

## **Cultural diffusion in humans and other animals**

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Recent years have seen an enormous expansion and progress in studies of the cultural diffusion processes through which behaviour patterns, ideas and artifacts are transmitted within and between generations of humans and other animals. The first of two main approaches focuses on identifying, tracing and understanding cultural diffusion as it naturally occurs, an essential foundation to any science of culture. This endeavor has been enriched in recent years by sophisticated statistical methods and surprising new discoveries particularly in humans, other primates and cetaceans. This work has been complemented by a growing corpus of powerful, purpose-designed cultural diffusion experiments with captive and natural populations, that have facilitated the rigorous identification and analysis of cultural diffusion in species from insects to humans.

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## Highlights

- Decades-long field studies yield evidence of widespread animal cultures
- New statistical approaches track the cultural diffusion of animal innovations
- From insects to primates, diffusion experiments rigorously confirm cultural diffusion
- Sophisticated statistical approaches trace human cultural diffusion on micro and macro scales
- Diffusion experiments analyze the what, who, when and how of human transmission

## **Introduction**

At the core of the phenomenon of culture, whether in humans or non-human animals (henceforth ‘animals’), are processes whereby entities including behaviour patterns, ideas and artifact designs spread between or within generations, maintaining some recognizable consistency of form. Such entities are often described as ‘traditions’, and the underlying social learning processes as ‘cultural diffusion’ or ‘cultural transmission’ [1-4]. The field has expanded enormously in recent years, often driven by methodological advances and maturing long-term field studies, generating multiple major advances [1-9].

These have often highlighted increasingly strong links between animal and human phenomena [1,2,8,9]. However, the unique aspects of human culture remain sufficiently distinctive that we review animal and human studies in turn.

### **Cultural Diffusion in Animal Field Studies**

As long term field studies have matured in recent decades, putative cultural differences between subpopulations have been delineated, particularly in avian, cetacean and primate species [8-10]. These typically reflect stable patterns, so opportunities to record the actual diffusion of spontaneous innovations are rare. However, cases have begun to be published.

The cultural basis of some have been identified through new techniques of ‘network-based diffusion analysis’ (NBDA), in which diffusion following the lines of social networks implicates transmission via social learning from close associates [11,12]. Pioneering examples include tracing of the diffusion of ‘lob-tail feeding’ from its first occurrence in humpback whales, to its spread along networks among 653 whales over 27 years, based on over 73,000 observations [13: see Figure 1]. At the other extreme, the invention and diffusion of using moss as a tool for sponging water by wild chimpanzees was tracked across a sequence of just days by a variant of this network-based technique [14,15].

\*\*\* insert Figure 1 about here \*\*\*

Diffusion has also been inferred from inter-group transfers. A recent example among chimpanzees is the spread of a novel form of ant-fishing from one community to its neighbours [16]. By contrast, female chimpanzees in the Tai Forest moving to a neighbouring community were shown to conform to local preferences in the selection of hammer materials for nut-cracking [17]. A major question is thus what throws the switch between incomers conforming, and incomers' behaviour instead being adopted by residents [15]. A recent striking example of the conformist alternative in the vocal domain is immigrant chimpanzees converging on local 'referential' vocalization styles that signal high-quality foraging options [18].

A dramatic contrast to the conservatism suggested by many studies of animal culture also comes from the vocal domain. The songs of humpback whales are similar across large areas of ocean, yet may change and diffuse rapidly, constituting 'cultural revolutions' [19]. Recently such changes have been observed to diffuse across the Pacific ocean like 'cultural ripples' [20]. Songs originating near Australia in 1998 and 2002 spread to French Polynesia by 2001 and 2004 respectively, being recorded at four intermediate locations in between.

### **Animal Cultural Diffusion Experiments**

It is often difficult to confidently identify a causal role for social learning in observational field studies, whereas this is precisely what controlled experiments can do. Such experimental studies of animal social learning have a history of over a century, but for a long time involved only single subjects observing a single model. Relevance to the 'macro' scale of culture required a different approach, which later developed in three main forms [3-4]: (i) diffusion (or transmission) chains, that begin with a trained model and then follow a sequence in which observers successively become models for a next observer in the chain; (ii) open diffusion, where the means by which traits spread from trained models or spontaneous innovators is left open; and (iii) replacement designs where, over successive 'generations', some group members are replaced with naïve incomers. These designs each tell us something different and are complementary.

Whiten and Mesoudi [3] reviewed 33 animal diffusion experiments conducted from 1972 to 2008, spanning fish, birds, primates and rodents. The rate of such studies has since escalated, such that supplementary table S1 lists a further 30 experiments

2009-2015, extending the taxonomic coverage to insects as well [21]. There is a welcome increase in field experiments, from 3/33 in 2008 to 14/30 now. We cannot comprehensively review these studies here but Table S1 offers terse summaries of each study's contribution. Advances on several fronts deserve mention.

A first cluster of advances are methodological. The 2008 review [3] systematized the 33 experiments reviewed into a matrix structured by the three kinds of experiments outlined above, and seven different contrasts among experimental and control conditions. Studies were found to span as many as 15 of the resulting 21 cells in the matrix. It is noticeable that 27 of the 30 more recent studies have converged on one of the three approaches, open diffusion. This might suggest a developing view that this is the most valuable of the three, arguably representing many natural situations, such as when an individual with a novel skill immigrates into a new group. However it may simply be that diffusion chains (just 3/33 studies) can be hard to engineer in animals that have the potential for aggression between pairs put together, such as chimpanzees [22]. The open diffusion experiments are now commonly coupled with the strongest condition contrasts advocated in ref [3], which have two different behavioural options seeded in two or more groups (Figure 2), ideally with the addition of a no-model control condition.

