity index can be expressed as

$$\text{Cultural homogeneity index} = \sum_i x^{(i)^2}.$$

This index is a number between 0 (when no two individuals share the same variant) and 1 (when all individuals share the same variant); accordingly, high values of the index correspond to the presence of customary cultural variants.

For simplicity, we assume that there are m different solutions to a problem such as opening a nut or building a sleeping platform, and that all these variants are equally likely to be individually learnt (i.e. each of the m cultural variants can be invented by an individual with probability a/m). We denote the frequency of variant i by $x^{(i)}$. Then the dynamical system in an infinite population where each individual has a single learning trial is described by

$$x_{t+1}^{(i)} = px_t^{(i)} + \left(1 - \sum_{i=1}^m px_t^{(i)}\right)a/m, \quad \text{for } i = 1, 2, \dots, m.$$

Straightforward analysis gives that in equilibrium all variants are present at the same frequency:

$$x_\infty^{(i)} = \frac{a/m}{1 - p(1 - a)} \quad \text{for } i = 1, 2, \dots, m$$

yielding a cultural homogeneity index of

$$\left(\frac{a}{1 - p(1 - a)}\right)^2 / m, \tag{13}$$

which, of course, is always less than $1/m$. Consequentially, this model does not produce any impressive degree of customary culture, even when innovation rates are very high. This result does not rely on the population being infinite; in a finite population there will be fluctuations around this equilibrium, but typically all possible cultural variants will be present in a sufficiently large population, although not all individuals will acquire one of the

variants. The conclusion generalizes to any number of learning trials.

Effect of Several Cultural Parents

As we have seen before, the potency of social learning increases markedly if individuals have several cultural parents instead of one (and similarly with repeated learning trials). In this situation, one innovation may get lucky and spread through the population without having any a priori advantage, resulting in a high cultural homogeneity index and a customary cultural variant.

To illustrate this phenomenon we have run repeated simulations of 300 generations of cultural evolution in a population where individuals have several learning trials, each time with a new cultural parent drawn at random from the entire population. We assume that there exist a small number of variants of a cultural trait, each of them equally difficult to learn. For one set of parameter values, Fig. 5 shows the resulting cultural homogeneity index (as well as the total frequency of all cultural variants). It is obvious from the figure that the effect of increasing the number of cultural parents (which corresponds to the number n of learning trials) is a rapid increase in the cultural homogeneity index.

In the simulations reported in Fig. 5a, the number of learning trials equalled the number of cultural parents. However, it may be

more realistic that there is just a small set of potential cultural parents, each of whom may be the object of several learning trials. For instance, one can imagine the set of potential cultural parents to be limited to the two biological parents. To explore whether the number of potential cultural parents is an important factor, we carried out the same simulations when each individual obtains a random sample of a small number of potential cultural parents; for each of n learning trials the individual then tries to learn from a cultural parent drawn at random from this set. The results are shown in Fig. 5b, which clearly shows, first, that there is a positive relation between the number of cultural parents and the cultural homogeneity index, and, second, that the major step is that from a single cultural parent to two cultural parents.

The clear take-home message from these simulations is that, in the absence of transmission biases, multiple cultural parents are necessary for customary cultural variants and any substantive degree of cultural homogeneity.

DISCUSSION

We have used mathematical models to explore the conditions under which learning from a single cultural parent can lead to stable culture. Our analysis leads us to the view that it is surprisingly difficult for uniparental cultural transmission to maintain cultural traditions. We have shown that unbiased social learning from a single cultural parent alone can neither establish nor maintain culture in a population. The reason for this is that only those individuals who happen to choose a cultural parent carrying the trait will have the opportunity to learn, and since social learning is not perfect, the proportion of individuals with the trait will always tend to decrease. Our general result is robust even when an advantageous trait is transmitted, asocial learning compensates for transmission losses and biased transmission favours the trait. Our general conclusions are, to some extent, based on assumptions about typical levels of cultural transmission fidelity. However, the available evidence strongly suggests that cultural traits of sufficient fidelity to support uniparental transmission are, at best, extremely rare. While certain forms of transmission bias can maintain culture through a uniparental mechanism, such mechanisms can only do so when multiple individuals are sampled, which in many respects is equivalent to individuals having multiple demonstrators. For instance, conformity can maintain the stability of transmission of common cultural traits (Whiten et al. 2005), but this process, by definition, requires individual to monitor multiple models, rather than learn from a single parent. While our 'one cultural parent' illustrative examples are reliant on vertical transmission (i.e. sons learning from fathers, daughters from mothers), since most claims of uniparental transmission fall in this category, our conclusions apply equally to horizontal and oblique transmission, for which the conditions under which a single cultural parent can lead to stable culture are equally restrictive. Our analyses do not imply that learning from a single cultural parent is impossible; merely that it does not lead to stable culture. Note also that our models do not allow for the forgetting of cultural traits, which would make it even harder for uniparental transmission to lead to stable culture. In summary, when individuals attend solely to a single cultural parent stable culture will not result.

