Establishing an experimental science of culture: animal social diffusion experiments

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Review

Establishing an experimental science of culture: animal social diffusion experiments

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A growing set of observational studies documenting putative cultural variations in wild animal populations has been complemented by experimental studies that can more rigorously distinguish between social and individual learning. However, these experiments typically examine only what one animal learns from another. Since the spread of culture is inherently a group-level phenomenon, greater validity can be achieved through 'diffusion experiments', in which founder behaviours are experimentally manipulated and their spread across multiple individuals tested. Here we review the existing corpus of 33 such studies in fishes, birds, rodents and primates and offer the first systematic analysis of the diversity of experimental designs that have arisen. We distinguish three main transmission designs and seven different experimental/control approaches, generating an array with 21 possible cells, 15 of which are currently represented by published studies. Most but not all of the adequately controlled diffusion experiments have provided robust evidence for cultural transmission in at least some taxa, with transmission spreading across populations of up to 24 individuals and along chains of up to 14 transmission events. We survey the achievements of this work, its prospects for the future and its relationship to diffusion studies with humans discussed in this theme issue and elsewhere.

Keywords: culture; cultural transmission; social learning; diffusion experiments; diffusion chains; transmission chains

1. INTRODUCTION: MIND THE GAP

The study of cultural processes in animals can now boast approximately half a century of achievement, generally considered to have been launched by the famous efforts of Japanese researchers to document the spread of novel behaviour patterns among groups of macaque monkeys (Itani & Nishimura 1973; McGrew 1998). Reports of cultural phenomena in other mammals, birds and fishes have since accumulated, their frequency rising in recent years as decades of field research on some species have facilitated the identification of regional variations in behaviour, attributable to social learning (learning from others; Whiten & van Schaik 2007; Laland & Galef 2008). Where there is evidence that such variations are sustained (e.g. across generations) they are typically referred to as traditions or cultural variations.

Such phenomena are of considerable theoretical significance for evolutionary biology, because they offer (i) a means of inheritance and adaptation much more rapid than the genetic transmission processes on whose shoulders they have evolved and (ii) the prospect of a secondary form of behavioural evolution at the cultural level (Whiten 2005; Mesoudi *et al.* 2006). The animal studies are additionally of interest in identifying the roots of the cultural processes that are so distinctive in our own species (Whiten in press).

However, purely observational studies of wild populations are constrained in the inferences they can draw about the social learning mechanisms involved. Owing to this, a complementary corpus of experimental studies has arisen, in which the role of social learning can be robustly tested by comparing a condition permitting observational learning with one that offers no such opportunities. The literature based on this kind of approach now spans over a century and accommodates scores of studies identifying and differentiating various forms of social learning in different animal taxa (Galef & Heyes 2004). We think this literature suffers a major limitation, however, in relation to the topic of culture. Typically, researchers examine only what a single animal learns from another: in other words, they study only a single transmission event. Given that by its nature, culture requires multiple transmission episodes, examining social learning only at the dyadic level falls far short of the methodology that is needed. Hence our exhortation to 'mind the gap'. There is a yawning gap between the dyadic norm of the experimental literature and the typical, and proper, focus of observational field studies

on group-level phenomena. The latter, which include regional differences among groups and diffusion of novel behaviour patterns through groups, are what cultural analyses should properly be concerned with.

We propose that the best opportunity currently available to us to bridge this gap is the cultural diffusion (or 'transmission') experiment. Here, rather than focusing on only a model–observer dyad, experimentally controlled innovations in behaviour are seeded into *groups* of individuals and the spread (or otherwise) of the innovation is tracked and documented. Such approaches have been represented in the research literature for some time, but only sparsely and spasmodically in comparison to the dyadic design. We advocate here that the current interest in animal culture means that their time has come. They combine the power of experimental control with group-level analysis. Accordingly in §2 we offer a brief resumé of the history of these experiments, which in turn leads to an effort to systematize the variations in design that have proliferated.

2. DEVELOPMENT AND EVOLUTION OF DIFFUSION EXPERIMENTS

The first clear example of a diffusion experiment appeared in the celebrated work of Bartlett (1932), who studied how story narratives were either preserved or modified as they were transmitted along a chain of human subjects. Bartlett recognized and discussed the relevance of this approach for investigating cultural transmission, but his primary interest was in what the successive transmissions told us about the nature of memory. Over the next decade or so, Bartlett's pioneering methods were adopted and developed by numerous disciples, but then the transmission experiment temporarily faded from the literature. It was rejuvenated as a tool to study cultural transmission by Jacobs & Campbell's (1961) explicitly titled 'perpetuation of an arbitrary tradition through several generations of a laboratory microculture'. Through the remainder of the century other human studies steadily built on this, but only recently has the power of such 'laboratory microculture' diffusion experiments with human subjects been fully appreciated and a rapid expansion of this literature occurred. In a companion paper to the present one (Mesoudi & Whiten 2008) we review this corpus of human diffusion studies from Bartlett to the present day.

In the non-human animal (henceforth, 'animal') diffusion literature, the first study most commonly cited in the cultural transmission literature that followed it is the work of Curio *et al.* (1978a,b). These authors conditioned blackbirds to make alarm calls in relation to novel stimuli and showed that such responses would pass along a transmission chain of six successive pairs of birds (A–B, B–C, C–D and so on) without decrement, contrasting with baseline rates of alarm calls. The authors interpreted these results as support for a 'cultural transmission hypothesis'.