\*\*\* insert Figure 2 about here \*\*\*

Perhaps most surprising is the absence of replacement designs in the present table, because these also represent a common scenario in real world animal groups shaped by immigrations, emigrations, births and deaths. However a new approach in some studies is to incorporate multiple models. At one extreme, all existing members of whole groups of monkeys were trained in food preferences, followed by testing of maturing naïve infants and immigrants with opposing preferences [23]. This revealed potent social learning effects [23] echoing the spontaneous conformity in chimpanzees noted above [17]. Similar findings have been observed in species as diverse as great tits [24] and drosophila [21]. Several field studies introducing only single models found more fragile social learning effects, so the multiple-model approach – which is

consistent with other evidence for conformity-to-majority effects in animals [25] – may repay more research in future.

Other pioneering methods advancing our understanding have included extending the use of video models to field conditions [26] and combining social network analyses like NBDA with diffusion experiments [24, 27]. Whilst as in 2008 most of the animal social diffusion experiments were addressing only the (fundamental) question of the capacity for cultural diffusion in the species and context studied, these newer studies analyzing social networks illustrate a shift to tackling the underlying decision rules. For example, squirrel monkeys central in the social network tended to be the first to participate in the diffusion of new behavioural variants [27] and chimpanzees preferentially learned from high ranking and knowledgeable group members [28].

### **Cultural Diffusion in ‘Real-world’ Human Populations**

Efforts to trace the diffusion and cultural evolution of human technologies, languages and other cultural phenomena have a history of well over a century, including historical, archaeological, anthropological and sociological studies spanning the whole gamut of the humanities and social sciences. Recent advances have been generated by the application of increasingly sophisticated statistical methodologies, in some cases derived from other scientific domains like evolutionary biology [1,2,6,7,29,30].

These have taken perspectives ranging from the ‘micro’, concerned with observable diffusion processes at the inter-personal level, to ‘macro’ analyses spanning large geographic areas and/or time scales that may extend to centuries. A pioneering recent example of relatively ‘micro’ analysis charted transmission networks for particular skills like fishing and herbal medicine in traditional village societies, finding a shift from learning from parents in early childhood to selective learning from relevant experts with age [31].

A longer-term perspective comes from archaeology, where the focus is on directly tracing records of diffusion over often large regions and timeframes. For example a recent study found that the S-shaped curve characterizing the slow, then accelerating, then plateauing diffusion of innovations identified in many more modern studies is also observed in prehistoric hunter-gatherer societies, exemplified in this case by the diffusion of pottery designs, but spread over several centuries across the western

Great Basin of America [32]. Shennan [33] and Lycett [34] offer up-to-date reviews of research of this kind and the value of an evolutionarily-informed approach to the archaeological analysis of cultural diffusions.

Other approaches search for the signatures of cultural phylogeny in present day cultural variation. One recent study targeted socio-political structures across SE Asia and the Pacific, finding evidence for the cultural diffusion and evolution of four escalating levels of political structure across this vast region [35]. Arguably the biggest strides have been made in cultural phylogenetic studies of language evolution, for example tracing language diffusion and evolution accompanying the migration of populations across this same Pacific region [36] and others [37]. On the grandest scale, such approaches based on over 500 languages have generated evidence for an African origin of all today's languages [38].

### **Human Cultural Diffusion Experiments**

Parallel to their review of animal studies [3], Mesoudi and Whiten reviewed 34 adult human diffusion experiments extant by 2008 [4]. Table S2 lists 61 more studies of this kind published since that review, confirming the explosion of interest and achievement in this area. Whilst only a handful of the animal experiments go beyond checking the capacity of the species concerned for cultural transmission, this can be assumed for humans and the human experiments go further in asking a variety of questions about the "what, who, when and how" of diffusion, extending a trend already apparent in 2008 [4: see Figure 3 for an example]. Perhaps the closest comparison between the two sets of studies comes from the addition of child experiments in the new human corpus, often following a similar design and rationale to the primate experiments and in some cases facilitating direct comparison [39-40].

\*\*\* please insert Figure 3 about here \*\*\*

The growing human literature defies comprehensive review in the space available here. Instead, we highlight some welcome developments that strike us. First, in addition to the incorporation of children [39-40 and Table S2], participation has been extended to overdue cross-cultural comparisons, finding more use of social learning in

East Asian samples known for their more collectivist attitudes [41]; moreover in several studies, marked individual differences in reliance on different social learning strategies and even in reliance on social learning per se, have been identified [42-44]. The content of what is transmitted has further diversified, ranging from the technical like tool use [39-40] and even flint-knapping [45] to the social, such as stereotypes [46] (see also Kirby, in this issue, on language transmission and evolution). By 2008, the “how” question concerning diffusion remained little tackled, but more recent studies dissect social learning into categories like imitation [47-49] and teaching [45]. Studies have also explored the effects of the size and nature of the pool of models from whom participants can learn [50-53].

In the growing suite of diffusion experiments examining the factors affecting cumulative cultural evolution in laboratory micro-societies [47-53], accumulation is generally expected to involve an increase in complexity or sophistication in the phenomena at hand, such as escalating heights of constructed towers [47]. However, the new corpus of diffusion experiments has been widened by several studies of communicative conventions, ranging from artificial languages [54] to graphical images [55] and here, the principal change along diffusion chains instead typically involves some kind of simplification or stylization that facilitates remembering, communication and transmission. A similar effect is the focus of a single animal study, to date [56].