Neither can uniparental transmission generate customary cultural traits (cultural variants adopted by a large proportion of the population) or cultural homogeneity. Rather, the stable maintenance of cultural traits and the adoption of cultural variants by a substantial fraction of the population both seem to require multiple cultural parents. Several cultural parents (and/or repeated social learning) are necessary to establish and maintain customs and cultural homogeneity, both because individuals become more
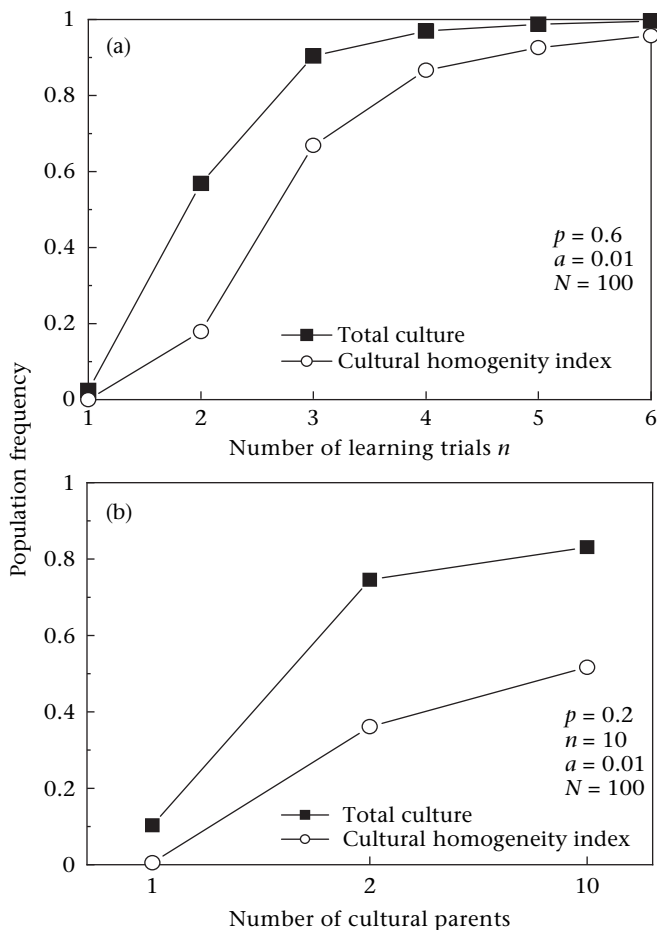
Figure 5. The diagrams show the total number of individuals in possession of a cultural variant (squares) and the cultural similarity index (circles) in a situation with six different cultural variants. These entities are shown as functions of (a) the number of learning trials and (b) the number of cultural parents. Each learning trial uses a new cultural parent drawn from the parent population (see text). The values are the averages from 100 simulations of the values obtained after 300 generations.

likely to pick up cultural traits with more cultural parents (and/or more social-learning trials) and because, if losses of culture are compensated for through individual learning, the resulting culture will not involve the same shared variant. In simple terms, uniparental transmission does not make for culture as we know it.

While these findings are broadly consistent with what is known about human cultural learning (Richerson & Boyd 2005), there are some reports in humans of traditional crafts and skills that are acquired from a single parent. These include the making of hunting techniques, manufacture of arrowheads, glass working, construction work (all reported as transmitted from fathers to sons), and pottery, weaving and bag manufacture (all reported as transmitted from mothers to daughters; see Shennan & Steele 1999 for a review and references). However, it is not clear to what extent such reports challenge the theory. First, in most cases the mode of transmission has not been evaluated empirically. Second, in many instances, while these are the primary routes for information transfer, there are other kin, or nonkin, from whom individuals also learn, that potentially reinforce the stability of information transmission. For instance, Hayden & Cannon (1984) reported that, in the Maya, while in 64% of cases sons acquired hunting skills from fathers, 13% were from other kin and 23% were from nonkin. Third, as in the famous case of the apprentice to the sushi chef (De Waal 2001), long periods of observation and training may allow humans uniquely to achieve a transmission fidelity close to perfect in some cases. Fourth, in the human case, even lower transmission fidelity may be sufficient to retain cultural variants in the population until the variant has outlasted its usefulness and been replaced by an alternative.

