

# Imitation explains the propagation, not the stability of animal culture

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For acquired behaviour to count as cultural, two conditions must be met: it must propagate in a social group, and it must remain stable across generations in the process of propagation. It is commonly assumed that imitation is the mechanism that explains both the spread of animal culture and its stability. We review the literature on transmission chain studies in chimpanzees (*Pan troglodytes*) and other animals, and we use a formal model to argue that imitation, which may well play a major role in the propagation of animal culture, cannot be considered faithful enough to explain its stability. We consider the contribution that other psychological and ecological factors might make to the stability of animal culture observed in the wild.

**Keywords:** imitation; cultural evolution; animal culture

## 1. INTRODUCTION

Recent studies have convincingly established the existence of culture among social animals such as chimpanzees (*Pan troglodytes*), orang-utans (*Pongo abelii*), rats, birds and cetaceans by showing that they display community-specific behaviour (Fisher & Hinde 1949; Terkel 1996; Whiten *et al.* 1999; Noad *et al.* 2000; Rendell & Whitehead 2001; van Schaik *et al.* 2003; Krutzen *et al.* 2005). These behavioural variants cannot be readily attributed to genetic or environmental induction, thus suggesting a cultural character (Whiten *et al.* 1999; Lycett *et al.* 2007).

For acquired behaviour to clearly count as cultural, two conditions must be met: it must propagate in a social group, and it must remain self-similar or stable across generations in the process of propagation. Reiterated transmission (through imitation or other means), even with relatively low fidelity, is sufficient to explain propagation (or 'spread'). Among humans, for instance, rumours easily propagate through verbal communication even though their content typically keeps changing in the process. In contrast with true cultural traditions such as folk tales, most rumours fail to achieve intergenerational cultural stability (or 'persistence').

In animals, a variety of behavioural patterns have been shown both to spread and to persist across generations (e.g. Fisher & Hinde 1949; Kawai 1965; Terkel 1996), and it has been assumed that the same transmission mechanisms explain both the spread and the stability of animal culture. In particular, among the several forms of social learning, imitation is thought to exhibit a higher degree of fidelity and therefore play a major role. Once considered to be uniquely human, imitation has now been shown to exist in animals such as chimpanzees (for a review with a historical perspective, see Whiten *et al.* 2004).

The extent to which imitation explains cultural propagation and stability in animal cultures is a matter of controversy. Heyes (1993) and Galef (1988), in particular, have questioned the idea that imitation is a distinct

mechanism specially geared to the spread of cultural information. Galef (1995) has also argued that the spread and stability of cultural behaviour is contingent on their rewarding character rather than on the mechanism of their propagation.

The issue we want to raise here is a different and complementary one. Let us accept, at least for the sake of discussion, that imitation is more faithful than other forms of social learning found among animals. It could be, at least in principle, that imitation is so faithful that *in itself* it guarantees the stability of behaviour over several generations. Indeed, in the biological case, the relative stability or inertia of genes is to a very large extent explained by the extraordinarily high fidelity of gene replication, with typical rates of mutation ranging from  $10^{-4}$  to  $10^{-11}$ , although, even in this case, selection must be invoked to explain very long-term stability. But is the degree of fidelity of imitation high enough to explain cultural stability? Our aim is to investigate this question from both an empirical and a formal point of view.

It is commonly assumed that the degree of fidelity found in animal imitation, even if obviously much lower than in gene replication, is sufficient to explain cultural stability. Marino *et al.* (2007, p. 970), for instance, claim that

'Imitation is an important type of social learning that can readily lead to stable cultures'.

Horner *et al.* (2006, p. 13878) justly note that

'what we really need to establish is whether chimpanzees learn from each other with *sufficient fidelity* for behaviour to spread within a community' (emphasis added).