### **Conclusions, Further Reading and Future Prospects**

The field is clearly in robust health and displaying a growing richness in scope and understanding of the cultural transmission processes active in our own species and others. Two recent edited volumes incorporate a diversity of reviews by many leaders in the subject and are recommended to readers who wish to further explore the scope and potential of recent studies of cultural diffusion [6, 57].

Future prospects for this field are accordingly expansive and as our review suggests, now have at their disposal an array of exciting new methodological approaches to exploit and elaborate on. However whilst as noted there is a welcome expansion of the power of experiments into wild and natural context in animal studies, laboratory studies dominate the human arena and there is much scope for researchers on humans to emulate experimental animal ethologists in creating more ecologically valid

‘field experiments’ [39-40]. More generally, it must be remembered that there are two essential components of cultural evolution; innovation and dissemination. Experimental seeding of the kind we have reviewed is perfect for elucidating the latter but by its very nature excludes the innovation element. Advancing ecological validity by bringing innovation into a more comprehensive experimental science of culture is a needed but challenging prospect.

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Uses 27 years of observation to track the spread of a foraging innovation from its beginnings; its spread along independently identified social networks implicates social learning, making it a compelling case of cultural diffusion.

\*\*[14] Hobaiter C, Poisot T, Zuberbuehler K, Hoppitt W, Gruber G: **Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees.** *Plos Biology* 2014, **12**:1-12.

Exploited a rare occurrence of an innovation in tool use (using moss to make sponges to obtain water from a pool) to track its spread across the group, following social network lines and confirming it as a case of cultural diffusion.

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Shows that differences in preferred natural hammer materials between neighboring communities that are not explained by available materials are adopted by females who typically migrate to other communities once sexually mature. The differences thus appear to represent local cultural norms that diffuse to immigrants, hence maintain inter-community differences.

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Chimpanzees employ grunts described as functionally referential when they signal differences in the quality of food sources discovered. A group of chimpanzees introduced into a Zoo community initially used recognisably different vocalisations for this purpose than the residents, but over time converged on the local vocal conventions.

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- Took the novel approach of training whole groups (instead of the usual single, seeded individual) to prefer one of two feeding options and investigated the effect on naïve infants and immigrant males. All infants adopted the preference of their mothers, and most surprisingly, males trained on one option and moving to a group with the alternative preference, immediately conformed to that local norm.
- \*\*[24] Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC: **Experimentally induced innovations lead to persistent culture via conformity in wild birds.** *Nature* 2015, **518**:538-541.
- Seeding different communities of wild great tits with alternative foraging behaviours generated consistent differences that endured across seasons. As in Ref [23], many immigrants conformed to the local norms: these two studies are the first to demonstrate this effect in wild primates and birds respectively.
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Combined two-action diffusion experiments with statistical modelling to reveal evidence for preferential learning from high-ranked and knowledgeable (successful) models, and biases towards social learning when of low rank or when uncertain.