Observations from the animal social-learning literature are also broadly consistent with our theoretical findings. First, the vast bulk of animal social learning does not appear to involve learning from a specific individual (e.g. from fathers or mothers). To the contrary, animal social learning appears to be largely horizontal or oblique in character, with individuals learning from unrelated individuals rather than specific others with whom they have a close relationship (Lefebvre & Palameta 1988; Laland et al. 1993). However, it is fair to say that in the vast majority of studies the number of cultural parents is unknown. Second, in those cases where there is clear evidence for vertical transmission we can often also see evidence for additional individual learning, or more than one cultural parent, being involved. For instance, a well-known case of vertical transmission is pine-cone stripping in black rats, *Rattus rattus* (Terkel 1995), where individuals fail to learn on their own but do acquire this skill from their mothers, provided there is plenty of opportunity for additional asocial learning. Another nice example is provided by marsh tits, a species in which the female as well as the male sings. Here the mother sings almost exclusively at the time just after fledging, when copying takes place, and moreover sings a virtually identical song to the father (Rost 1990). This observation fits extremely well with the finding that more than one cultural parent is required for stable transmission. Third, in animal social-learning experiments the fidelity of cultural transmission is known to be affected by the number of demonstrators. For instance, guppies, *Poecilia reticulata*, are considerably more likely to adopt the behaviour shown by several members of a shoal of fish than an alternative behaviour shown by a single demonstrator, and the likelihood of copying increases with the number of demonstrators (Sugita 1980; Laland & Williams 1997). Similar patterns are reported in Norway rats (Beck & Galef 1989) and pigeons, *Columba livia* (Lefebvre & Giraldeau 1994). Fourth, the observation that additional asocial learning can buttress a variant's stability but does not lead to customary traditions, fits nicely with the evidence that social learning is primarily deployed for difficult or costly tasks, and not for traits that are simple to learn on one's own (e.g. Coolen et al.

2003; Kendal et al. 2005; Webster & Laland 2008). This pattern may reflect the fact that it will be difficult to detect a social influence on learning in cases where the probability of asocial learning is high (compared to low) since, as the above theory demonstrates, the incremental increase in the frequency of trait carriers is proportionally smaller. Alternatively, the pattern may reflect a history of selection against reliance on social learning for easy to learn traits, where, by the above reasoning, the incremental fitness benefits are likely to be small relative to costly to learn traits, but the costs of copying (e.g. the possibility of picking up inappropriate or outdated information) do not differ.

There are, perhaps, grounds for being cautious regarding our conclusion that uniparental transmission cannot lead to cultural homogeneity, since there are several additional potential pathways to customary cultural variants that we have not considered. For instance, only one variant may be possible in some cases, or there may be significant fitness benefits conferred by a certain cultural variant, or a direct bias among individuals for a cultural variant, for instance if it yields a higher payoff or is easier to adopt, or there may be an indirect bias for a cultural variant via a bias for social learning from a key individual or a preference for the common type. Such processes will increase the frequency of a single variant in the population. However, our analysis of the maintenance of cultural traits, which found that supplementary mechanisms such as fitness benefits, and biases in learning, did not greatly enhance the efficacy of uniparental transmission, leads us to the view that multiple cultural parents are necessary in order for cultural traits to reach a high frequency. While experimental studies have established that multiple social-learning mechanisms can act to reinforce each other and enhance the fidelity of information transmission from the same cultural parent (Laland & Plotkin 1993), this interaction is merely equivalent to an increase in the fidelity of a single social-learning mechanism, and hence cannot lead to stable culture unless multiple demonstrators are involved. As mentioned in the Introduction, there are several species of birds in which the males are thought to acquire their song from their father; however, we know of no case for which it has been experimentally established that such learning is exclusively from the father, and additional learning from neighbouring males remains a credible possibility in most cases.

Our analysis of the spread of cultural variants in a population of finite size leads to several points of interest. First, new innovations are likely to be lost immediately. In the simulations depicted in Fig. 3, the vast majority of the innovations that occur do not spread and hence do not become customary. This is in line with the results on innovation in nonhuman primates, which show lots of evidence for innovations, including highly functional traits, which only very rarely seem to spread and become part of a cultural tradition (Kummer & Goodall 1985; Reader & Laland 2001). The expectation that functional innovations can easily be lost because of stochasticity has not always been apparent to researchers studying the diffusion of foraging innovations in animals, who have regarded the failure of most innovations to spread, particularly those beneficial to the inventor, as a mystery (Reader & Laland 2003). In fact, the observation that the majority of beneficial innovations are frequently lost is exactly what this analysis predicts (see also Tanaka et al. 2009).