Controlled experiments have indeed shown that chimpanzees can learn new and complex behavioural patterns from the observation of conspecifics (Sumita *et al.* 1985; Huffman & Hirata 2004; Horner *et al.* 2006). Further experiments have focused on repeated transmission (Whiten *et al.* 2005, 2007; Horner *et al.* 2006;

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Bonnie & de Waal 2007; Dindo *et al.* 2008). Whiten *et al.* (2007, p. 1038) conclude:

we provide robust experimental evidence that alternative foraging techniques seeded in different groups of chimpanzees spread differentially not only within groups but serially across two further groups with *substantial fidelity*. Combining these results with those from recent social diffusion studies in two larger groups offers the first experimental evidence that a nonhuman species can *sustain* unique local cultures, each constituted by multiple traditions. (emphasis added)

If fidelity of imitation is to explain not just the spread but also the stability of different traditions in different communities in the wild, what level of fidelity must be involved? Has such a level of fidelity been achieved in experiments on social transmission? Here, we answer these questions by means of a simple model and a review of relevant experimental evidence. We argue that the level of fidelity of imitation observed in an experimental setting would not be sufficient to secure the stable differences observed among laboratory communities if the chains of transmission were allowed to extend for more than a few steps and to proceed more spontaneously. Therefore, we claim, this level of fidelity falls quite short of explaining the stable behavioural differences found between communities in the wild (e.g. Mercader *et al.* 2002).

## 2. TRANSMISSION CHAIN STUDIES IN CHIMPANZEES

The study of the spread of the ‘potato-washing’ behaviour among macaques (*Macaca fuscata*) is the paradigmatic example of the diffusion of a new behaviour in a community and can easily be compared with laboratory experiments (Kawai 1965). Briefly stated, in 1953, Japanese primatologists observed a female macaque washing sweet potatoes in water to remove sand from it. This new habit slowly spread among other monkeys and led to several changes in the lifestyle of the community. The potato-washing behaviour is an example of a persistent cultural difference between communities of macaques since it has now been observed for more than 50 years.

Unfortunately, there are very few well-studied cases of the spread of novel behaviour in animals in the wild, in part because it is rare and in part because it requires long-term field studies. But can we transpose this natural situation in the laboratory? To do so, Whiten *et al.* devised an artificial fruit from which chimpanzees could gain food by using two alternative techniques, either use a stick to lift a hook to release food from the fruit (the so-called ‘lift’ technique) or insert a stick into a trap and push to gain access to food (the ‘poke’ technique). Using this artificial fruit, Whiten *et al.* performed an experiment with three different groups of chimpanzees. In one group, they introduced an individual trained to use the lift technique; in a second group, they introduced an individual trained to use the poke technique; in the control group, they introduced an untrained individual. While in the control group, no individuals managed to gain food from the artificial fruit, in both the lift and poke groups naive chimpanzees managed to learn how to open the artificial fruit by observing the model. Furthermore, in

both the lift and poke groups, most individuals used the technique of the model. Note however that this was far from being universal. In the lift group, for instance, eight chimpanzees used only lift, four used only poke, four used both techniques, and one did not use the artificial fruit at all (Whiten *et al.* 2005, fig. 2*b*).

Whiten *et al.* (2005, p. 738) take their results as evidence of the strength of social learning in creating lasting community-specific behaviour:

‘To our knowledge, these data provide the first robust experimental demonstration of the *spread and maintenance* of (1) alternative traditions in any primate, and (2) alternative tool-use techniques in any non-human animal’ (emphasis added).

We agree with Whiten *et al.* that their experiments show that new behavioural variants can spread through a community of chimpanzees, even under laboratory conditions, by means of social learning. This is relevant for field studies because it supports the idea that community-specific behaviour is spread through social learning. However, while these experiments are highly relevant to understanding the *spread* of behaviour, they raise some questions when it comes to the *stability* of behavioural variants along the chains of transmission.

As we pointed out, not all animals imitated just the technique of the model. This is not mysterious. Observing the model using the lift technique may provide a naive individual with information about the actual behavioural sequence to be performed in order to open the artificial fruit, with imitation in a strict sense ensuing. It may also just indicate that food can be obtained by manipulating the artificial fruit in some specific way, which may give the naive individual the incentive to explore and rediscover the lift technique (or alternatively, the poke technique). This would be imitation only in a looser sense, and could more precisely be described as emulation (Tomasello *et al.* 1987). Even learning by imitation in the strict sense, say, the lift technique would cause the animals to interact more often and more spontaneously with the artificial fruit and would thereby increase their chances of discovering the alternative poke technique by individual learning. Given this range of possibilities, it is unsurprising that not all animals in a community used the technique of the model. If anything, it is remarkable that most animals did, and it shows that indeed chimpanzees can and do imitate in a wide and possibly also in a narrow sense of the term (where it contrasts with emulation). Still, given that a few individuals ended up discovering the alternative method, and given that the animals had only a few opportunities to interact with the artificial fruit over a relatively short period of time (compared to natural conditions), these experiments cannot be said to establish that the level of fidelity in social learning experimentally demonstrated in chimpanzees is sufficient to explain cultural stability.