The next controlled diffusion experiments concerned foraging behaviour in pigeons and rats. Lefebvre (1986) released pigeons trained to peck through food covers into whole flocks of naive birds.

In this way, he showed that the piercing technique was learned rapidly by some observing birds, contrasting with control birds that saw no model, and in the seeded population it continued to spread in the ensuing weeks. Laland & Plotkin (1990, 1992, 1993) returned to the principle of the linear diffusion chain, applying it to the transmission of digging up pieces of hidden food through consecutive expert–novice pairings of rats.

These studies cited the earlier experiments of Curio *et al.* (1978a,b) and over the last 15 years a reasonably thorough 'citation genealogy' has been built on these foundations. However, what appears to be the first true diffusion experiment in animals remained uncited until recently. In this study, Menzel *et al.* (1972) investigated habituation to two anxiety-inducing objects by juvenile chimpanzees, applying a 'replacement method' that started with a founder group of three chimpanzees that avoided the novel objects. One chimpanzee was then replaced by a naive chimpanzee and this process was repeated through 17 consecutive trios. Between the fourth and eighth 'generation' in this process, habituation occurred in some chimpanzees and gradually became pervasive, such that later trios routinely engaged with the objects. Menzel *et al.* accordingly concluded that 'a culture-like process was at work'. This first study effectively underlines why the diffusion method is indispensable for studying cultural transmission; the changes identified by Menzel *et al.* would never have been documented in a merely dyadic study because they were inherently cumulative.

Building on these pioneering foundations, diffusion studies have appeared with accelerating frequency (nearly half in the present century). They have now extended to a variety of species of fishes, birds and mammals and a diverse assortment of behavioural categories including predator avoidance, foraging, tool use, route choice and communication, which are of considerable potential adaptive significance. Below we survey this growing corpus of studies and, most importantly, offer the first systematization of the diversity it encompasses. In the electronic supplementary material (table S1), we offer detailed information about the scope of each of these studies. Table 1 below is a succinct overview derived directly from table S1 in the electronic supplementary material.

3. CLASSIFYING THE EMERGING PARADIGMS

Our approach to systematizing these studies involves two broad sets of distinctions that are constituted, respectively, by the columns and rows of table 2. The value of this operation is that, after a period in which this small field has grown by the gradual accretion of a number of individual studies, we can now start to survey all the methodological options 'in the round', together with their various limitations, pay-offs and prospects for more informed and strategic work in future.

(a) *Transmission designs*

We distinguish three broad types of experimental design that form the columns in table 2.

Table 1. Chronological table of diffusion experiments. (This table is directly derived from table S1 in the electronic supplementary material, which offers a comprehensive survey of methods and conclusions, together with Latin names of species studied, and further evaluative comments. Des. str. = design strength, following the scheme described in table 2 and explained fully in the text, where higher numbers represent designs judged more powerful in identifying diffusion based upon social learning: those of levels 3 and above incorporate control conditions that discriminate social from non-social learning, and are represented in italics. The column 'cultural diffusion' summarizes evidence for diffusion of the behaviour pattern of interest, where des. str. = 3 or more. Numbers of transmissions within chains are shown in parentheses; ? = number of transmissions unknown. For detailed information see table S1 in the electronic supplementary material.)

study content	species studied	publication	des. str.	cultural diffusion? (no. of transmissions)
Successive replacements in trios exposed to alarming objects	chimpanzees	Menzel et al. (1972)	3 B	habituation effect stable (17)
Transmission chains, seeded with alarm calls to arbitrary object	blackbirds	Curio et al. (1978a,b)	3 C	alarm calling stable (6)
Whole groups exposed to novel cues to buried food; spread of discovery in groups documented	baboons, vervets	Cambefort (1981)	1 A	?
Three nut-cracking chimpanzees mixed with nine naive ones	chimpanzees	Sumita et al. (1985)	2A	?
Models pecked through paper covers, in wild and captive flocks	pigeons	Lefebvre (1986)	4 A	piercing stable over 55 days
Spread of spontaneously initiated nut-cracking recorded in group	chimpanzees	Hannah & McGrew (1987)	2 A	?
Transmission chains seeded with models digging up carrot pieces	rats	Laland & Plotkin (1990)	4 C	digging stable (8)
Replication of 1990 study but incorporating a 24 hour delay	rats	Laland & Plotkin (1992)	4 C	stability less, with delay
Opportunity provided for group to use tools to probe for honey	chimpanzees	Paquette (1992)	1 A	?
Rearing conciliatory stump-tailed macaques with rhesus, among whom reconciliation is relatively rare	rhesus macaques	de Waal & Johanowicz (1993)	5 A	effect stable over six-week post-model phase
Transmission chains seeded with rats preferring different flavours	rats	Laland & Plotkin (1993)	7 C	transmission shown (8) but fidelity variable
Nuts cracked elsewhere introduced; spread in group recorded over several years	chimpanzees	Matsuzawa (1994) and Biro et al. (2003)	1 A	?
Successive replacements in groups with initial flavour preferences	rats	Galef & Allen (1995)	5 B	transmission shown, with slight waning (over 14)
Wild groups seeded with individuals trained to open specific small doors to feed	magpie jays (wild)	Langan (1996)	7 A	door opening stable over 3 days, but not door chosen
Spread of dipping for honey with specific natural tool documented	chimpanzees	Tonooka et al. (1997)	1 A	?
Founder shoals were seeded with preference for one of two routes	guppies	Laland & Williams (1997)	5 B	differences transmitted (7) but waned by half
Similar to 1997 paper but more efficient alternative available	guppies	Laland & Williams (1998)	5 B	differences transmitted (7) but waned
Groups with mixed naive and experienced fishes created	guppies	Reader & Laland (2000)	2 A	?
Young cowbirds housed with adults singing either of two different songs; repeated once first cohort became adults (models)	cowbirds	Freeberg (1998) and Freeberg et al. (2001)	5 A	?
Spread of route preference: models in familiarity and experience	guppies	Swaney et al. (2001)	2 A	?
Spread logged off using either of two routes to escape a threat	guppies	Brown & Laland (2002)	7 A	social transmission not found
Flocks exposed to models feeding on blood from mock hen	chickens	Cloutier et al. (2002)	4 A	rapid waning over three transitions
Wild, banded birds exposed to model using novel foraging method	keas (wild)	Gajdon et al. (2004)	3 A	no significant evidence of social transmission
Captive chimpanzees given rough leaves used medicinally in wild	chimpanzees	Huffman & Hirata (2004)	1 A	?