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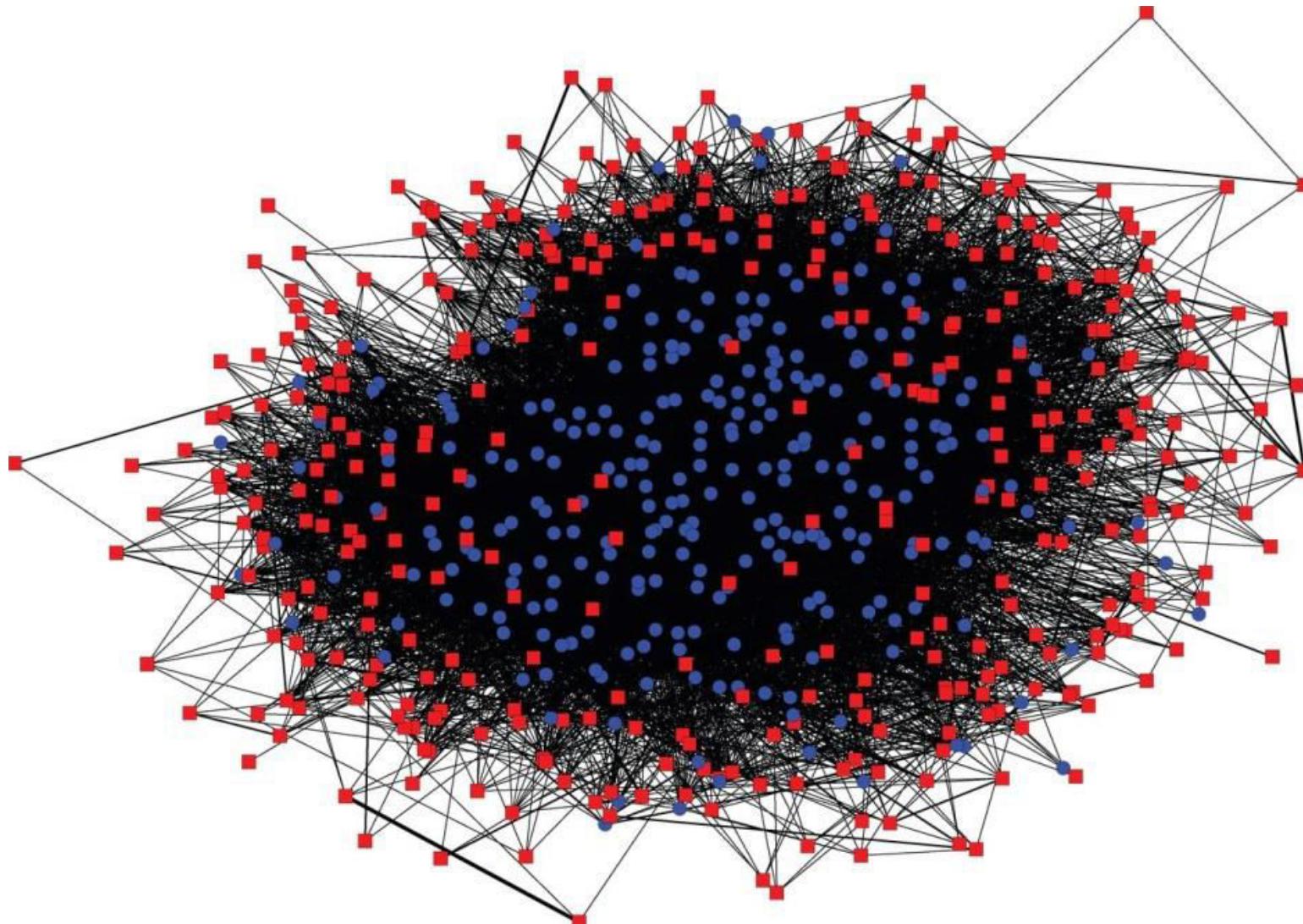
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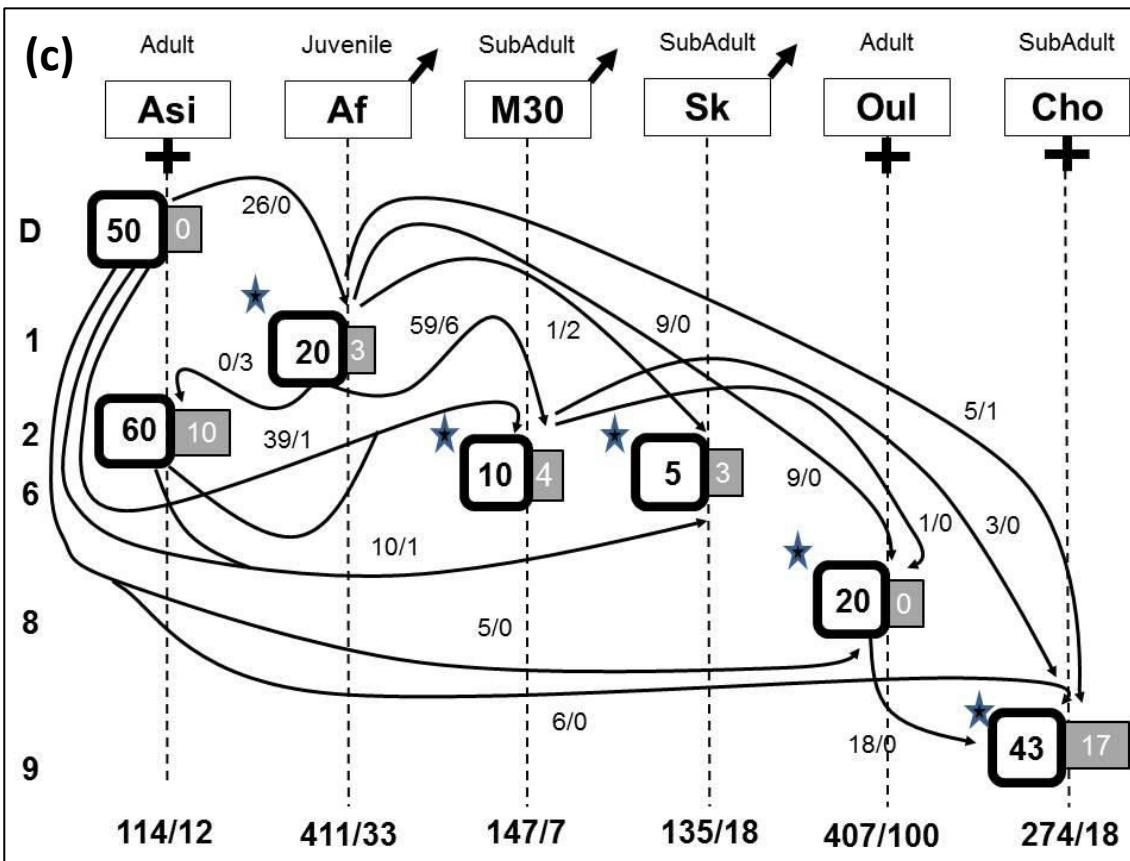
Figure 1. Diffusion of lob-tail foraging in a social network of humpback whales. Individuals close to the centre of the network plot are well connected with the others; blue nodes are those observed lob-tail feeding at least 20 times, red nodes those never observed lob-tail feeding. After Allen et al. 2013.

Figure 2. An ‘open’ diffusion experiment with wild vervet monkeys.  
 (a,b) Vervet monkeys opening an artificial fruit (‘vervetable’) by alternative methods of lift versus slide, seeded in trained models in different groups. (c) Inferred information flow through group AK, seeded with ‘lift’ approach. Each column represents one vervet and each row represents a session day (numbered), with entries diagonally left to right expressing each individual’s first opening techniques on the relevant session: on left in white box, number of lifts; on right in grey box, number of slides. The bold frame indicates the most common action in each case. Arrows tracked backwards show whom an individual had been in a position to observe before starting to open vervetables, and the relative numbers of ‘lift’ versus ‘slide’ they were thus inferred to have witnessed before their first successful opening, so arrow heads indicate inferred information flow. Numbers across the bottom of the diagram show the total frequencies of alternative actions in the whole series of sessions. Stars indicate whether the first action done was lift or slide. After van de Waal et al. 2015, cited in Table S1.