Whiten *et al.* might point out that they retested the lift and the poke groups after two months and found that some differences remained across groups. They might argue that this speaks not only to the issue of propagation, but also to that of stability. We rather see this interesting finding as providing evidence that chimpanzees

remembered the method they had been using two months earlier, not that these differences would have remained stable had the artificial fruit been available throughout this period.

What would happen if the animals in these artificial communities had unrestricted access to many baited artificial fruits over an extended period of time? We would expect most chimpanzees to end up preferring the most efficient of the techniques if there is one, or using either or both techniques if they are equivalent. In all cases, it should not matter to the long-term outcome which of the poke or the lift technique was introduced in the first place. Imagine for instance that the model had used lift in the first place but that poke is more efficient for chimpanzees. This is actually what is suggested by the fact that more chimpanzees switched from the lift to the poke method than vice versa (Whiten *et al.* 2005). Provided that some individual did discover the poke technique, it should end up spreading to the whole group and more or less replacing the lift technique. In a community where poke had been introduced first, the accidental discovery of lift should not, on the other hand, result in the abandonment of the more efficient poke. In the long run, therefore, both types of communities should be using the same technique. Some evidence that this is indeed what would happen is provided by a follow-up study (Hopper *et al.* 2007). Similar considerations apply to comparable studies of transmission in chimpanzees (Bonnie & de Waal 2007; Whiten *et al.* 2007).

Studies conducted among rats, fishes and humans give further reasons to doubt that imitation and other forms of social learning are sufficient to secure cultural stability. We review this evidence in the next section.

### 3. TRANSMISSION CHAIN STUDIES IN OTHER SPECIES

In a pioneering transmission chain study, Curio *et al.* (1978) taught a captive blackbird (*Turdus merula* L.) to express a fear response to a stuffed Australian honeyeater (*Philemon corniculatus*). This bird, hereafter named the teacher, was then shown the honeyeater in the presence of another naive blackbird (staying in another aviary). Curio *et al.* showed that the naive bird learned to fear the innocuous honeyeater by observing the teacher's behaviour. To see whether the strength of the fear response decreased through multiple transfers, they performed a transmission chain study of six steps, with the naive individual at step  $n$  serving as the teacher at step  $n + 1$ . The results suggested that the fear response could propagate without loss of intensity (Curio *et al.* 1978).

Following a procedure similar to that of Curio *et al.*, Laland & Plotkin studied the transmission of 'digging' behaviour in Norway rats (*Rattus norvegicus*; Laland & Plotkin 1990, 1992). They contrasted four different conditions (Laland & Plotkin 1990).

- (i) In the 'standard transmission' condition, the first 'teacher' rat was trained to uncover buried carrots. A naive individual was then given the opportunity to learn to dig and find carrots by observing the teacher. The naive individual at step  $n$  then served as the teacher at step  $n + 1$ .

- (ii) The 'additional individual learning' condition was similar to the standard transmission condition except that the naive individual was given further time to search for buried carrots alone.
- (iii) In the 'innovator' condition, the initial teacher was untrained and left to discover by itself how to uncover buried carrots.
- (iv) Finally, in the 'control' condition, every naive rat was paired with an untrained individual that had had no carrots buried in its cage.

Rats found more carrots in the three transmission conditions than in the control condition, suggesting a sustained effect of social learning. What is of particular relevance to the present discussion is that the difference between the innovator condition and the other two transmission conditions disappeared after five to six transmission events. In the standard transmission and in the additional individual learning conditions, the level of digging behaviour was very high at the beginning, in line with the fact that the first teacher was trained to dig carrots. This high level of activity progressively decreased and stabilized after five to six transmission events. In the innovator condition, on the other hand, the first teacher was untrained and the level of digging activity was therefore very low initially. This level subsequently rose and stabilized. Remarkably, in all three transmission conditions the digging activity reached the *same level*. Starting from different initial conditions and different transmission protocols did not lead to persistent differences between transmission chains, but on the contrary to the very same stabilized endpoint. Experimentally modifying the social cues available to rats changed the speed at which difference between groups disappears, but it does not prevent this disappearance (Laland & Plotkin 1993; Galef & Whiskin 1995).