(Continued.)

Table 1. (*Continued.*)

study content	species studied	publication	des. str.	cultural diffusion? (no. of transmissions)
Juveniles exposed to adults using either of two methods to get juice	brown capuchins	Fragaszy et al. (2004)	6 A	techniques spread but social learning unclear
Two groups each seeded with model using tool in different way	chimpanzees	Whiten et al. (2005)	7 A	moderate fidelity but stable over two months
Two transmission chains; opening artificial 'fruit' using alternative methods, plus control condition lacking model	chimpanzees children	Horner et al. (2006)	7 C	stable (8)
Two groups, each seeded with arbitrary convention to obtain food	chimpanzees	Bonnie et al. (2006)	7 A	spread to half group: stable, one corruption
As for 2005, but transfer between groups in foraging techniques	chimpanzees	Whiten et al. (2007)	6 A	stable, spread across three groups
Replication of Whiten et al. (2005), with one untrained model	chimpanzees	Hopper et al. (2007)	7 A	minimal evidence of social transmission
Two groups each seeded with a different foraging technique (via video)	colobus monkeys	Price & Caldwell (2007)	6 A	stable after 5 days with no model, one corruption
Replication of Horner et al. (2006) with appropriately modified task	brown capuchins	Dindo et al. (2008)	7 C	stable (4)
Successive replacements of fishes focused on novel food task	guppies, playfish	Stanley et al. (2008)	4 B	stable (13)

(i) *Open group diffusion* (*column A*)

Here, a behaviour of interest is introduced into a whole group, as in the study of Lefebvre (1986) described above. Rather than exert experimental control over the potential channels of social learning such as was done in the work of Curio *et al.* (1978*a*), the open group approach leaves open for investigation which other individuals might attend to, learn from and possibly adopt the behaviour they see (figure 1). The open group approach thus scores high in ecological validity, reflecting a situation common in nature, where an individual skilled in some technique is observed by naive individuals, as in intergroup migration.

Weighing against this approach is that the results are likely to be more 'messy' than those of more constraining methods described below. At the stage where a second and third individual adopts the seeded behaviour, it may already have been difficult to distinguish whether the third learned it from the first or the second (or both), and with each new learner, the question of who learned by observing whom may become difficult to disentangle.

(ii) *Linear chain* (*column C*)

We address this next because it represents an opposite extreme to the open group approach. As in the study of Curio *et al.*, each step in the diffusion is constrained to involve just one model and one naive observer, with the latter then becoming the model for the next in the chain, and so on, resembling the children's game 'Chinese Whispers' or 'Telephone' (figure 1). This is sometimes referred to as a 'diffusion chain' or 'transmission chain' method. It allows the experimenter to track precisely what happens at each step in the diffusion process, and identify, for example, at what point a particular level of corruption occurs, contrasting with the complex interactions that may occur in an open diffusion context. The cost of this might be thought to be a loss of the kind of ecological validity inherent in the open group approach; however, there are many cases in the wild where transmission may routinely be one to one, as in some parent–offspring relationships. For these, the linear chain design can be seen as simulating repeated intergenerational transmission, collapsing what in the wild may take decades into a diffusion chain experiment that may occupy only weeks (Horner *et al.* 2006).

Excluding the studies in parentheses (which identified chains of social learning only via examining transmission across three groups) in column C, table 2 records the completion of only four true linear-chain experiments in the animal literature. This contrasts with numerous transmission chain studies in the human literature (Mesoudi & Whiten 2008). One reason for the paucity of such experiments in animals may be that it is necessary to ensure that each pair in the chain is both comfortable with being isolated from the remainder of their group and compatible with each other. Experience indicates that in primates at least, these can be very exacting requirements (Horner *et al.* 2006; Dindo *et al.* 2008).

