



# Do Animals Have Memes?

*[Simon M. Reader](#) & [Kevin N. Laland](#)*

Sub-Department of Animal Behaviour, [Department of Zoology](#)  
[University of Cambridge](#)

Madingley, Cambridge, CB3 8AA, UK.

Tel: +44 (0) 1954 210301, fax: +44 (0) 1954 210247

[smr1001@cam.ac.uk](mailto:smr1001@cam.ac.uk), [kn11001@hermes.cam.ac.uk](mailto:kn11001@hermes.cam.ac.uk).

## [Abstract](#)

### [1 - Introduction](#)

### [2 - Imitation and the meme](#)

### [3 - Reconstructed memes](#)

### [4 - Information versus phenotype](#)

### [5 - Birdsong: a special case?](#)

### [6 - Memes in non-human animals](#)

### [7 - Conclusions](#)

## [Acknowledgments](#)

## [References](#)

---

## Abstract

Imitation has been put forward as a defining feature of memetic transmission. Since there is currently poor evidence for imitation in non-human animals, such definitions have been interpreted as restricting meme theory to the study of human behaviour patterns and birdsong. We believe this is a mistake. Human capacities for imitation, teaching and language may well account for the extraordinary diversity of human culture compared with animal proto-cultures, but imitation is simply one mechanism of transmitting acquired information between individuals. As long as information is transmitted with sufficient fidelity to be replicated in the brain of the receiver, any social learning process will do. Non-human animals may be poor imitators, but many are excellent social learners. We argue that the meme concept can, and should, be applied to animal cultural transmission.

**Keywords:** social learning, cultural transmission, acquired information, animals,

imitation, replicator, meme.

---

# 1 Introduction

In her recent book *The Meme Machine* Susan Blackmore ([1999](#)) suggests that what makes humans special in comparison with other animals is our extraordinary capacity for imitation. According to Blackmore, imitation is the linchpin of meme transmission, and as evidence for imitation in animals is weak, humans alone can be regarded as possessing and transmitting memes.

In this article we present a counter position to Blackmore's, arguing that animals should be allowed the right to carry memes. We present our arguments, not as a criticism of Blackmore's position, but rather in an attempt to open up an informed debate over this interesting issue. We agree that evidence for non-human animals routinely imitating is weak, but argue that imitation need not, and should not, be the defining feature of a meme. Transmission fidelity, not the psychological process underlying transmission, is a determining feature of whether a meme can spread and replicate.

---

## 2 Imitation and the meme

The definition of the term 'meme' has been the subject of some controversy (e.g. [Rose 1998](#)). However, transmission of acquired information by imitation is a common element to many definitions. For example, a meme has been defined as "*an element of a culture that may be considered to be passed on by non-genetic means, esp. imitation*" (Oxford English Dictionary), as "*a unit of imitation*" ([Dawkins 1989](#), p.192), and as "*whatever it is that is passed on by imitation*" ([Blackmore 1999](#), p. 43). In these definitions the use of the term 'imitation' is frequently qualified by the phrase "*in the broad sense*" ([Dawkins 1989](#), p.194; [Blackmore 1999](#), p.7 and p.43). Indeed, Dawkins's first definition of the term appears to equate imitation with all kinds of cultural transmission processes ("*[a meme is] a unit of cultural transmission, or a unit of imitation*", [Dawkins 1982](#), p.192, reversed original italics), and includes examples of cultural transmission such as the spread of milk bottle opening in British tits ([Fisher & Hinde 1949](#); [Dawkins 1982](#), p.109). Other authors do not specifically address this issue, but use the term 'imitation' to refer to social learning processes in general ([Bonner 1980](#), p.18 & p.165; [Goodenough 1995](#)) and agree that animals possess memes ([Bonner 1980](#), p.188). Blackmore however explicitly excludes all non-imitative forms of social learning as capable of transmitting memes, and so, with the exception of birdsong, restricts memes to humans ([1999](#), p.49).