Adapting the methodology of Jacobs & Campbell (1961) (whose experiment we discuss below), Galef & Allen (1995) extended the results of Laland & Plotkin by using two diets, Jh and Cp, which were equally liked by Norway rats (i.e. naive rats presented with both diets on average ate an equal amount of each). They taught two groups of four rats an aversion for Cp in one case and for Jh in the other. Each group of rats served as 'founding colony' members and were placed in a cage with two bowls, one of Cp diet and the other of Jh diet. After 24 h, they weighed the amount of Jh and Cp diet eaten and replaced one founding member with a new, naive rat. After four such replacements, they replaced the individual that had spent the longest time in the colony by a new one. In the first experiment, Galef & Allen showed that the difference between the two groups of rats disappears through time, in a way consistent with Laland & Plotkin's findings and with our general argument.

Moreover, Galef & Allen (1995) established a new result highly relevant to transmission studies: when rats were given unlimited access to the food, the difference between the two groups disappeared much faster than when they were given the food for only 3 hours a day. This is indeed crucial because, if the experiment had only been performed with the 3 hours-a-day condition, one could have come to the wrong conclusion that once a majority of rats prefer one diet, this preference is

*faithfully* transmitted to novel individuals. This could have led one to the further unwarranted conclusion that the very same mechanisms of social transmission that explain propagation of behaviour also explain the stable community traditions and between-community differences observed in the wild. What these experiments tend to show is that the more individuals rely on social learning, either because the social cues are more prominent or because they have less time to explore the environment, the longer it takes for between-group differences to vanish, but in the absence of other factors of stabilization, these differences end up vanishing anyway.

Laland & Williams (1998) performed an experiment with guppies (*Poecilia reticulata*) similar to that of Galef & Allen with rats. They trained 'colony founder' guppies to use one of two available routes of different lengths to get to a feeder. In some colonies, the founders were trained to use the longer route and in others to use the shorter route. In each of the conditions, after 24 hours, a founder, or, if there were no more founders, the oldest individual in the colony was removed and replaced by a naive individual. Unsurprisingly, in light of the previous results in rats, the percentage of times the short route was used remained high when the founders had been trained to use the short route and progressively increased when the founders had been trained to use the longer route. Thus, the differences between the short and the long groups rapidly diminished through time (Laland & Williams 1998).

It could, at first, seem surprising that naive guppies did not simply use the shortest route to get to the feeder, independently of what the other fish were doing. However, Bates & Chappell (2002) have shown that when left alone in the aquarium, naive fish mostly use the shorter route. It is only in the presence of a group of fish that they follow the group. This could be because the predation risk is lower in a group, suggesting that guppies have a natural tendency to stay within a group whenever available (Day *et al.* 2001; Bates & Chappell 2002). Assuming this interpretation to be correct, it is notable that, in spite of a strong incentive to stay within the group, individuals progressively changed their behaviour, making the whole group more and more likely to use the shortest route to reach the feeder. What is even more surprising is that when both routes are of equal length, the difference between the groups also tends to disappear, the group using alternatively one or other, equivalent, route (Laland & Williams 1997).

The above examples strongly suggest that, in animals, the initial differences experimentally introduced between groups vanish through successive transmission events. This has been shown for different species (rats and guppies), for different behavioural variants (such as feeding techniques, food preferences and foraging preferences) and with different levels of reliance on social information. One could still argue that social learning in rats and guppies takes place through stimulus enhancement or emulation that are imitation only in a broad sense and may not have a high enough degree of fidelity, whereas in the case of chimpanzees, as in the case of humans, imitation in a stricter sense is involved and is faithful enough to secure the persistence of between-community heterogeneities for long periods of time.

This was precisely the assumption of Jacobs & Campbell (1961) regarding humans. They reasoned that many human norms seem to be completely arbitrary, group-specific and nevertheless stable through time. They further postulated that the stability of these norms could be explained by a tendency of individuals to be influenced by other members of their community. To test this hypothesis, they used a visual illusion (Sherif 1936): if a participant sees a light spot in a completely dark room, the light appears to move. This illusion is very robust, but when participants are asked to evaluate the distance travelled by the light, they lack confidence and can easily be influenced. Jacobs & Campbell thought that:

so labile is the autokinetic experience or at least the translation of it into judgments of linear extent, that one reading the reports of studies employing it might expect that an arbitrary group norm once established would be passed on indefinitely without diminution; that once well indoctrinated, the naive group members would become as rigid and reliable spokesmen for the norm as were the confederates who preceded them; that each new generation would unwittingly become a part of a self-perpetuating cultural conspiracy propagating superstition and falsehood.