(iii) *Replacement* (*column B*)

The replacement method, such as the linear chain, involves a systematic series of steps or 'cultural

Table 2. Experimental designs used to study the spread of traditions. (Criteria for inclusion are that a behaviour pattern is either facilitated (row 1) or explicitly seeded, usually through training of an initial model (rows 2–7), and the spread of such patterns is subsequently documented. Experimental designs are classified according to (i) experimental versus control conditions (condition designs: rows 1–7) and (ii) methods used to examine the spread of any traditions emerging (transmission designs: columns A–C), distinctions fully explained in the text. Studies marked with a single asterisk showed spread within a first group in an open diffusion design (column A) then on to a second or third group, thus demonstrating a chain of transmission (column C). For more information on each study see table 1, and table S1 in the electronic supplementary material.)

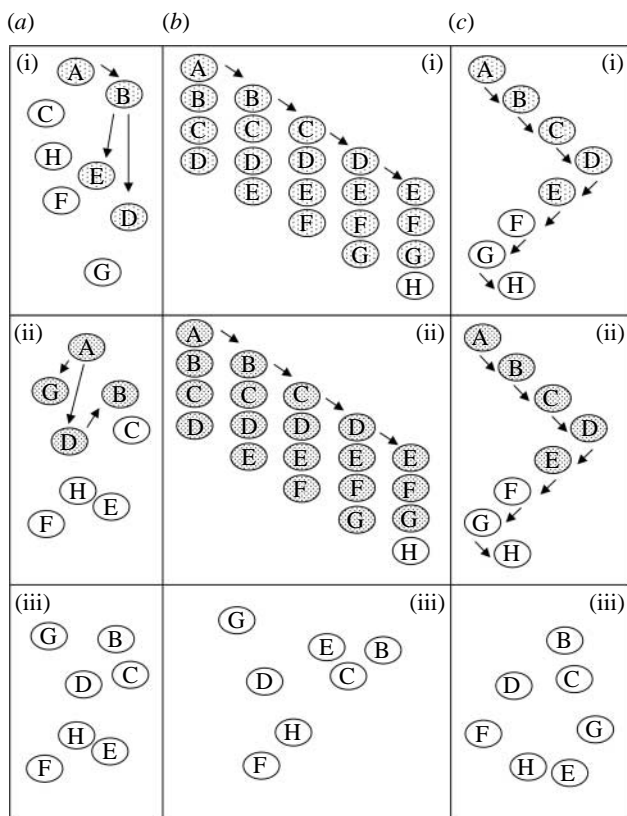| condition designs (1–7)	transmission designs (A–C)		
	A. open group	B. replacement	C. linear chain
1. one group, presented with novel learning opportunities	Cambefort (1981), Paquette (1992), Tonooka *et al.* (1997), Biro *et al.* (2003) and Huffman & Hirata (2004)		
2. action explicitly seeded in one group but no baseline	Sumita *et al.* (1985), Hannah & McGrew (1987), Reader & Laland (2000) and Swaney *et al.* (2001)		
3. one experimental group with one trained, seeded action, following no-model baseline	Gajdon *et al.* (2004)	Menzel *et al.* (1972)	Curio *et al.* (1978*a*)
4. one experimental condition with one trained, seeded action, versus no-model control condition	Lefebvre (1986) and Cloutier *et al.* (2002)	Stanley *et al.* (2008)	Laland & Plotkin (1990, 1992)
5. two experimental conditions, with alternative actions seeded in each	de Waal & Johanowicz (1993), Freeberg (1998) and Freeberg *et al.* (2001)	Galef & Allen (1995) and Laland & Williams (1997, 1998)	(Freeberg (1998), Freeberg *et al.* 2001 ∗see also Col. A)
6. two experimental conditions, with alternative actions seeded in each, after baseline, no-model control period	Fragaszy *et al.* (2004), Price & Caldwell (2007) and Whiten *et al.* (2007)		(Whiten *et al.* (2007), ∗see also Col. A)
7. two experimental conditions, with alternative actions seeded in each, plus third, no-model control condition	Langan (1996), Brown & Laland (2002), Whiten *et al.* (2005), Bonnie *et al.* (2006) and Hopper *et al.* (2007)		Laland & Plotkin (1993), Horner *et al.* (2006) and Dindo *et al.* (2008)

Figure 1. Three principal diffusion experiment designs. (*a*) Open diffusion with one model seeded in each group and all members free to observe, learn or not; (*b*) replacement method with an experienced individual replaced by a naive one at each step; (*c*) linear chain with order of any transmission determined by experimenter. (i,ii) (corresponding to the designs described in row 7 of table 2) Seeding with a model acting in different ways (shaded); (iii) a no-model control group limited to individual learning. Arrows illustrate hypothetical diffusion of information, beginning with seeded model 'A'.

generations' that are experimentally imposed, unlike in the open diffusion approach. However, at each step, one naive individual replaces one of a group of experienced individuals, so that in this respect there are resemblances to the open group context; the experimenter will not necessarily know from which of the available models the novice learns, or if it learns from several; and again, the more experienced individuals may be influenced by how the later recruits behave. The replacement method can thus be regarded as something of an intermediate design, lying between the open group and linear chain approaches in our table (table 2 and figure 1).

One important aspect of this method is that if the animals being studied are influenced by the number of models they witness, being predisposed to 'copy the majority' (a form of conformity, discussed further below), then positive social learning effects might be documented by a replacement approach, yet missed in a linear design that fails to sufficiently stimulate the social learning mechanisms available. In general, the replacement approach provides a good model of natural situations in which there is gradual turnover in a group. A human example is in the present issue (Caldwell & Millen 2008).