Figure 3. Cultural differences transmitted along laboratory diffusion chains: spaghetti towers created by participants in Caldwell & Millen (2010a, cited in Table S2). Each row displays the complete set of towers that were produced by one chain of participants. The towers are ordered from left to right, in the order in which they were produced (i.e. the first participant’s tower is on the far left, and the tenth on the far right).

Supplementary Tables S1, S2 – are in separate files.





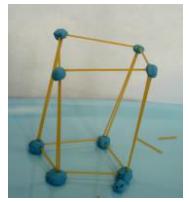
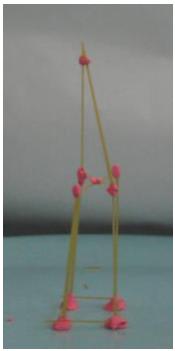
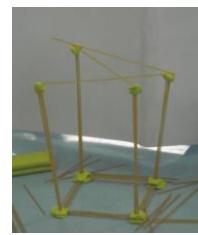
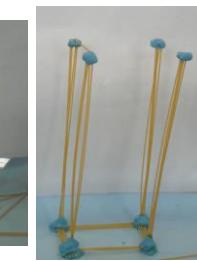
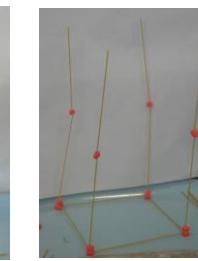
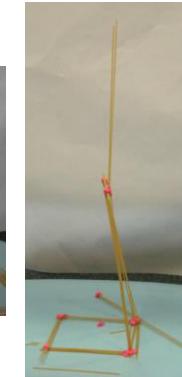
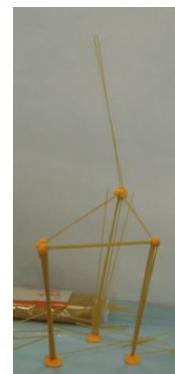
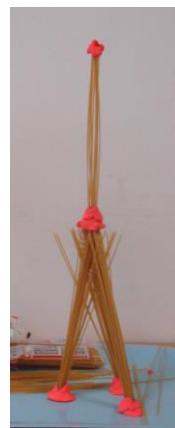
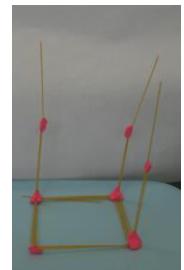
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Table S1. Cultural diffusion studies with non-human animals 2009-2015 (n = 30). \* = field study of wild subjects (n = 14); group seeded = open diffusion with trained model(s) seeded in group(s); chain = diffusion chain. Effects are reported when statistically significant.

authors	species	design	content and findings
Thornton & Malapert 2009a	meerkat *	group seeded	Wild meerkat groups were seeded with individuals trained to use one of two alternative landmarks to find food. Initially these spread in the groups to create incipient traditions, but individuals explored, discovered both alternatives and the differences eroded.
Thornton & Malapert 2009b	meerkat *	group seeded	Models were trained either to enter an apparatus by a flap, or climb to the top and break into a paper cover to obtain food. Individuals in three groups with each kind of model were faster to obtain food and tended to acquire the seeded method so that groups differed accordingly in their profile of foraging methods.
Dindo et al. 2009	capuchin monkey	group seeded	Monkeys in each of two groups seeded with alternative methods to open an artificial fruit primarily adopted the methods seeded, despite 17/21 successful monkeys discovering both of the two effective methods.
van de Waal 2009	vervet monkey *	group seeded	Trained opening of an artificial fruit by models either lifting one door or sliding another spread to others in the groups so long as the model was a resident female.
Kendal et al. 2010	ring-tailed lemur *	group seeded	An idiosyncratic technique to obtain food from an artificial fruit emerged in a subset of lemurs that were close associates, implicating social learning.
Horner et al. 2010	chimpanzee	group seeded	Trained posting of tokens in two different receptacles to obtain food by reliable high ranking models spread to others in preference to those posted by low ranking models.
Hopper et al. 2011	chimpanzee	group seeded	Trained trading of either of two types of tokens to obtain food spread to others even when the option shown gained less quality rewards.
Battesti et al. 2012	fruit fly	group seeded	Trained preferences for either of two ovipositing site flavours in 8 flies per groups spread to 4 naïve flies. This occurred even when neither option was flavoured and even when all flies had prior experience of both.
Hoppitt et al. 2012	meerkat *	group seeded	A complex statistical technique, 'stochastic mechanism-fitting model', was applied to behaviour following trained modelling of two alternative methods to obtain food from either of two boxes. Evidence of social learning included emulation, enhancement and effects on perseverance at the most commonly observed options.
Schnoell et al. 2012	red-fronted lemur *	group seeded	Individuals preferred whichever of two alternative techniques to open an artificial fruit was shown by a trained model in their group and in one of two unseeded groups a