(Jacobs & Campbell 1961, p. 650).

They tested their prediction by introducing confederates at the beginning of the experiment and progressively replacing them with naive participants until all the confederates were removed. The transmission then continued by replacing each time the 'oldest' participant in the group by a naive one. Confederates would always judge the light to have travelled a very long distance (about 16 inches whereas the mean uninfluenced answer is 4 inches). The results were clear:

The experimental comparisons were introduced in the expectation that induced cultures of differing strengths and persistence would be produced. In fact, there was some expectation that the strongest conditions might produce an arbitrary culture which would persist without apparent diminution. No condition produced a culture of any such strength, and among the three experimental groups starting with one naive respondent, the number of confederates in the groups had little if any clear-cut effect.

(Jacobs & Campbell 1961, p. 654).

While increasing the number of confederates had little effect, increasing the number of naive individuals had disproportionate effects (a result also found in guppies; Stanley *et al.* 2008). With two confederates and one naive individual, it took five steps for the difference from the control condition to vanish. With one confederate and two naive individuals, the same result was obtained in only two steps.

#### 4. WHY ARE CHIMPANZEE STUDIES DIFFERENT?

In all experimental transmission chain studies performed so far, not a single one has shown that arbitrary differences between groups could persist for a long time. This is all the more remarkable given that most studies did not last more than a few transmission steps (the longest involving 14 steps; Galef & Allen 1995). To help

explain what is happening, it is useful to distinguish two types of causal contribution affecting individual behaviour. An individual's behaviour is influenced by its constitution and situation, as they result from its biological make-up, its past experiences, acquired skills and dispositions and its idiosyncratic viewpoint. We will call this the 'individual propensity'. An individual's behaviour is also influenced by the recent or present behaviour of its conspecifics that it can observe and that can inform its own behaviour. We will call the influence that the recent or present behaviour of others has on an individual's behaviour the 'social influence'. The speed at which the differences between groups diminish is crucially dependent on the relative importance of social influence and individual propensity. The more important the social influence, the slower the erosion of the difference. Three factors affect the strength of social influence:

- (i) The greater the number of social cues converging towards the same alternative, the more important social influence is (Laland & Plotkin 1993; Galef & Whiskin 1995).
- (ii) The greater the time available to individuals to explore different alternatives, the less important social influence is (Galef & Allen 1995).
- (iii) The greater the proportion of naive individuals in the group, the less important social influence is (Jacobs & Campbell 1961; Stanley *et al.* 2008).

These provisional conclusions contrast sharply with those reached by Whiten and colleagues on the basis of chimpanzee studies. Two important methodological factors help explain this discrepancy. First, unlike the procedure followed in the transmission studies we have just reviewed and unlike the generational turnover in natural conditions, in Whiten and colleague's experiments, knowledgeable individuals were not progressively replaced with naive ones. So, individual conservatism (i.e. the tendency to stick to one technique once learned) could play an even greater role than in natural conditions (see, for instance, Marshall-Pescini & Whiten 2008). Second, the artificial fruits were presented a few hours per day (typically 3 hours) over a short period of time (typically 10 days), drastically limiting the opportunity for further exploration. In spite of these methodological factors, Whiten and colleagues still report evidence of erosion of between-group differences.

We therefore conclude that, at present, experimental evidence does not support the claim that artificially introduced arbitrary cultural differences can persist among captive communities of animals. Imitation and other forms of social learning fail to provide an adequate explanation of the stability of culture among wild animals. In the following section, we show that this conclusion is also supported by theoretical considerations on the role of the fidelity of social learning in explaining between-community differences.

## 5. HOW FAITHFUL MUST TRANSMISSION BE FOR CULTURAL DIFFERENCES TO PERSIST?

The pooling of individual propensity with social influence is, we want to argue, the driving force behind the transmission chain experiments. In the absence of other factors of stability and provided that the transmission

chain is long enough and that the individual propensity is not negligible, any difference between social influence and individual propensity will end up disappearing. How likely is it then that artificially introduced arbitrary differences between groups of animals persist for several generations, that is, achieve cultural stability?