There is little doubt that animals regularly acquire learned information from one another. The term 'social learning' refers to learning that is influenced by observation of, or interaction with, another animal or its products ([Box 1984](#)). Experimental investigations have revealed that imitation is just

one of several processes that can result in social learning ([Galef 1988](#)). There exist numerous reports of novel behaviour patterns spreading through animal populations through social learning processes (for reviews see [Lefebvre & Palameta 1988](#) or [Galef 1988](#)). Famous cases include terming in chimpanzees ([Goodall 1964](#)), food washing in Japanese macaques ([Kawai 1965](#)), the opening of milk bottles in British birds ([Fisher & Hinde 1949](#)), dietary preferences in rats ([Galef 1996](#)), birdsong ([Jenkins 1978](#)), and fear of snakes in rhesus monkeys ([Mineka & Cook 1988](#)). In the majority of cases where the transmission process is investigated, behaviour patterns are not transmitted by imitation, but instead result from other, simpler processes such as local enhancement, where an animal's attention is drawn to an object by the actions of another, in a manner that results in learning ([Galef 1988](#)). Yet animals clearly have behavioural traditions based on acquired information transmission. Moreover, many of these animal traditions appear to change over time (e.g. [Gibbs 1990](#)) in a manner perhaps consistent with the predictions of memetic evolution.

So why do researchers place such a premium on imitation? It would seem that, for Blackmore, the key to memetic transmission is that something is learned about the form of a behaviour rather than about the environment ([1999](#), p.49). For example, Blackmore argues that milk bottle opening in British birds is not a meme since *"the tits already knew how to peck; they only learned what to peck"* ([Blackmore 1999](#), p.49, reversed original italics).

However, while in the past definitions of imitation have stressed the learning of a new behaviour through observation (e.g. [Galef 1988](#)), it is now widely recognised that imitation is not solely, and may rarely be, concerned with learning a new motor pattern: imitation is also concerned with learning the context and consequences of an established motor pattern ([Heyes 1993](#); [Heyes 1996](#), p.381). For illustration, consider the case of someone learning to play tennis through imitation. Here the apprentice is not learning to run, hold racket like objects, hit things or wave their arms around - all of the required motor patterns are already part of their repertoire. They are learning to move their body in a particular way (for instance, to move the racket towards the ball), at a particular time (when the ball is approaching), to generate a certain result (to hit the ball in the desired manner). The tennis playing meme is not exclusively concerned with motor patterns: it is a complex of information that also concerns the location appropriate for the behaviour, the objects with which one interacts, and the consequences of the behaviour. To take another example, this time the 'making pumpkin soup' meme described by Blackmore ([1999](#), p.61), we have a case where the recipient of the new recipe is not preparing food, cooking, or even making soup for the first time. The cook is simply carrying out an existing motor pattern (that of making soup) with an ingredient novel to the soup-making context but familiar in other contexts.

Exactly the same logic applies to the milk-bottle-top opening birds. They are not learning to peck any more than the tennis apprentice is learning to run around or hold rackets: that motor pattern is already part of their repertoire. They are learning to peck a particular object (the milk-bottle), found in a particular location (on a doorstep), to generate a particular consequence (the cream reward). Similarly, Japanese macaques are not learning to move their hands in water, they are learning that if they move particular objects (the sand-covered sweet potatoes) in water they can generate a desirable reward (that is, sand-free food). Imitation is not a criterion upon which the meme-carrying of animals and humans can be distinguished.

---

## 3 Reconstructed memes

A second, but related, objection to allocating meme status to animals is that in cases of animal social learning most or all of the meme is not transmitted, but rather reconstructed. To quote Blackmore once more, "*other forms of social learning do not support a replication system with true heredity, because the behaviour is not really copied*" (1999, p.50). To remain with the milk-bottle-opening example, current experimental and theoretical analyses (Lefebvre 1995; Sherry & Galef 1984) concur with Fisher & Hinde's original conjecture that the majority of birds have learned the behaviour pattern in some way from comparatively few individual innovators. There is no evidence that the birds transmit any more information than a tip-off that milk bottles contain cream (Hinde & Fisher 1951), but that is enough for each observer to reconstruct the behaviour of milk-bottle opening. Here it is the meme for milk-bottle opening that is transmitted, not the specific opening technique, which is quite variable even within individuals (Fisher & Hinde 1949). This reconstruction process is very different from the direct copying of DNA, and leads Blackmore to question whether it is legitimate to describe such a process as replication. Yet while this particular meme may not be directly copied, it none the less appears to be replicated with unerring reliability. The first report of milk-bottle opening was in Swathling near Southampton in 1921 (Fisher & Hinde 1949) and since then, it has spread throughout Britain, into several other European countries, across to tens of other species, and is apparently still prevalent some 75 years later. If fidelity in the form of reliable reproduction is a criterion upon which memes are judged, milk-bottle-top opening will surely qualify. It is highly likely that cream-drinking is just one element of these birds' socially learned foraging repertoire, implying that other feeding memes may have exhibited a corresponding decrease in frequency. There is no reason to think that the birds could not institute a mutant variation to exploit some other food source.

