



ARTICLE



<https://doi.org/10.1057/s41599-020-0515-3>

OPEN

# Do guide dogs have culture? The case of indirect social learning

Dominique Guillo<sup>1,2</sup>✉ & Nicolas Claidière<sup>3</sup>

In the study of animal behaviour, culture is often seen as the result of direct social transmission from a model to a conspecific. In this essay, we show that unrecognised cultural phenomena are sustained by a special form of indirect social learning (ISL). ISL occurs when an individual B learns a behaviour from an individual A through something produced by A. A's behavioural products can be chemicals, artefacts, but also, we argue, behaviours of another group or species that are the consequence of A's actions. For instance, a behaviour—guiding a blind person—can be transmitted from dog A to dog B, because the fact that dog A learns the behaviour creates in the mind of the trainer representations about the efficacy of the training practice that can be transmitted to another human, who can then train dog B. These dog behaviours have all the properties of standard cultural behaviours and spread in some dog populations through the exploitation of the social learning capacities of another group/species. Following this idea requires a change in perspective on how we see the social transmission of behaviours and brings forward the fact that certain cultural practices can spread among animals through a cultural co-evolutionary dynamic with humans or other animals.

<sup>1</sup>African Center for Behavioral Sociology, Mohammed VI Polytechnic University, Rabat, Morocco. <sup>2</sup>CNRS, Paris, France. <sup>3</sup>Aix-Marseille Université, LPC, CNRS, Marseille, France. ✉email: [dominiqueguillo@yahoo.fr](mailto:dominiqueguillo@yahoo.fr)

## Introduction

The study of social learning (SL) and animal culture (defined in detail below) has come a long way over the past 20 years or so (Whiten et al., 2016). Field studies and experiments have flourished and shown that a broad range of animals socially learn a variety of skills (surveys of the literature can be found for instance in Hoppitt and Laland, 2013; Laland and Galef, 2009; Whiten et al., 2011). For instance, tandem running ants teach each other the location of food by waiting for each other (Franks and Richardson, 2006), capuchin monkeys learn to crack hard shelled nuts open with stones by observing knowledgeable individuals (Otoni and Mannu, 2001), female dolphins learn from their mother to use sponges to forage (Krutzen et al., 2005) and humpback whales sing song that they learn from neighbouring groups (Garland et al., 2011). In addition, numerous studies have emphasised the crucial evolutionary consequences of these SL capacities in animals (for a review, see Laland and Galef, 2009). Through SL, behaviour can spread in a population without relying on genetic inheritance, leading to the emergence of locally adapted skills, knowledge and customs. These skills, knowledge and customs are named in the literature traditions or culture. In this article, we propose to take the study of SL and animal culture even further but by looking at animals that are much closer to us: chiefly, dogs (*Canis familiaris*).

Recent studies have revealed that dogs have a remarkable capacity to interact and communicate with humans that allow them to *socially* learn from humans a broad range of behaviour (for a review see, Miklósi and Topál, 2012). For instance, dogs spontaneously initialise communicative interactions with humans, using eye contact, gaze alternation and visual orientation (Miklósi et al., 2003; Virányi et al., 2008). They can take into account the visual perspective of a human when fetching an object (Kaminski et al., 2009). They respond to several referential gestures performed by humans, such as pointing or head orientation, in a way similar to 18-month-old children (Lakatos et al., 2009). Dogs' communicative skills permit finely tuned interactions with humans, they allow guide dogs and their human partner to mutually adjust their behaviours by switching the role of leader and follower depending on the task for instance (Mondémé, 2019; Naderi et al., 2001). In addition, various social skills, like mimetic behaviour, anticipation, stimulus and local enhancement and attraction for what humans do (detour task, for example, Pongracz et al., 2001) allow dogs to build synchronised routines with their owner (Miklósi and Topál, 2012). Dog-human communication and interaction are reinforced by the specific strong affiliative relationship that dog can develop with their owner (Topál et al., 2005). For instance, the concentration of oxytocin—which is an indicator for the degree of social bonding—increases in both a human and his dog companion when they are interacting (Odendaal and Meintjes, 2003). This set of complex communicative and social skills make dog-human interaction a step by step constructive process (Miklósi and Topál, 2012) which greatly facilitate SL. For instance, unlike chimpanzees, and like children, dogs tend to replicate an inappropriate or ineffective behaviour exhibited by a human to achieve a specific goal, even when they are able to reach the same goal with more effective means (Kupán et al., 2011). More generally, dogs learn a broad diversity of behaviour through their interactions (teaching, training, conditioning, etc.) with humans, thus displaying an important capacity for SL.