The experiments we have reviewed so far can be classified according to whether the behaviour under study varies in a discrete or continuous fashion. For the sake of cogency, we focus on the lift versus poke experiment, an important paradigm in transmission chain studies. The model we outline is, however, quite general, and it extends straightforwardly to continuous behaviour.

In the lift versus poke experiment, two alternatives are considered. Let  $x_i$  be the behaviour of an individual  $i$ . If the individual  $i$  uses the poke technique,  $x_i = 1$ . If the individual uses the lift technique,  $x_i = 0$ . Let  $q_i$  be the probability that the individual  $i$  performs the poke technique during a given session. In other terms,  $q_i = P(x_i = 1)$ . Let  $q'_i$  be the probability that the same individual performs the same poke technique during the next session of the experiment.

To represent the fact that both social and individual factors contribute to determining the behaviour of an individual, we may write

$$q'_i = \alpha S_i + (1 - \alpha)P_i, \quad (5.1)$$

where  $S_i$  represents the social influence exerted on  $i$  and is a function of the behaviour of group members.  $P_i$  is the individual propensity;  $\alpha$  represents the fidelity of social transmission. If  $\alpha = 1$ , the individual behaves perfectly in accordance with the social influence  $S_i$ ; if  $\alpha = 0$ , it behaves only in accordance with its own propensity  $P_i$ . Importantly, equation (5.1) assumes that there is no conservatism: the behaviour of one individual in a new session is a function of what it has observed in the previous session ( $S_i$ ), not what it has done ( $x_i$ , see discussion below).

We will assume that social influence is linear and is well represented by the proportion of behaviour types an individual observes. Thus, if an individual  $i$  observes four pokes and two lifts, the social influence for that individual is  $S_i = 4/(4 + 2) = 2/3$ . For the sake of clarity, we will further assume that the group is large and that an individual observes many instances of behaviour (so that  $S_i = \bar{x}$ , see below). We will also assume that the individual contribution is fixed and is the same for all individuals,  $P_i = P$ .  $P$  is therefore the probability that an individual performs the poke technique when  $\alpha = 0$ .

Note that  $P$  is not the probability that an individual discovers a new technique but the probability that it performs one of two techniques when it knows both and there is no social influence. In the lift-poke experiment,  $P$  would represent the behaviour of individuals once they have learned the two techniques and are left alone; from the results, we can infer that it would probably be poke. In the case of the potato-washing behaviour, washing is an alternative to removing the sand from the potatoes by brushing them by hand. It seems plausible that individuals who know both techniques tend to use the washing behaviour because it is the most efficient one. In that case,  $P$  would be the washing behaviour. Finally, in a controlled field experiment, Thornton & Malapert taught

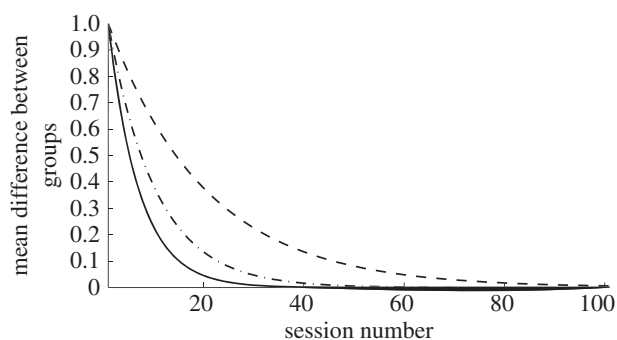


Figure 1. The effect of fidelity on behavioural stability. Three different levels of fidelity ( $\alpha$ ) are considered (table 1). We plot the evolution of the difference between two groups that are initially maximally different, and behave according to equation (5.2). Dashed line 0.95, fidelity found in rat experiment; dash-dotted line 0.90, fidelity found in guppy experiment; solid line 0.85, fidelity found in humans experiment.

demonstrator meerkats (*Suricata suricatta*) of seven different groups to retrieve food from one of two different landmarks (see also Thornton & Malapert 2009a,b). Naive individuals learned in contact of demonstrators to prefer the landmark used by the demonstrator. But at the same time, they progressively discovered the other landmark and started to forage on it. Hence, the difference initially introduced between groups progressively disappeared through time because individuals more and more foraged equally on both landmarks. In this natural setting,  $P$  would be the natural propensity to forage on one rather than the other landmark (here  $P$  would be  $1/2$  because individuals from control groups, without trained demonstrators, do not appear to prefer one or the other landmark).