(**b**) *Experimental conditions designs*

In the seven rows of table 2, we distinguish what we call 'conditions designs' on the basis of the experimental and control conditions applied. Each of rows 2–7 includes the introduction of a model, usually a trained one but sometimes capitalizing on the natural emergence of an innovator. Whether we have successfully captured all of the relevant published studies in the present paper or not, the criteria for inclusion of a study in each of these rows appear quite clear.

The same cannot be said of row 1, where the experimental approach is the most minimal, simply offering novel learning experiences in such a way that if an innovation occurs, its potential subsequent spread can be systematically tracked. In this row we have included studies that express this intent. For example, Paquette (1992) gave four chimpanzees the opportunity to use tools to dip for honey in an artificial 'termite mound' and recorded the emergence and spread of this behaviour. However, it could be argued that many other studies of the spread of behaviour patterns, not included here, share essential features with those listed in row 1. For example, the original Japanese macaque 'preculture' studies documented the spread of behaviour patterns elicited by novel learning experiences, such as washing human-supplied foodstuffs (Kawai 1965). Studies in table 2 are differentiated from these by the authors' intent to conduct an experiment tracing diffusion, but the evidence for social learning remains only of the weakest, circumstantial kind, owing to a lack of any control condition where social learning is not possible. In the Paquette study referred to above, for example, we cannot be sure that the spread of the dipping behaviour was not simply the result of each chimpanzee developing this on its own account, rather than through observing those already dipping for honey. Our principal interest in the present paper is thus in the lower rows of the table.

Broadly, as we further descend the rows of table 2, the power of the experimental designs to identify social learning, and in turn cultural transmission in the spread of the behaviour of interest, is enhanced. Row 2 differs from row 1 in that a known model is seeded, providing added focus about what behaviour pattern is to be subsequently tracked. However, the absence of a comparison with a control condition where there is no model means that evidence for social learning here still remains weak (see table S1 in the electronic supplementary material for details).

Row 3 is the first where we see the incorporation of a control condition for individual learning, in this case through an initial baseline phase of exposure to the problem of interest, before subjects witness a model in the experimental phase. As in the case of the original ape and avian experiments of Menzel *et al.* and Curio *et al.*, respectively, where responses changed dramatically between baseline and social learning conditions, compelling evidence of cultural transmission can here be obtained. However, the use of a baseline as the reference condition may remain weaker in some other contexts, wherein the behaviour is more likely to appear through exploration the longer the period of exposure; this may be the case for solving novel foraging problems, for example.

Row 4 overcomes this limitation through a between-subjects design: an experimental condition where seeding via a model takes place and with a separate control condition where no such model is available. Studies in this row thus have the power to provide clear evidence of social learning. Of course, whether cultural diffusion was found in each of these studies is a different matter, and indeed the extent of cultural spread documented varies across the studies. The important point for now is that the method has the capability to determine the extent of any cultural diffusion that occurs.

Rows 5–7 list studies that expose each of two populations to different models. This is an approach borrowed from dyadic studies of social learning particularly concerned to identify imitation, as opposed to simpler forms of social learning (Heyes 1996). The idea here was that whether subjects that observe a model using either a behaviour pattern A or pattern B subsequently show a significant tendency to preferentially match the pattern they saw, imitation is implicated. In the context of diffusion experiments, this kind of discriminatory power can be contrasted with the approach seen in row 4, where there is just one experimental and one control condition. Where a behaviour pattern spreads only in the experimental condition, we have good evidence the cause is social learning. However, the social learning could be of the simplest kind. For example, Laland & Plotkin's (1990) study demonstrated in this way that carrot digging by rats diffused socially along a chain of eight steps. However, the rats did not necessarily learn about digging: perhaps they learned only that there was buried food available. By contrast, in a design of the type shown in rows 5–7, the diffusion may start with two different techniques to recover the food: and if these each diffuse with significant fidelity, we know that the social learning is sophisticated enough to involve some degree of replication or copying of these alternative forms of behaviour. For example, Whiten et al. (2005) exposed groups of chimpanzees to either of two types of tool-based foraging techniques and found that each spread with significant fidelity in the group they were seeded in, creating different traditions.

However, each of any such pairs of techniques may be latent in the animals under study, and be merely elicited through witnessing a model (contagion). Conditions 6 and 7 therefore add the refinement of controls for individual learning—a baseline procedure in row 6 and a between-group control in row 7, paralleling those involved in the one-model designs of rows 3 and 4. For example, in the study of Whiten et al. (2005) noted above, chimpanzees exposed to the problem without benefit of a model failed to solve it, indicating that in the experimental conditions the different techniques spread to become local traditions because individuals acquired the techniques by observational learning.

In these respects, the approaches identified in rows 6 and 7 represent the most powerful designs so far developed for the experimental investigation of cultural transmission, and we advocate that in future they should be adopted wherever possible. The two could even be juxtaposed, using both baseline and between-group

controls to identify the role of social learning in particularly rigorous fashion.