This raises a policy decision for memetics. Should reconstructed memes count as genuine memes? We argue that they should for two reasons. First, virtually all memes, including those of humans, involve an element of reconstruction (Sperber 1996). Humans when they imitate rarely do so perfectly, and they are typically forced to re-evaluate and adjust their behaviour in the light of sensory feedback (Piaget 1962; Yando et al. 1978; Custance et al. 1995). To argue that largely reconstructed memes are not memes would require an arbitrary and unenforceable rule to be employed regarding just how much reconstruction is allowed before acquired information qualifies as a meme. Reconstruction cannot be quantified in any meaningful sense. Second, reconstructed memes fit the Darwinian model as effectively as perfectly transmitted memes. They too can replicate and evolve, and to eliminate them on arbitrary grounds at this early stage in the science of memetics risks eliminating a large number, maybe even the majority, of interesting cases of social transmission that may benefit from memetic analysis. What counts is not how transmission occurs, but whether the product is similar in the transmitter and receiver - in other words, what counts (amongst other things) is fidelity (Dawkins 1989).

---

## 4 Information versus phenotype

A further criticism of memetic definitions based upon imitation is that emphasis is shifted from the transmission of information to the transmission of that which is imitated, i.e. behaviour patterns, or the memetic phenotype. Delius ([1991](#)) was explicit on the fundamental nature of this distinction, stating, "*memes stress the transmittence of coded information rather than of behaviour itself*". Delius defines memes as "*synaptic patterns that code cultural traits*" (where cultural traits are "*behavioural items acquired through social learning*"). Boyd and Richerson made a similar point, arguing, "*the essence of culture is encoded information rather than the behaviours that result from this information*" ([1985](#), p.43). This discrimination is important, since it seems entirely feasible that the same meme could produce very dissimilar behaviour patterns in different individuals or in different circumstances (see e.g. [Boyd & Richerson 1985](#), p.41-43), and that identical information could be learned from different behavioural performances ([Sperber 1999](#)). For example, the meme for making pumpkin soup could be transmitted by a perfect demonstration of the technique, or by a demonstration riddled with obvious mistakes. Prior knowledge of cooking would ensure that the meme for soup making was reconstructed accurately, without the inclusion of such mistakes.

---

## 5 Birdsong: a special case?

Although animals in general are frequently regarded as not having memes, researchers commonly make an exception of birdsong. However, learning a song does not involve learning a novel motor pattern, and would appear on the surface to be inconsistent with Blackmore's criteria for memes. Yet perhaps we are being pedantic, since the acquisition of birdsong involves the social learning of novel behavioural elements, if vocalizations can be regarded as such. Moreover, no doubt, most birdsong meme enthusiasts regard song learning as a form of imitation. Yet social learning theorists have long made a distinction between vocal and motor imitation ([Galef 1998](#); [Heyes 1994](#)). The former is regarded as a less challenging form of social learning, since there is a greater correspondence between the sensory feedback from the learner's own vocalizations and those of its tutors than in motor imitation, for which the sensory experiences of *doing* and *seeing others do* are typically very different. What is more, birdsong is a highly restricted form of social learning, different from the general capacity for social learning found in humans. The processes underlying song acquisition allow birds to learn song and nothing else. That is not to say that songbirds are incapable of other forms of social learning, but rather that these other forms probably rely on alternative mechanisms to song learning. Whatever the processes underlying birdsong, there is no evidence that they are more similar to the processes underlying human culture than other forms of animal social learning.

So why is an exception made of birdsong? We suggest two reasons, both unconnected to the psychological processes that underlie learning. First, Dawkins mentions birdsong in *The Selfish Gene* ([1989](#), p.189). Dawkins's authority carries a great deal of weight in memetics, and if he says birds have memes that is enough for many. Second, birdsong has been subject to some of the most elegant empirical work on memes (e.g. [Burnell 1998](#); [Lynch 1996](#); [Lynch et al. 1989](#)). It turns out that



birdsong lends itself to the meme concept beautifully, perhaps better than almost anything else, even human culture. We would welcome similar memetic analyses of other forms of animal social learning.