Usually in transmission chain studies, what is of interest is the average behaviour of the groups during each session. We call  $\bar{x}$  and  $\bar{x}'$  the proportion of poke performed during two successive sessions, respectively, with  $\bar{x} = (1/n) \sum_i x_i$ . We compute the average change ( $\Delta\bar{x}$ ) between two sessions

$$\Delta\bar{x} = (1 - \alpha)(P - \bar{x}). \quad (5.2)$$

Equation (5.2) states that the change in the average behaviour of the group is proportional to the difference between the individual propensity ( $P$ ) and the mean social behaviour ( $\bar{x}$ ). Thus, after some time, the mean behaviour in the community will be identical to that based on individual propensity alone. Importantly, the fidelity of social learning ( $\alpha$ ) determines the rate at which the difference between social influence and individual propensity erodes. More precisely, the distance between two groups is a geometric progression with ratio  $\alpha$  (figure 1). The fact that the mean behaviour in the group converges towards the individual propensity is a very robust and indeed trivial result. If at every time step the behaviour of an individual in the group is a function of the behaviour of the group and of individual propensity, we should always expect the average behaviour of the group to converge towards the individual propensity. The only source of directional change is in that direction. The interesting question, which the model helps address, is that of the rate of convergence towards individual propensity. When this rate is low

Table 1. The fidelity of social transmission is usually high (greater than 80%) in the four cases reviewed. We used a linear regression analysis by the least-squares method to estimate  $\alpha$  (the degree of fidelity) in the four studies reported. In each experiment, we focused on the longest, more detailed and more faithful condition. Following the order of the table from top to bottom, we used figs 2, 3, 5 and 4 of the respective papers.

reference	species	fidelity of social transmission	number of observations
Laland & Williams (1998)	guppy	0.89	7
Laland & Plotkin (1993)	Norway rat	0.9	7
Galef & Allen (1995)	Norway rat	0.95	10
Jacobs & Campbell (1961)	human	0.86	5

enough for differences to persist across generations, then cultural stability is largely explained by fidelity of transmission. When this rate is high, then the explanation of cultural stability must crucially involve other factors.

To give a rough idea of the degree of fidelity found in experiments on social transmission chains and of the rate of erosion it determines, we fitted our model to the experiments reviewed above. The results are recapitulated in table 1. Although the estimates are not really accurate because of the relatively limited number of observations, the results show that the degree of fidelity varies according to species and to experiment but nevertheless remains generally quite high (in all cases above 80%). In spite of this high degree of preservation, none of the studies reviewed so far managed to produce a culture-like phenomenon.

Taken together, these formal results and the available evidence cast serious doubts on the claim that cultural stability can be explained by the same mechanism that explains cultural propagation, be it imitation or some other form of social learning. Of course, it could be that imitation is more faithful in the wild than in the laboratory. It could be that conservatism is very high, meaning that once animals have acquired a given arbitrary technique, they almost never depart from it in their lifetime either through exploration or through imitation of individuals using another technique. While a high degree of conservatism has been experimentally demonstrated over relatively short periods of time (two months in the case of Whiten *et al.* 2005), there is also evidence of individuals changing their technique (Whiten *et al.* 2005; Hopper *et al.* 2007). With very high fidelity and very high conservatism, culturally transmitted techniques could remain stable for several generations. However, at present, experiments do not support the conclusion that this is indeed what happens.

## 6. FACTORS EXPLAINING CULTURAL STABILITY

Other factors, beside the relative fidelity of transmission, may be—we would argue, *must* be—invoked in explaining

the persistence of cultural differences. While random factors, and especially innovation rate, also deserve discussion, here we focus on four types of factors: ecological availability, reward-based factors (that combine an ecological and a psychological aspect), content-based psychological factors and source-based psychological factors (Sperber & Claidière 2008).