Having said that, a final word in this section should be said in support of one aspect of the approach illustrated in row 1. It is important to remember that cultural processes must rely on both social learning and on innovation (Reader & Laland 2000). Only once innovations emerge can social learning drive the spread of new cultural variations. In table 2, the lower rows represent the more powerful means of identifying social learning and row 1 lists the weakest; however, the approaches in the lower rows all depend on the experimenter creating, through training or other means, the initial innovation. Thus, these procedures really focus on identifying just one 'side' of the culture process, social learning. Perhaps, with ingenuity, it may be possible in the future to combine the key elements of row 6 or 7 with the element of spontaneous innovation that is in play in the works listed in row 1. In the present issue, McElreath et al. (2008), in human studies, has offered a different approach to dealing with important, spontaneously generated social information.

4. THE SCOPE OF DIFFUSION EXPERIMENTS TO DATE: METHODS, TAXONOMIC COVERAGE AND TYPES OF BEHAVIOUR STUDIED

Inspection of table 2 shows that some of the methods distinguished remain to be exploited by more than a handful of studies. Among the main transmission designs distinguished in columns A–C, open diffusion is the most common with 23 studies, whereas replacement and linear chain designs account for only five and six studies, respectively. Moreover, several cells in the table, denoting the intersection of specific transmission designs with specific condition designs, remain empty. We count only 11 studies that have employed the most powerful condition designs (rows 6 and 7).

Taxonomic coverage shows a primate focus typical of the field of social learning: there are 17 primate studies (12 of them on chimpanzees) but just 4 on other mammals (all rodents) and only 7 and 6 on birds and fishes, respectively. However, the extent of the primate bias is a very recent phenomenon: in fact, until 2005 none of the approaches with control conditions (rows 3–7) had been extended to primates.

There is a marked homogeneity in the types of behaviour that existing studies focus on. The early study of Curio et al. remains the only one concerning responses to predators, that of Menzel et al. the only one on habituation to alarming objects. The two avian studies by Freeberg and colleagues concern courtship, focusing particularly on vocalizations. The bulk of the studies—the other two dozen—all concern foraging behaviour (including drinking behaviour and ingestion of putative medicinal items), in nine cases through the use of tools.

In sum, the present corpus of studies is patchy and uneven in its coverage of methods, taxa and types of behaviour. Nevertheless, the field has generated a sufficient diversity of methods and findings to populate a table already as elaborate as table 2, providing a working map of the variety of methodological routes that further investigations may consider following or

surpassing, as well as the areas where there is still a low density of coverage taxonomically and behaviourally.

The limited size and uneven distribution of the existing corpus of diffusion studies make it premature to attempt any very systematic comparative analysis of the findings they have generated. However, some initial generalizations and repeating themes are worth highlighting at this stage.

5. PRINCIPAL QUESTIONS ADDRESSED
(a) *How well do traditions spread in the species and context studied?*
The primary question driving all diffusion studies is essentially about how well the seeded behaviour patterns do or do not spread. If they spread, are they maintained at the levels seeded, or are they instead degraded or corrupted in some fashion, or even lost altogether at some point? That these basic questions are those of the studies to date is no doubt due to the youth of the field, and contrasts with the wider range of questions tackled by studies with human subjects (Mesoudi & Whiten 2008). In human studies the existence of cultural transmission is of course already assured, whereas for the animal studies this remains the core issue.

Questions about the success with which seeded behaviours are transmitted will be addressed in different ways according to the transmission design. In the case of linear chains, one can count the number of transmission episodes through which the behaviour of interest passes, at levels significantly above those of baseline or other control conditions, and/or one can examine the fidelity to the founder patterns as the chain proceeds, as Flynn (2008) has done for children elsewhere in this issue. In the case of replacement studies, one can proceed in a similar fashion as successive replacements are examined. In open diffusion studies, however, it may be difficult or impossible to enumerate the number of transmission events; instead, one can consider the extent to which seeded behaviour spreads across the groups studied and whether behavioural mutations emerge.

In surveying the results of the studies from this perspective, we focus on rows 3–7, where the incorporation of controls allows relatively clear answers to be given to questions concerning social transmission.

(i) *Linear transmission chains*
We address studies using this design first since it gives the most direct answer to the question of fidelity of transmission across cultural generations. Interestingly, a majority of the studies of this kind have demonstrated statistically significant diffusion relative to control conditions along all or most of the chains. This fidelity has also been maintained along all or most of the chain steps tested in the studies (chains have included up to four (Dindo *et al*. 2008), six (Curio *et al*. 1978*a*; Horner *et al*. 2006) or eight steps (Laland & Plotkin 1990, 1992, 1993)). These studies involve an eclectic mix of species (birds, rats and primates) and behaviour patterns (mobbing and varied aspects of foraging). The latter, coupled with the small numbers of studies completed, means that no substantial comparative

conclusions are yet warranted. The focus has been to establish whether a functional degree of fidelity of transmission is maintained along significant chains for the species and task examined.

(ii) *Replacement 'chains'*
There are just five replacement studies completed with fishes, rats and primates but they include some of the higher numbers of transmission steps, in this case counted as the number of replacements made. However, in such cases, it is not so straightforward to denote how many cultural generations or transmission episodes are involved. How long it takes for a group to completely replace its cultural ancestors depends on the size of groups and how many are replaced at each step. In the study of Menzel *et al*. (1972) for example, 17 replacements were completed, creating a series in which six successive sets of trios, each involving different chimpanzees, existed over time (as in the first and the last of the initial series of individuals 123, 234, 345, 456) and the habituation to novel objects that were built up by the replacements 4–8 (depending on the stimulus) were maintained throughout the remainder of the transitions. In the rat diet study of Galef & Allen (1995), 14 consecutive replacements likewise generated four entire group replacements over the course of the study and the differential dietary (flavour) preferences of the rats were sustained, although it waned throughout this period.