All these observations show that dog learning from humans is “social” in a much stronger sense than most of the learning processes traditionally regarded by ethologists as producing animal *cultures*, for example the learning of opening of milk bottles in some blue tits (Fisher and Hinde, 1949), of variants of song in some birds (Aplin et al., 2012) or of specific ways to eat pine

cones in some black rats: in this last case, individuals do not necessarily interact (Aisner and Terkel, 1992 and see below our comments).

However, surprisingly, dogs are scarcely ever mentioned in research on animal culture, i.e. on the consequences at the level of the population of animal's SL capacity (Laland and Galef, 2009). The evolutionary outcomes of dog social capacities remain unstudied, although they are unquestionably huge, creating important and quickly changing behavioural differences between dog populations. If a dog is helping a blind person to cross a road for instance, is this a cultural behaviour of dogs? Being helped by a dog to cross a road is a cultural behaviour of humans, but is the behaviour of the dog, the action of helping a blind person, in that context, parts of dog's culture?

In the following, we want to explore this question in detail.

We start by examining a well-documented example, based on historical research, of the diffusion of a behaviour in dogs and we defend the idea that this behaviour represents an interesting example of dogs' culture. This example further demonstrates how a behaviour can spread by SL in species with limited intra-specific SL capacities (dogs) through a special mechanism of diffusion—indirect social learning (ISL) mediated by behaviours—that has not yet been clearly identified and studied in detail.

Next, in the “Discussion” section, we discuss the objections that can be raised against the view we are defending here.

Finally, in the last sections of the article, we consider some of the consequences of this view. In particular, we think that the study of SL and culture would benefit from a more balanced view going beyond intraspecific copying, towards the study of *all* the behaviours that spread in a population as a consequence of social interactions, indirectly as well as directly, by interspecific as well as by intraspecific transmission.

## The diffusion of the guiding dogs' complex set of behaviour during the XXth century

In this section, our goal is to introduce the transmission process we want to highlight—ISL mediated by behaviours—by relying on a real chain of interactions, documented by historians (Putnam, 1997; Fishman, 2003; Ostermeier, 2010): the transmission chain that connects the first guide dog to current ones.

In 1915, a German military doctor, Gerhard Stalling, noticed that his German shepherd seemed to help blind veterans during his visits to hospitals for war wounded (Ostermeier, 2010). Drawing on the observations made on his dog, in 1916 Dr. Stalling opened the first guide school for blind people in Oldenburg, Germany. He chose the dogs among the 25,000 German shepherds used during World War I for many tasks. This school was a great success. Other schools were opened in a dozen German cities, including Potsdam (Ostermeier, 2010) and in 1927, 4000 dogs served as guides for the blind persons in Germany (Fishman, 2003). The diffusion of “guide dog” behaviours in certain canine populations crossed a new historical level at the end of the 1920s through the efforts of Dorothy and George Eustis (Ostermeier, 2010; Putnam, 1997). Dorothy Eustis had in the 1910s a German Shepherd of which she had noted the speed of learning and docility (Ostermeier, 2010). This dog gave her the idea of systematically producing very effective working dogs, obtained by selecting docile puppies with good learning abilities and by providing a rigorous training method. She and her husband set up one of their experimental training centre in Switzerland, in Vevey, named Fortunate Field, which supplied dogs to the police and the Swiss army. After visiting the Potsdam guide dog school, Dorothee Eustis wrote an essay “The seeing eyes” (published in 1927) to make known the usefulness of working