Second, there are many reports of cultural traditions among nonhuman primates where different behavioural variants have become established in different populations, although environments are reported to be very similar (Whiten et al. 1999; Perry et al. 2003; van Schaik et al. 2003). Currently, such variation is interpreted as a manifestation of a cultural selection process, with individuals biased towards adopting the local or parental variants (Whiten et al. 1999). However, our finding that most cultural traits

go extinct at an early stage suggests that these differences between populations need no other explanation than the stochasticity that exists in real world social learning. Conceivably, cultural drift may explain the different behavioural traditions reported in common chimpanzees (Whiten et al. 1999).

Third, Tomasello (1994) has argued that our species' unique capabilities for language, teaching and efficient imitation allow us to transmit cultural knowledge with higher fidelity than observed in other animals. He argued that this transmission fidelity helps to explain the existence of cumulative culture (or 'ratcheting') in humans but not other animals. However, hitherto it has not been apparent why high fidelity should necessarily favour ratcheting (Laland et al. 2009). Our analysis potentially plugs a gap in this argument. Since refinements of cultural traits are only likely to occur if the original trait is present in the population, a longer persistence time would seemingly create greater opportunities for refinements to appear, leading to cumulative culture. From Fig. 3, it can be seen that a small increase in the fidelity of transmission can lead to substantially longer persistence times for cultural traits. One implication of this finding is that, to the extent that the human capacity for effective imitation, teaching, language and other human-specific mechanisms that promote information transmission significantly enhance the transmission fidelity of social learning, then this could partly explain the orders of magnitude greater volume of culture associated with our species than with other animals, as well as the longevity of some human cultural traits, and human culture's uniquely cumulative character. Moreover, these factors are likely to reinforce each other: more culture means greater opportunity for borrowing of ideas and technologies from other conceptual lineages, potentially fuelling innovation and refinement, and instigating further cumulative culture. Thus it is possible to envisage how a small increase in the fidelity of cultural transmission could have made a large qualitative difference to the character of human culture. It can also be seen (Fig. 3) that larger population sizes possess steeper curves, with traits reaching higher expected longevities for lower transmission fidelity than smaller populations. This too would serve to promote more culture in human populations than in other animals, since the former are typically more populous.

Conversely, a great deal of animal culture has been characterized as short-lived foraging traditions (Laland et al. 1993), the majority of which are thought to be transmitted by comparatively simple social-learning processes, such as local enhancement, a mechanism not generally considered to promote high fidelity transmission, and observed in small populations. Our analyses lead us to predict that such traditions will indeed exhibit low fidelity of social learning (low *p*).

Finally, there are also some practical implications of this work for the study of social learning. A typical social-learning experiment, in both animals and humans, has a design reliant on transmission in demonstrator − observer dyads (i.e. a single cultural parent!). If our theory is correct, this would seem to be inappropriate for two reasons. First, a demonstrator − observer dyad will be suboptimal with respect to information transmission, and in extended transmission chains (e.g. Laland & Plotkin 1990, 1993) will eventually lead to loss of the trait. Employing multiple demonstrators should greatly enhance the likelihood of social learning taking place. Second, if uniparental transmission is indeed rare in nature, experiments deploying a single demonstrator lack ecological validity.

Acknowledgments

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APPENDIX

Proposition 1. The dynamical system $x_{t+1} = 1 - (1 - px_t)^n$ has a fixed point in the half-open interval $0 < x \leq 1$ (with the entire interval as its basin of attraction) if and only if $np > 1$.

Proof. Fixed points are solutions to the equation

$$f(x) := 1 - (1 - px)^n - x = 0$$

We are always assuming that $0 < p < 1$. The first and second derivatives are

$$f'(x) := np(1 - px)^{n-1} - 1$$

and

$$f''(x) := -n(n-1)p^2(1 - px)^{n-2}$$

Evidently, $f''(x)$ is negative for all $x \leq 1$. Hence $f'(x)$ is a decreasing function in this interval, and $f'(0)$ is positive if and only if $np > 1$. We have $f(0) = 0$ and $f(1) < 0$. Consequently, there will exist a solution to the equation in the interval $0 < x \leq 1$ if and only if $np > 1$. Another consequence is that in this interval, $1 - (1 - px)^n$ will be greater than x to the left of the fixed point and less than x to the right of the fixed point, so the basin of attraction is the entire interval.