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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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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

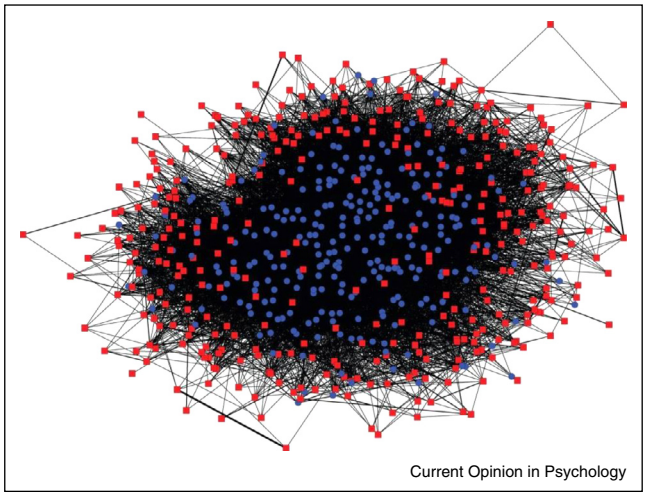
As long term field studies have matured in recent decades, putative cultural differences between subpopulations have been delineated, particularly in avian, cetacean and primate species [8–10]. These typically reflect stable patterns, so opportunities to record the actual diffusion of spontaneous innovations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

The cultural basis of some has 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].

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

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.* [13••].

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.

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•].