dogs through the exemplary case of the guide dogs of Potsdam (Putnam, 1997). Reading this essay, a man from Nashville, Morris Frank offered her to start a similar school in the United States. In April 1928, Frank travelled to Vevey, to train himself up with a dog named Buddy. After 5 weeks of training, Frank and the dog travelled back to America. Frank founded the first guide dog school in America—The Seeing Eye. This school became famous worldwide and prompted the opening of many schools of the same type, especially during the Second World War, for helping blind veterans again (Ostermeier, 2010; Putnam, 1997). This one century long interspecific chain of interactions led to the current, 25,000 guide dog partnerships (according to the International Guide Dog Federation).

### Is the behaviour of guiding dogs part of dogs culture?

In the study of animal behaviour, a cultural behaviour is often characterised by the following properties (Laland and Hoppitt, 2003; Lycett et al., 2007; Whiten, 2005; Whiten et al., 1999): (i) the behaviour can be present in some populations and not in others; (ii) the acquisition of the behaviour is not fully explained by genetic differences between individuals; (iii) the behaviour must be socially transmitted, i.e. the behaviour must be socially learned, broadly speaking, and not learned from interaction with physical environment; and (iv) an individual learning the behaviour increases the likelihood of other individuals learning the behaviour as well (i.e. the behaviour is not independently re-discovered by different individuals).

As the example above shows, the behaviour of guide dogs easily respects the first three of these conditions: it is present in certain populations of dogs and not in others (i); it is not genetically determined (ii); and it is socially learned by dogs through interactions with humans who train them to cooperate with blind persons (iii) (Mondémé, 2019; Naderi et al., 2001).

What seems rather strange in the idea that guiding a blind person is part of dog's culture is that naïve dogs do not learn this behaviour through interactions with other dogs. They learn to guide when interacting with humans. Should we conclude from the absence of interactions between dogs that these traits are not part of dog culture? This view overlooks the fact that a dog successfully learning the behaviour—as Dr. Stalling's German Shepherd—affects the probability that humans perform and transmit the training practice to other humans—George Eustis, Dorothy Eustis and Maurice Franks—who then apply it to new dogs—e.g. Buddy. The presence of a dog learning guiding skills therefore plays a causal role in the apparition of the same behaviour in another dog through an *indirect* chain of interactions involving humans. Thus, a dog learning guiding skill increases the probability of another dog learning the same behaviour, i.e. property (iv) above. Guide dog behaviour therefore respects the four properties of a cultural behaviour. “Helping a blind to cross a road” is a cultural trait specific to the guide dog population, which distinguishes it from other dog populations.

Note that arguing that dogs have culture does not extend the concept of culture to artefacts or living beings physically shaped by humans, like stone axes or trimmed trees. Like dogs, a stone axe can play a causal role in the apparition of another stone axe through social transmission between humans of the idea of “carving a stone”. But such a “trait”—“being carved”, for a stone—lacks two properties shared by guide dog traits—properties that are essential for a trait to be considered as cultural. Firstly, “being carved” for a stone or “trimmed” for a tree are morphological and material traits, not behavioural ones, unlike “helping a blind person to cross a road”. Secondly, they are not *socially learned* from humans, unlike guide dogs' behaviours. In contrast to trees and stones, dogs are *actively* socially learning new behaviours

adjusted to those of humans (Miklósi and Topál, 2012; Mondémé, 2019; Naderi et al., 2001; see also, below, “Discussion” section).

In the following section, we will explore the very particular and unnoticed transmission mechanism through which dog SL from human makes behavioural traits spread within dog populations.