- (i) *Ecological availability.* Subtle differences in the environment can cause the stabilization of different culturally propagated techniques. Differences in ant-dipping among chimpanzees, for instance, were once thought to be unrelated to ecological variation (Whiten *et al.* 1999). Recently, however, careful examination of the behaviour of ants has revealed that, depending on ants' aggressiveness, chimpanzees adapt the length of their collecting stick and the technique used to eat from the sticks (Humble & Matsuzawa 2002; see also Schöning *et al.* 2008; Yamamoto *et al.* 2008). Chimpanzees use different techniques when harvesting species of ants that differ in their global aggressiveness but also when harvesting the same species in different conditions such as when ants are in their nest or on a foraging trip (Humble & Matsuzawa 2002).
- (ii) *Reward-based factors.* The rewarding effect of behaviour is the best known factor in its reinforcement. It is also, at a population level, a major factor in its stability. Chimpanzees' 'leaf-swallowing', for instance, consists of swallowing rough leaves in order to expel intestinal parasites. The spread of the behaviour is probably linked to social learning, but the stability of the behaviour can be explained by the relief produced by the disappearance of parasites (Huffman & Hirata 2004). Similarly, in all the animal experiments we have reviewed, the behaviour artificially introduced was a rewarding one, and this is an important factor of explanation of its social success that deserves to be emphasized (Heyes 1993; Galef 1995).
- (iii) *Content-based factors.* Psychological disposition may cause certain techniques to be more easily learned or performed than others and hence, *ceteris paribus*, more likely both to spread and to stabilize. Hunt and colleagues, for instance, have shown that New Caledonian crows are laterally biased and prefer to use the right-hand side of *Pandanus* leaves to manufacture tools (Hunt 2000; Hunt *et al.* 2001; see also Weir *et al.* 2004). Furthermore, different populations of crows use tools that differ in their complexity. Hunt and colleagues have shown that the more complex the tool design, the stronger the laterality bias (Hunt *et al.* 2006).
- (iv) *Source-based factors.* Source-based factors are important when individuals acquire their behaviour from specific others (Coussi-Korbel & Fragaszy 1995). In the case of chimpanzees, for instance, Bonnie & De Waal have argued that the spread of the 'hand-clasp grooming' behaviour was determined by the proximity between individuals (McGrew *et al.* 2001; Bonnie *et al.* 2006;

Leca *et al.* 2007; Nahallage & Huffman 2007). They showed that the more chimpanzees spend time together, the more likely they are to learn the hand-clasp grooming technique from one another (see also Nakamura & Uehara 2004). Source-based factors can also vary in time and through development. Kawai, for instance, has argued that female Japanese macaques first learned the potato-washing behaviour from their daughters, but subsequently the pattern was reversed and the behaviour spread from mother to daughters and sons (Kawai 1965).

Attributing to individuals a conformist tendency to prefer a behaviour already adopted by the majority is a general source-based factor that might greatly contribute to explaining the stability of culture (Whitehead 1998; Byrne *et al.* 2004; Whiten *et al.* 2005; Bonnie *et al.* 2006; Thornton & Malapert 2009*b*). The effects of conformism in humans and its possible evolution by natural selection have received some theoretical attention, in particular by Boyd & Richerson (Boyd & Richerson 1985; Henrich & Boyd 1998; Eriksson *et al.* 2007; Nakahashi 2007; Wakano & Aoki 2007). The existence and possible stabilizing effects of conformism in animal culture deserve more investigation.

Distinguishing the propagation and the stability of behaviour and also different types of factors of stability should be of relevance to laboratory research on animal culture. Reward is the most obvious factor accounting for tool-use differences (Galef 1992). We have given examples of ecological availability and content-based factors that also play a clear role in the stabilization of specific cultural traits. The role of source-based biases, conformism in particular, in animal culture is more speculative but potentially quite relevant too.

## 7. CONCLUSION

Imitation, as other forms of social learning, refers to a process through which individuals acquire new behavioural variants. In agreement with Galef, we think it is quite important to dissociate explanations regarding the origin and spread of behaviour from explanations of its stability (Galef 1988, 1995). Here, we have reviewed relevant experimental and theoretical work and argued that imitation and other forms of social learning have not been shown to be, and are unlikely to be, faithful enough to support cultural stability. The state of the art is such, we conclude, that not only mechanisms of social learning—and in particular imitation—but also a variety of ecological and psychological factors must be investigated as potential contributors to the stability and hence to the very existence of animal culture.

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