			stable tradition focused on one technique emerged.
van de Waal et al. 2012	vervet monkey	group seeded	Four groups with model trained to open artificial fruit in each. Most used mouth to open fruit, but in group with model showing manual opening, this method spread to be more common; in group using cord to pull fruit apart, this likewise spread.
Dean et al. 2012	chimpanzee, capuchin monkey	group seeded	An artificial fruit with three escalating levels of difficulty and reward was made available. In conditions where models proficient in the highest level were introduced, these did not spread, unlike in children in parallel experiments.
Aplin et al. 2013	blue tit *	group seeded	Groups seeded with alternative foraging methods showed associated spread of the techniques. Differences in social learning disposition were correlated with innovativeness and social learning was stronger in females and juveniles.
Hopper et al. 2013	squirrel monkey	group seeded	Groups seeded with trained models pushing a door left or right to obtain food tended to adopt the method witnessed. Monkeys exposed instead to a ‘ghost control’ in which the door moved without an agent did not succeed in gaining rewards.
Claudiere et al. 2013	squirrel monkey	group seeded	Two groups with model trained to open artificial fruit by lift versus swing door. These methods spread differentially with a bias for those well connected in the social network to open the fruit earlier and use the method they witnessed.
van de Waal et al. 2013a	vervet monkey *	group seeded	Four groups with model trained to open artificial fruit in each. Methods of lifting door versus sliding left or right spread more commonly in the group corresponding to seeded model.
van de Waal et al. 2013b	vervet monkey *	group seeded	Whole groups were trained to avoid either pink or blue coloured maize corn made bitter. Naïve infants later tested with no bitter additive nevertheless copied maternal preference. Immigrant males switched quickly, conforming to new group preference.
van Leeuwen et al. 2013	chimpanzee	group seeded	Chimpanzees that had individually learned to use either of two alternative tokens to gain rewards, or in other experiments use either of two targets for tokens, did not change their token use when exposed to a majority using the other option (they did not conform to a majority) but did switch when the alternative yielded a great payoff.
Schnoell et al. 2014	red-fronted lemur *	group seeded	Some individuals in groups seeded with either of two methods to obtain food from an artificial fruit maintained the seeded preference over two years, others fluctuated in showing a preference or none, but none switched between preferences.
Boogert et al. 2014	starling	group seeded	The social network in perching but not foraging networks predicted the spread of either of two trained methods to obtain food.
Gunhold et al. 2014a	marmoset *	group seeded	Naïve individuals tended to adopt whichever of two alternative techniques to open an artificial fruit that the remainder of the whole group had learned X months earlier and

			maintained the preferences Y months later.
Gunhold et al. 2014b	marmoset *	group seeded	Groups seeded with alternative foraging techniques through video displays in the forest exhibited associated bias in spread of these.
Battesti et al. 2015	fruit fly	group seeded	Naïve flies exposed to flies trained to prefer one of two alternative oviposition sites adopted this in proportion to the extent of interaction with models, but models were also affected by interaction with untrained flies so that group differences eroded (c.f. Thornton and Malapert 2009a).
Aplin et al. 2015	great tit *	group seeded	Groups seeded with alternative foraging techniques exhibited strong bias in spread of these, extending to a second year. Immigrants tended to conform to local method.
Kendal et al. 2015	chimpanzee	group seeded	Statistical models fitted to the results of open diffusion experiments with two alternative techniques to obtain food seeded from trained models
van de Waal et al. 2015	vervet monkey *	group seeded	Replication of 2013 van de Waal et al. paper with wild vervet monkeys. Lift door and slide door methods spread preferentially in groups seeded with these methods.
Feher et al. 2009	zebra finch	chain	Isolates, unexposed to species-typical song during development, produced impoverished songs in adulthood. Juveniles paired with these adult isolates were then used as tutors for further juveniles. Songs evolved towards wild type in three to four such generations.
Lindeyer and Reader 2010	zebrafish	chain	Groups of fish tended to follow whichever of two escape routes was chosen by a trained model. Along transmission chains, escape responses were transmitted but choice of route decayed.
Dindo et al. 2011	orangutan	chain	Each of two different methods to open an artificial fruit (lift door versus slide door) spread preferentially along chains of five and six individuals respectively.
Claudiere et al. 2014	Guinea baboon	chain	Patterns of pixels on a screen remembered by subjects became the stimuli for next animal in chain. Patterns became progressively structured, described as cumulative cultural transmission. Different lineages developed different regular patterns.

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Table S2. Examples of cultural diffusion experiments with human participants 2008-2015 (n = 61). chain = diffusion chain; repl = replacement design; group seeded = open diffusion with trained model(s) seeded in group(s); group = closed group with no replacement and innovations relying on spontaneous emergence;. Effects are reported when statistically significant. Note the marked differences in the distributions of different types of experimental design between these human experiments and experiments with animals listed in Table S1.