---

## 6 Memes in non-human animals

We end with three illustrative examples of cultural transmission in non-human animals to which meme theory may profitably be applied. First, an example from the apes. In a recent synthesis of long-term field studies of chimpanzees across Africa, Whiten et al. ([1999](#)) documented "*significant cultural variation*" after ecological explanations for this variation were discounted, with 39 different behaviour patterns identified that are traditional in some communities but absent in others. An earlier paper by McGrew ([1994](#)) reached similar conclusions. Whiten et al. ([1999](#)) argue that these behaviour patterns are most likely acquired by a mix of imitation and other processes that can result in social learning, but Whiten (personal communication) agrees that these different behaviour patterns can be classed as memes, as defined by the Oxford English Dictionary, especially in the sense that Boyd and Richerson ([1985](#)) emphasized. For example, the essential 'idea' of ant-dipping by the two-handed method used at the Gombe National Park has been observed in several successive generations, despite minor variations in its manifestations (Whiten, personal communication). Cultural variation has previously been identified only for single behaviour patterns in non-human animals, such as the local dialects of song-birds, and it may be possible to examine the dynamic relationships between the different memes which make up chimpanzee proto-cultures.

The meme concept need not be restricted to animals phylogenetically close to humans. In an experimental study, Curio et al. ([1978](#)) demonstrated that observer birds could learn to mob a non-raptorial bird, and even a plastic bottle, as a consequence of witnessing another bird mob at its presentation. This behaviour was transmitted along chain of six individuals, with each individual acting as a demonstrator for the next bird in the chain. Here a meme for the context in which mobbing is an appropriate response is transmitted. However, there were limitations to what could be transmitted. For example, birds did not learn to mob an empty cage, and learned to mob the plastic bottle stimulus less strongly than the bird stimulus. There may be similar restrictions on the successful transmission of human memes.

Third, an example from fish. Mating sites of the bluehead wrasse (a coral reef fish) have remained in daily use over 12 years (four generations) without changing location ([Warner 1988](#)). There was no obvious correlation of sites with resources, and many more potential mating sites available. Entire populations were experimentally replaced, and the transplanted populations chose new sites; but where females were transplanted to locations containing native females, the newcomers only mated at established sites, implying that tradition rather than resources is important in determining mating site location. After further experiments Warner proposed that these arbitrary traditions were probably transmitted by females following one another ([Warner 1990](#)), a very simple social learning process. Here we have an example of a long-lived, arbitrary tradition transmitted without imitation. Again, we can consider the mating site preference that each fish learns as a discrete, replicating unit of

information, and examine the diffusion dynamics of these memes.

---

## 7 Conclusions

We argue that a defining feature of a meme is that of a culturally transmitted replicator. The proposed memes in our examples show the three characteristic qualities of replicators detailed by Dawkins: copying-fidelity, fecundity, and longevity ([1989](#), p.194; see also [Dennett 1995](#), p.343). As such, these proposed memes seem as likely as any human meme to undergo evolutionary processes through heredity, variation, and selection. Hence we believe that memetics should not prematurely rule out these animals' memes. Indeed, animal social learning may be a useful testing ground for the meme concept. After all, it is entirely plausible that in future years animal social learning may eventually be judged to fit the meme model better than human culture.

---

## Acknowledgments

This work was supported by a BBSRC studentship to Simon Reader and a Royal Society University Research Fellowship to Kevin Laland. Jeremy Kendal made helpful comments on the manuscript.

---

## References

- Blackmore, S. (1999). *The Meme Machine*. Oxford, Oxford University Press.
- Bonner, J. T. (1980). *The Evolution of Culture in Animals*. Princeton, NJ, Princeton University Press.
- Box, H. O. (1984). *Primate behaviour and social ecology*. London, Chapman and Hall.
- Boyd, R. & P. J. Richerson (1985). *Culture and the evolutionary process*. Chicago, University of Chicago.
- Burnell, K. (1998). Cultural variation in savannah sparrow, *Passerculus sandwichensis*, songs: an analysis using the meme concept. *Animal Behaviour*, **56**:995-1003.
- Curio, E., U. Ernst & W. Vieth (1978). The adaptive significance of avian mobbing II. Cultural transmission of enemy recognition in blackbirds: Effectiveness and some constraints. *Zeitschrift für Tierpsychologie*, **42**:184-202.