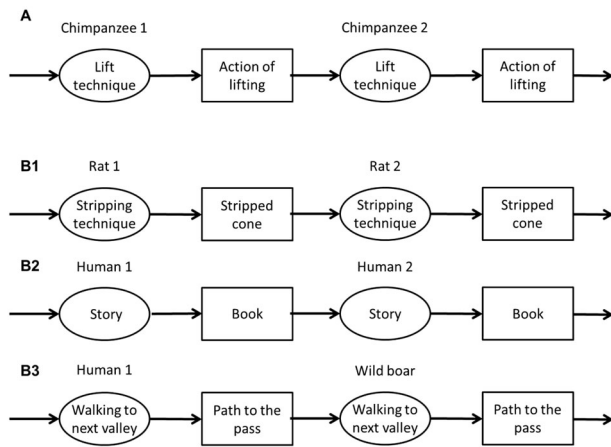
### Direct social learning (DSL) and indirect social learning (ISL)

SL is often defined as “learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products” (Heyes, 1994; see also Shettleworth, 2009). The most studied case of SL is the one in which an individual is learning from the *direct* contact with a conspecific (see for instance Whiten and Mesoudi (2008) for a review of transmission chain studies)—emulation, imitation and teaching for example—and various species have been shown to be able to learn new behaviours by *directly* interacting with other individuals—‘models’—that perform the behaviour (Birds: Curio et al., 1978; Ants: Franks and Richardson, 2006; *Drosophila*: Mery et al., 2009; Fish: Pike et al., 2010; Primates: Whiten et al., 2005; Tortoise: Wilkinson et al., 2010; Bumblebees: Worden and Papaj, 2005).

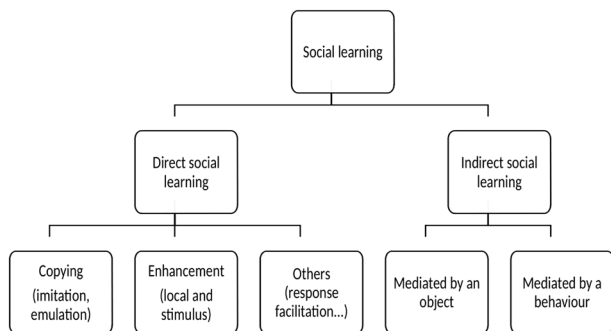
However, animals have also been reported to be able to learn from the *products* of other's behaviour (conspecifics or not), as noticed in the classical definition of SL given above. In its simplest form, learning from the products happens when ants for instance learn the location of a food source by following the chemicals left by other ants (Jackson and Ratnieks, 2006) or when fish are alerted to the presence of a predator through chemical cues emitted by other fish (Brown, 2003). These instances of SL create local and ephemeral traditions which are cultural only to a very limited extent since they concern only a few individuals and for a short lapse of time (Leadbeater et al., 2006; Sperber and Claidière, 2008). However, more elaborate forms of cultural behaviour can also result from product learning. For instance, Aisner and Terkel (1992) showed that black rats had developed a new technique to eat pinecones efficiently by learning from already partially eaten pinecones. In that case, individuals might have been able to learn socially from the products (partially eaten pinecones) of their conspecifics' behaviours (and maybe from individuals of distinct species, such as squirrels; see Fig. 1).

We will use the terms “ISL” in a broad sense to refer to SL that occurs from the products of others' behaviours (Fig. 2). The terms have been used in this sense previously by Lefebvre (1995) for instance when describing the possibility of blue tits learning to open milk bottles from the exposure to previously opened ones by other individuals. They have also been used to refer to stimulus and local enhancement (Castro and Toro, 2004), which is not incompatible with the sense we intend to convey here given that in stimulus or local enhancement the learner's attention is directed to the part of the environment that was affected by another individual (Heyes, 1994). With enhancement however, the presence of another individual is necessary to direct the attention of the focal subject (Want and Harris, 2002; Whiten et al., 2004). For the purpose of this article we will leave open the possibility that ISL includes enhancement (this has no bearing on the present discussion; see Fig. 2).