<b>authors</b>	<b>design</b>	<b>content and findings</b>
Flynn 2008	chain	Children watching a single adult model are disposed to ‘overimitate’ even visibly causally unnecessary actions. However in child-to-child diffusion chains, such causally irrelevant actions were parsed out early as diffusion proceeded along the chain. But contrast differences in causally necessary actions were faithfully replicated.
Flynn & Whiten 2008	chain	Different techniques for tool use were transmitted with fidelity along child-to-child diffusion chains, more so in five-year-olds compared to three-year-olds and in boys compared to girls.
Griffiths et al. 2008	chain	Participants shown category exemplars were required to select a hypothesis from multiple possibilities regarding category membership. Selected hypotheses were used to generate exemplars for the next participant. Over generations probabilities of particular hypotheses shifted towards known human biases for category learning.
McGuigan & Graham 2009	chain	Irrelevant actions on a puzzle box were faithfully transmitted along chains of 3-year-olds for both opaque and transparent boxes. For 5 year-olds, irrelevant actions only persisted for opaque boxes.
Reali & Griffiths 2009	chain	Word-object associations were transmitted over generations, seeded with training data in which two words were paired with each object. Regularisation occurred over generations such that objects became reliably associated with one of the two words.
Hopper et al. 2010	chain	One of two alternative forms of tool use seeded by a trained model, spread along 20 “cultural generations” of children in a diffusion chain. Further experiments showed that merely observing the results of the technique was typically insufficient for the underlying social learning to take place.
Smith & Wonnacott 2010	chain	An artificial language that initially showed unpredictability in plural marking showed increases in predictability as it was transmitted along diffusion chains.
Xu & Griffiths 2010	chain	A series of four experiments including diffusion chains delineated the effects of prior memory biases on the reproduction of simple one-dimensional aspects of images.
Tan & Fay 2011	chain	Bidirectional social interaction was found to increase fidelity of transmission of narratives along diffusion chains, compared to a unidirectional, non-interactive context.
Kempe et al. 2012	chain	Handaxe images were transmitted along chains of participants instructed to copy their size exactly. Handaxe size drifted within bounds predicted by the inaccuracy of human perception.

Matthews et al. 2012	chain	Using a payoff structure intended to motivate participants to identify, and be identifiable to, their in-group members, identifiability of artifacts (tower designs) emerged over generations within chains originally seeded with random designs.
Eriksson & Coultas 2012	chain	Stories were transmitted with higher fidelity when participant hear the story from two demonstrators, compared to hearing the story twice from the same demonstrator.
Imada & Yussen 2012	chain	When transmitting narratives, chains of American participants retained more individualistic information and chains of Japanese participants retained more collectivist information, consistent with cultural values.
Kashima et al. 2013	chain	Stories transmitted over conversational communication chains retained more stereotype-consistent information, compared with stereotype-inconsistent information.
Xu et al. 2013	chain	Initially random labels for different colours gradually converged on a small number of terms that match naturally-occurring colour terminology systems observed cross-culturally.
Hunzaker 2014	chain	More negative stereotype-consistent statements were retained, compared with stereotype-inconsistent statements, in transmission chains which re-told narratives with negative outcomes, compared with positive outcomes.
Muthukrishna et al. 2014	chain	Chains with more demonstrators per generation maintain more complex cultural traits (tying knots and using an image editor).
Eriksson & Coultas 2014	chain	A disgust bias operates to favour the transmission of disgusting urban legends, and this bias operates at multiple stages of transmission (choosing to receive, encoding and retrieving, choosing to transmit).
Martin et al. 2014	chain	Information about novel social targets (aliens) was passed along chains. Gradually ‘stereotypes’ formed as a means of making the information more easily learnable.
Caldwell & Eve 2014	chain	Rates of change in the construction of spaghetti-and-plasticine towers (see Caldwell and Millen 2010) were reduced when participants were uncertain about the outcomes of later stress tests, and particular existing design styles tended to be preserved in this condition.
Kempe & Mesoudi 2014	chain	The opportunity to learn from multiple rather than single models enhanced the cumulative transmission of solutions to a puzzle.
Tennie et al. 2014	chain	In unseeded chains of children, tool choice (for rice transportation) was faithfully transmitted, with different tools preferred in different chains. In some chains seeded with an inefficient method the inefficient tool was rejected in favour of one used by the children in the unseeded chains.
Verhoef et al. 2014	chain	Twelve whistle patterns were transmitted, with combinatorial structure emerging over generations such that elements were reused as building blocks across different whistles, suggesting that iterated learning creates pressure for the combinatorial nature of human languages.

Oishi et al. 2014	chain	A hedonic story about a woman partying was transmitted marginally better than a non-hedonic story about a woman studying.
Miton et al. 2015	chain	Three studies showed that blood-letting as a medicinal treatment was transmitted better than other forms of therapy (e.g. emetic plants or ritual prayers), and certain features of blood-letting (e.g. that it is intentional rather than accidental) make it more likely to persist.
Moussaid et al. 2015	chain	Negative information about risks associated with an antibiotic was transmitted better than positive or neutral information.
Kempe et al. 2015	chain	In transmission of visual patterns along diffusion chains, children required more inherent structure to maintain similar levels of transmission to adults, and accordingly such structure emerged earlier in child than adult chains, an effect attributed to children's more limited cognitive processing powers.
Kirby et al. 2015	chain	Pairs of participants were trained on signal-meaning associations, and used these to communicate. Communicated signals were used as training materials for the next pair. Structured compositionality of signal systems increased with transmission in chains.
Stubbersfield et al. 2015	chain	'Urban legend' items were found to be transmitted more powerfully along diffusion chains when containing survival, and particularly social, information, predicted by evolutionary theory.
Tamariz et al. 2015	chain	Transmission of initially meaningless drawings ('squiggles') along chains tended to become simpler and more symbolic where they had to be remembered before reconstruction, whereas where direct viewing remained possible, they tended to retain the meaningless and form of the original.
Morgan et al. 2015	chain	Learners were assigned to one of five different regimes for transmitting along a diffusion chain the skill of knapping sharp flint flakes from a core. Those limited to imitation performed no better than in a baseline emulation condition, whereas various kinds of teaching facilitated significantly better achievements along the chain.
Caldwell & Millen 2009	repl	Chains of learners made paper planes designed to fly as far as possible. Chains achieved as much cumulative success when imitation was disallowed in the transmission process in favour of emulation based on viewing results only, challenging the idea that imitation is critical for cumulative culture.
Caldwell & Millen 2010a	repl	Different chains of learners building towers as high as possible using spaghetti and plasticine generated designs idiosyncratic to groups; those in a condition imposing uncertainty on the viability of towers under stress conformed most to a group design and showed less cumulative progress along the chain.
Caldwell & Millen 2010b	repl	Chains of learners made paper planes to fly as far as possible, in three conditions with varying rates of replacement and corresponding cohort size. Conditions with higher replacement rates and larger cohorts showed no advantage over smaller cohorts with lower replacement rates.
Caldwell & Smith 2012	repl	Iconic graphical signs passed along small groups subject to replacement changes became