- Custance, D., A. Whiten & K. Bard (1995). Can young chimpanzees (*Pan troglodytes*) imitate arbitrary actions? Hayes and Hayes (1952) revisited. *Behaviour*, **132**:837-859.
- Dawkins, R. (1982). *The Extended Phenotype*. Oxford, Oxford University Press.
- Dawkins, R. (1989). *The Selfish Gene*, 2nd edition. Oxford, Oxford University Press.
- Delius, J. D. (1991). The nature of culture. In *The Tinbergen Legacy*, M. S. Dawkins, T. R. Halliday & R. Dawkins (eds.), 75-99. London, Chapman & Hall.
- Dennet, D. C. (1995). *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. New York, Touchstone.
- Fisher, J. & R. A. Hinde (1949). The opening of milk bottles by birds. *British Birds*, **42**:347-357.
- Galef, B. G. (1996). Social enhancement of food preferences in Norway rats: a brief review. In *Social Learning in Animals: the Roots of Culture*, C. M. Heyes & B. G. Galef (eds.), 49-64. London, Academic Press.
- Galef, B. G. J. (1988). Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. In *Social Learning: Psychological and Biological Perspectives*, T. Zentall & B. G. Galef (eds.), 3-25. Hillsdale NY, Erlbaum.
- Gibbs, H. (1990). Cultural evolution of male song types in Darwin's medium ground finches, *Geospiza fortis*. *Animal Behaviour*. **39**:253-263.
- Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, **201**:1264-1266.
- Goodenough, O. R. (1995). Mind viruses: culture, evolution and the puzzle of altruism. *Social Science Information*. **34**:287-320.
- Heyes, C. (1993). Imitation, culture and cognition. *Animal Behaviour*, **46**:999-1010.
- Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews*, **69**:207-231.
- Heyes, C. M. (1996). Genuine imitation? In *Social Learning in Animals: the Roots of Culture*, C. M. Heyes & B. G. Galef (eds.), 371-390. London, Academic Press.
- Hinde, R. A. & J. Fisher (1951). Further observations on the opening of milk bottles by birds. *British Birds*. **44**:393-396.
- Jenkins, P. F. (1978). Cultural transmission of song patterns and dialect development in a free-living



bird population. *Animal Behaviour*, **25**:50-78.

Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates*. **6**:1-30.

Lefebvre, L. (1995). The opening of milk-bottles by birds: evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission. *Behavioural Processes*, **34**:43-53.

Lefebvre, L. & B. Palameta (1988). Mechanisms, ecology and population diffusion of socially learned, food-finding behaviour in feral pigeons. In *Social learning: Psychological and Biological Perspectives*, T. Zentall & B. G. Galef (eds.), 141-163, Erlbaum.

Lynch, A. (1996). The population memetics of birdsong. In *Ecology and Evolution of Acoustic Communication in Birds*, D. E. Kroodsma & E. H. Miller (eds.), 181-197. Ithaca, New York, Cornell University Press.

Lynch, A., G. M. Plunkett, A. J. Baker, et al. (1989). A model of cultural evolution of chaffinch song derived with the meme concept. *American Naturalist*, **133**:634-653.

McGrew, W. C. (1994). Tools compared: the material of culture. In *Chimpanzee cultures*, R. W. Wrangham, W. C. McGrew, B. M. de Waal & P. Heltne (eds.), 25-39, Harvard University Press.

Mineka, S. & M. Cook (1988). Social learning and the acquisition of snake fear in monkeys. In *Social Learning: Psychological and Biological Perspectives*, T. Zentall & B. G. Galef (eds.), 51-73. Hillsdale NY, Erlbaum.

Piaget, J. (1962). *Play, Dreams and Imitation in Childhood*. London, Routledge & Kegan Paul.

Rose, N. (1998). Controversies in meme theory. *Journal of Memetics - Evolutionary Models of Information Transmission*. **2**. <[http://jom-emit.cfpm.org/1998/vol2/rose\\_n.html](http://jom-emit.cfpm.org/1998/vol2/rose_n.html)>

Sherry, D. F. & B. G. Galef (1984). Cultural transmission without imitation: milk bottle opening by birds. *Animal behaviour*, **32**:937-938.

Sperber, D. (1996). *Explaining Culture: a Naturalistic Approach*. Oxford, Blackwell.

Sperber, D. (1999). The future of 'meme': retirement or redefinition? Paper presented at King's College Research Centre Forum, Do Memes Account for Culture?, University of Cambridge, UK.

Warner, R. (1988). Traditionality of mating-site preferences in a coral reef fish. *Nature*, **335**:719-721.

Warner, R. (1990). Male versus female influences on mating-site determination in a coral-reef fish. *Animal Behaviour*. **39**:540-548.

Whiten, A., J. Goodall, W. C. McGrew, et al. (1999). Cultures in chimpanzees. *Nature*, **399**:682-685.

Yando, R., V. Seitz & E. Zigler (1978). *Imitation: A Developmental Perspective*. Hillsdale, NJ, Erlbaum.