ISL mediated by objects is ubiquitous in humans and is responsible for an important part of cultural transmission. It happens for instance when we read a book or use the internet: a behaviour is transformed into material products and traces that can be used by other individuals. Experiments have also shown how participants improve through ISL by the simple observation of the results of other participants' behaviour (for instance Caldwell and Millen, 2008; Caldwell et al., 2012; Osiurak et al., 2016; Zwirner and Thornton, 2015). ISL mediated by objects does not always require advanced technologies; it can also be present



**Fig. 1 Contrast between direct and indirect social learning (“cultural causal chains” (based on the framework developed by Sperber, 2006)).** **a** Example of direct social learning (DSL): Chimpanzees can, in certain circumstances, acquire new foraging techniques by watching others use that technique (Hopper et al., 2007; Whiten et al., 2005). The presence of the demonstrator is necessary for the transmission to occur (Hopper et al., 2007). **b** Example of indirect social learning (ISL): Individuals leave traces in the environment such as partially eaten pinecones (B1), books (B2) or paths (B3) that are used by others. Circled: mental representations (internal to the individual). Boxed: public productions (accessible to other individuals).



**Fig. 2 Classification of social learning mechanisms.** Social learning (SL) can be divided into direct (DSL) and indirect (ISL) forms based on the co-presence, or not, of the two individuals. Indirect social learning can be further divided according to the medium that supports the transmission, either artefactual or behavioural. This classification is inspired by the one proposed by Whiten and coll (Whiten et al., 2004, 2009).

less conspicuously when humans or animals trace path on the ground for instance. When walking a path an individual uses the result of others behaviour as guidance and at the same time maintains the path and leaves traces for others to follow the same path in the future. This creates a local tradition that can persist for years, be interspecific and trans-generational.

More broadly, it is possible to consider the distinction between ISL and DSL on a continuum running from cases in which there is no contact and no relationship between the two individuals involved in the transmission of information (in the case of a path created in the environment for instance, or the black rat eating pinecones) towards cases in which there is a close relationship and interaction between the individuals (in the case of teaching in meerkats or ants for instance (Franks and Richardson, 2006; Richardson et al., 2007; Thornton and McAuliffe, 2006). Intermediate examples involve local enhancement for instance, as in

the case of British tits learning to open milk bottles (Fisher and Hinde, 1949; Sherry and Galef, 1990).

So far, ISL has been illustrated by cases in which the transmission is mediated by material products left in the environment (pinecones, books, etc.) but we can extend the notion of product to behaviours produced in individuals of a different population (Fig. 3; note that the mental representations of these behaviours are also material products of course but in a less trivial sense).

In the simplest example, individuals from two populations of different species, P1 (dogs) and P2 (humans), have tight social interaction patterns (Fig. 3).

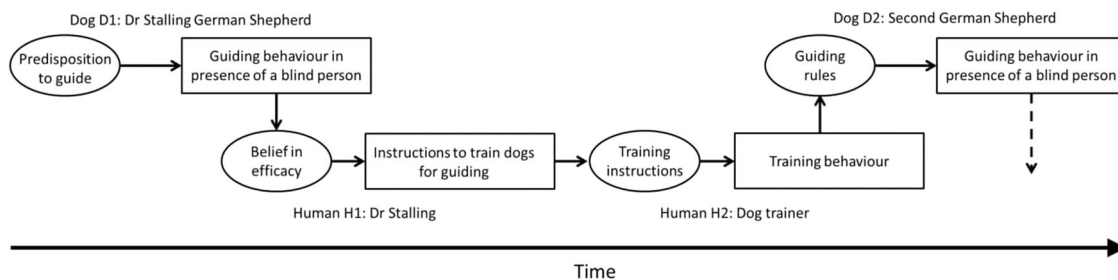
The causal chain that links a first dog D1—for example, Dr. Stalling’s German Shepherd—to a second dog D2—a guide dog trained in one of Dr. Stalling’s schools—can be decomposed as follows. First, the dog D1—Dr. Stalling’s German Shepherd—exhibits a new behaviour—guiding a blind veteran—in front of a human H1—Dr. Stalling. Then he gives this human H1—Dr. Stalling—the idea of a new human behaviour *HB*: training dogs to guide blind people. Secondly, H1 trains D1 to learn a specific set of dog behaviour (*DB*: guiding a blind man). This successful learning then causes in H1’s mind the belief in the efficacy of the behaviour *HB* regarding the way to train guide dogs. Thirdly, H1—Dr. Stalling—trains other dogs (D2–D4) to guide a blind person and at the same time causes the belief in the efficacy of *HB* in another human (H2)—a dog trainer in one of Stalling’s schools. Finally, this dog trainer, by performing *HB*, causes *DB* in other dogs (D5, D6, D7, etc.) (see Fig. 3). *HB* then can spread in P2, and *DB* in P1. Instances of human training behaviour—performed by Dr. Stalling and dog trainers from his schools—are behavioural products caused by dogs that will, in turn, affect new dogs.