Laland & Williams (1997) likewise showed that over seven replacement episodes, preferences of guppies to adopt one route over another were sustained, although they waned in their magnitude. In this case, approximately half the difference between the two experimentally initiated preferences for one route over the other eroded over this period, suggesting that such alternative traditions would no longer exist after roughly twice this many transitions.

The extent to which animal traditions are transitory or sustained in the long term are of paramount theoretical significance. The answer in any one case is likely to depend on a multitude of factors, including the behavioural and psychological constitution of the species, the nature of the behavioural features (as simple as diet choice, for example, or as complex as use of a tool set), spatio-temporal variance in the environment and the costs and benefits of the behaviour relative to alternative options. This has been little addressed so far, but an illustrative, systematic attempt was made by Laland & Williams (1998), working with guppies. These authors compared the sustainability of traditions across seven replacements in which fishes had a choice of two doorways to travel through, each coupled with either a short route to food or a route that was three times longer and thus more costly. When the routes were short, the founder fishes' trained preferences for one door over the other were strongly maintained over the seven replacements, but when the routes taken were maladaptively long, the alternative traditions steadily eroded and were non-significant after five replacements.

(iii) *Open diffusions*
Open diffusion experiments provide important information about the extent to which traditions spread across

potential recruits, and how much loss or corruption occurs in relation to the founding behaviour patterns.

The studies available in this category (column A, rows 3–7 in table 2) reveal extensive variation in these respects. At one extreme, Whiten *et al.* (2007) documented the spread of two alternative foraging techniques first to each of two groups of chimpanzees, and then to two further groups in each case without corruption to the alternative technique. One technique spread across a total of 24 individuals, with only 4 others never succeeding in mastering the task. At the other extreme, Gajdon *et al.* (2004) found no evidence of uptake and transmission of a novel foraging technique by wild keas exposed to a founder model, despite the trainability of this (wild) model and the readiness of captive birds to acquire the technique. Other studies found intermediate degrees of spread (table 1, and table S1 in the electronic supplementary material). The factors that determine the extent of spread are important theoretically but remain little studied as yet. They should be priorities for future studies building on the foundation of the first tranches of studies reviewed here.

(b) *What are the underlying social learning mechanisms?*

Diffusion experiments are designed primarily to answer questions about whether behavioural variations spread and how faithfully they do so, rather than what social learning mechanisms are responsible. The latter may be regarded as an orthogonal, but important supplementary question to the more basic one concerning the extent to which cultural transmission is experimentally demonstrated in the first place. If transmission is demonstrated, it may in principle be due to a range of alternative learning mechanisms that then become of interest.

At first sight, this principle may appear to conflict with our earlier statement that the two-action procedures described in rows 5–7 of table 2 can discriminate some of the most basic processes that might underlie diffusion. For example, Whiten *et al.* (2005) found that in one chimpanzee group seeded with a model that used a 'poke' tool-use technique to release food trapped in a 'pan pipes' foraging device, this technique spread, but it was not discovered by a control group that saw no model. That result by itself equates to the designs listed in row 4 of table 2. It demonstrates diffusion due to social learning. However, the social learning could be of the most basic kind, in which the observer had merely learned that a tool could be used to extract food, and they then applied a method already within their repertoire to achieve this. By contrast, the introduction of a model employing a different ('lift') technique into a second group, where this alternative technique spread preferentially (Whiten *et al.* 2005), implicates a more structured social learning process capable of producing copies of the poke and lift techniques. An additional no-model control condition in which chimpanzees performed neither technique showed further that what the naive chimpanzees learned involved more than merely eliciting an existing functional response.

The two-action methods of rows 5–7 thus tell us something about the nature of the social learning in

operation. Nevertheless, this is limited to a fairly crude specification. Numerous alternatives known within the social learning literature (Whiten *et al.* 2004) might be operating and the diffusion experiment itself is largely mute on which are involved. One approach taken by a few investigators has been to complete a group-level diffusion experiment and then, if cultural transmission has been demonstrated, to use separate, dyadic experiments to tease out the mechanisms involved. In the case of the pan pipes study described above, 'ghost experiments', in which the relevant tools and other objects were experimentally operated without the agency of a chimpanzee model, showed that observers were not able to learn to emulate these physical effects, suggesting that imitation of the actions of a model is more likely involved in the diffusions documented earlier (Hopper *et al.* 2007). In similar fashion, Lefebvre (1986) demonstrated diffusion of pecking through covers to access grain among pigeon flocks, and in separate dyadic experiments Palameta & Lefebvre (1985) showed that watching another bird execute the piercing and feeding was significantly more effective than observing piercing behaviour alone.

Incorporating such investigations directly into the conduct of a diffusion experiment is more challenging and has been attempted little to date. Perhaps the only good example so far concerns the diffusion of food flavour preferences demonstrated in rats by Laland & Plotkin (1993). These authors went on to show that diffusion was facilitated both by gustatory cues on the rats' breath and by excretory cues, and that these factors can interact to produce more robust transmission. We encourage further studies that experimentally dissect learning mechanisms within an ongoing diffusion in this fashion, rather than separately.