		progressively simplified and tended to evolve into symbols as the process progressed.
Wasielewski 2014	repl	In apparent contradiction to the results of Caldwell and Millen 2009, the opportunity for transmission through imitation produced better evidence of cumulative culture than those limited to observing outcomes, in an unfamiliar, relatively opaque task of building a weight-bearing device.
Flynn & Whiten 2010	seeded group	This paper introduces the idea of child-based open-diffusion studies as described in detail in Whiten & Flynn 2010 and discusses the rationale and benefits of the approach.
Whiten & Flynn 2010	seeded group	An earlier study of cultural transmission of alternative tool use techniques in chimpanzees (Whiten et al. 2005) was replicated in child nursery groups. Groups seeded with alternative techniques initially generated different traditions but further exploration and innovation corrupted these; however new innovations then diffused, and overall most children copied the action type they witnessed most.
Flynn & Whiten 2012	seeded group	The influences of a variety of biographic, cognitive and social factors in the open group diffusion described in Whiten and Flynn 2010 were investigated. Social transmission effects including watching others more, being watched more and adopting witnessed actions were enhanced in older children and in more popular and dominant children.
McGuigan & Cubillo 2013	seeded group	Gossip was transmitted more frequently than knowledge items amongst groups of 10 and 11 year old children, especially by male sources. More dominant males tended to transmit to friends and less dominant males to others of higher peer regard.
McElreath et al. 2008	group	In a computer-based decision making task, participants exhibited a hierarchical strategy of first copying successful others (payoff bias), otherwise copying the majority (conformist bias).
Toelch et al. 2009	group	In a 3D maze task, participants tended to follow the routes of virtual demonstrators under conditions of low environmental variability, as models predict.
Fay et al. 2010	group	Within groups, individuals experienced repeated pairings with different group members, creating graphical ways of communicating concepts (see also Tamariz et al. 2014). This led to the creation of shared sign systems within groups, which varied between groups.
Toelch et al. 2010	group	Participants tasked with locating a reward in one of three locations tended to copy the choices of others that were rapidly increasing (a ‘copy-increasing-traits’ strategy).
Mesoudi 2011	group	Some participants copied the virtual artifacts of successful other participants (i.e. payoff-biased social learning) but only minority, the rest preferring to use individual learning.
Toelch et al. 2011	group	Participants who could view the high scores of other players in a 3D maze task showed greater exploration of the options than participants shown low scores or no scores.
Morgan et al. 2012	group	In a series of tasks that could be solved by social or individual learning, participants were more likely to copy others when there were more demonstrators, when the demonstrators agreed with each other,

		when participants were unconfident in their own judgement, and when individual learning was costly.
Atkinson et al. 2012	group	Participants chose to learn from models who had been viewed most by other group members, despite those looking times being fictional. Evidence of prestige-biased social learning.
Derex et al. 2012	group	Groups with access to process information (how to construct an artifact) outperformed groups with access only to the end product (finished artifact) as well as individual controls.
Derex et al. 2013	group	Larger groups maintained higher levels of cultural complexity in a virtual artifact-design task.
DiFonzo et al. 2013	group	Participants in groups exchanged opinions about rumours under conditions of uncertainty; rumours persisted over time, and homogenous clusters formed according to social network structure.
Wisdom et al. 2013	group	Participants assembled teams of creatures that competed in a league, with success dependent on the combination of creatures. Social learning enhanced both individual and group performance when participants could copy others' successful combinations (payoff bias).
Tamariz et al. 2014	group	Within groups, individuals experienced repeated pairings with others, creating graphical ways of communicating concepts like 'soap opera'. Evolving signs were influenced by an interaction between personal biases to use certain signs and experience of more effective sign content.
Derex et al. 2014	group	Groups of social learners in a between-group competition condition exchanged more information with group member, compared with a within-group competition condition. Both conditions performed better than an individual learning control.
Molleman et al. 2014	group	Consistent individual differences in participants' use of social information, with some focusing on demonstrator success and others on demonstrator behaviour.
Toelch et al. 2014	group	Participants who relied more on social information in computer-based decision tasks tended to score more highly on measures of collectivism.
DiFonzo et al. 2014	group	Participants exchanged opinions about group stereotypes (e.g. about Republicans and Democrats); stereotypes persisted more when participants were clustered according to those groups (Republican/Democrat) than when groups were not clustered.
Cook et al. 2014	group	Participants who relied more on social information in a computer-based decision task tended to score more highly on measures of social dominance (i.e. use of Machiavellian tactics to manipulate others).
Mesoudi et al. 2015	group	People from mainland China show higher rates of social learning than people from Hong Kong and the UK, and Chinese immigrants in the UK.
Derex et al. 2015	group	Groups of social learners outperformed individual controls in a virtual artifact-design task because they combine and transform information from multiple demonstrators.
van den Berg et al. 2015	group	Participants differ in social learning strategy: some show payoff biased social learning, others conformist social learning, with the latter more likely to cooperate in a social dilemma.

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