(c) *Comparative and evolutionary analyses of the content of cultural behaviour*

Elsewhere we have recently offered broad-ranging analyses of the relationships between biological and cultural evolution (Mesoudi *et al.* 2006) and the comparative scope of cultural phenomena in humans and non-human animals (Whiten *et al.* 2003; Whiten 2005). Here our comparative focus is the tighter one of diffusion experiments.

If we focus only on transmissibility, there is considerable comparability of findings across the fish, bird and mammal studies reviewed here. Some of the longest chains demonstrating fidelity of transmission are in the fish and bird studies (see table S1 in the electronic supplementary material for details). This suggests that human culture, although of course vastly more complex than anything seen in non-humans, may have evolved from a biological base that supports the social transmission of information in widespread ways among vertebrates.

However, when we look more closely at the content of what is transmitted, we note significant differences between major taxa. The fish studies all concern the following of a particular route, and whether this requires social learning in the full sense can be questioned. Although the naive fishes in these experiments are often described as 'observers' and the experienced ones as 'demonstrators', there is no evidence that the former

learn from the latter by observing what they do: rather, the fishes have a preference to shoal together and so the naive fishes come to learn the route they follow (by individual learning) as they swim along with the experienced fishes. This appears to fit what Whiten & Ham (1992) denote as 'social influence', rather than 'social learning' in which naive individuals learn directly *from* models (e.g. by observing what they do). However, this means that the studies of Laland & Williams (1997, 1998) are interesting in showing that even such social influence can be sufficient for the diffusion of traditions of route choice.

Among the bird and mammal studies there is evidence of observational learning, as when particular foraging techniques are acquired. There appears to be broad comparability between the experimental diffusions involving birds learning to open flaps (Langan 1996), rats learning to dig up hidden food (Laland & Plotkin 1990) and primates learning to open 'artificial fruits' (Horner *et al.* 2006; Dindo *et al.* 2008). Diffusion through such forms of observational learning thus appears to reflect a functionally important and fundamental capacity shared with much of human cultural transmission (Hurley & Chater 2005).

Two ways in which the primate studies go beyond those in other taxa appear worth remarking on so far. In chimpanzees, these have involved extensive diffusion of (i) different kinds of tool use (Whiten *et al.* 2005, 2007) and (ii) techniques that involve hierarchically organized sequences of different subcomponent actions (Whiten *et al.* 2007). Each of these may reflect more specific shared cognitive ancestry with humans, although the corpus of studies available remains so small that until more comparative studies are completed these must remain as only tentative hypotheses.

6. CONCLUSIONS

Given the state of the field reviewed, we see a principal contribution of the present paper as methodological, systematizing the current corpus of diffusion studies in the manner summarized in table 2. A majority (15) of the 3×7 array of options we distinguish there correspond to one or more of the small set of published studies, although these are inevitably spread thinly across the table, as yet.

We think the distinctions among the columns and the rows in the array we have arrived at are of differential significance. On the one hand, each of the three transmission designs corresponding to the three columns has made an important contribution to our understanding; indeed, an ideal study can now be seen to profitably apply all three in turn, for each offers different and complementary information, as has been discussed. By contrast, when we turn to the rows in the table, we conclude that the lower ones, particularly 6 and 7, offer greater analytical power than those above and in general should be preferred for future studies.

However, we note that by far the majority of the studies so far have been completed in captivity that limits the validity of the field as a whole. This may be another correlate of the youth of this field, but ethology has an illustrious history of field experiments and it is to

be hoped that as their methodological and theoretical significance becomes better appreciated, the future will see more diffusion experiments completed in the wild. This will require better solutions to the practical and logistic difficulties entailed, such as training alternative models without observation by other group members. Tables 1 and 2 list only three such field studies and we note that in contrast to the overwhelming proportion of positive diffusion results for the captive studies, two of the three field studies found no (Gajdon *et al.* 2004) or restricted (Langan 1996) diffusion from the models so industriously introduced into the wild populations. The existence of only three field experiments is too few to elicit real concern over a laboratory/field mismatch, and in any case Lefebvre (1986) found more extensive diffusion in feral than captive pigeons, so the negative outcomes may be the result of contextual factors that are not yet well understood. More field experiments are clearly needed.

Beyond the current set of demonstrations that cultural transmission can be experimentally established in a wide variety of species and types of behaviour, our conclusions about similarities and differences in the forms this takes across animal taxa must be viewed as very tentative. Above (and in detail in table S1 in the electronic supplementary material) we summarized the current picture for fishes, birds, rodents and primates as it currently appears, suggesting both that elementary forms of cultural transmission are widespread across this taxonomic range, and that more complex contents and mechanisms are identifiable in the avian and mammal studies, particularly in the primate ones where they extend to tool use and more elaborate manipulative and foraging techniques. This pattern suggests a series of phases in the evolutionary elaboration of cultural transmission that paved the way for human culture. However, the principal function of this paper is to provide a first overview of the contribution of diffusion experiments that can guide future research in this area in a more informed fashion. We expect diffusion experiments to provide an increasingly productive and robust bridge between observational studies of animal cultures in the wild, the extensive and well-established field of dyadic social learning experiments and the literature on human diffusion experiments illustrated elsewhere in this issue.

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