This kind of ISL is special and has rarely been evoked in the literature about animal cultures despite the fact that it corresponds to the standard definition of ISL (Freeberg, 1998; see also Hoppitt and Laland, 2013). It differs from more traditional examples of SL in two ways. Firstly, the product that induces the learning in a new individual—a new dog in this example—is not an object or a material trace; it is a behaviour of an individual of a different group or species—a human. Secondly, the process through which the behaviour is passed on between individuals—dogs—does not consist in copying: Dog D2 did not learn *DB* from observing dog D1, because they did not even meet (copying is defined in Fig. 2).

Note that these behaviours are socially transmitted in a very strong sense, comparing to behaviours transmitted by ISL mediated by objects. The transmission chain of ISL between two dogs is composed of consecutive sequences of DSL, i.e. sequences of interactions that are all *social* (interactions between dogs and trainers, and between humans (see Fig. 3)). This is not the case in occurrences of ISL mediated by objects. This kind of ISL is social in a weak sense, comparing to the guide dog case. In the black rat case, for example, the transmission chain between two rats is made of two consecutive sequences of interaction, both being between a rat and an object (a pinecone), i.e. non-social interactions. Considered as a whole, the chain formed by these interactions is social, rats interacting indirectly, through an object. But none of these interactions are social.

We believe that these special types of ISL—mediated by behaviour—have an important cultural potential. In these cases, the complex combination of SL skills of two different species leads to the spread in each of them of traits that have all the properties of culture. Furthermore, the cultures sustained by this indirect mode of social transmission force us to think about animal and human culture in a more complex, more complete and richer way. We explore some of the consequences of this view in the remainder of the article.





**Fig. 3** Decomposition of the initial spread of guiding behaviour in dogs through indirect social transmission, as described in the text.

**The importance of ISL mediated by behaviour**

If helping a blind person to cross a road is part of dog’s culture, then so is much of dogs’ behaviour learned in contact with humans, such as walking with a leash, hunting with a human, playing with children, detecting explosives or drugs. Of course, if dogs have culture, then so do other domestic species, like cats, horses—circus horses, ride horses, farm horses—, chicken—farm chicken, pet chicken—and even non-domestic ones, like apes that have frequent social interactions with humans, in laboratories, zoos or even forests. For instance, Akita et al. (2016) showed that the Sika deer (*Cervus nippon*) in Nara Park (Japan) developed a bowing behaviour that influence their feeding by human visitors. This behaviour develops both through positive reinforcement (the provision of food when the behaviour is observed by visitors) and through observational learning (the frequency of the behaviour increases after having seen another individual bow). On the human side, visitors are informed that deer perform this behaviour and acquire costly cookies in anticipation, thereby maintaining a high frequency of bowing. These examples suggest that ISL mediated by behaviour could be quite important for animals that regularly interact with humans, whether domesticated or not. This is expected, given the prevalence of SL among humans. But ISL mediated by behaviour may also exist between different animal species that closely interact. The difficulty however is to show that the complementary behaviours are spreading through SL, something that is already difficult with one species and one behaviour. Nonetheless, some research hints at such phenomenon, for instance in the study of interactions between birds and their predators (Hetrick and Sieving, 2012).

Moreover, ISL can potentially play an important role in interactions between different groups within the same species. For instance, the use of baby bottles by babies or the young children’s habit of playing with plasticine can be considered with the same logic as being part of babies’ and young children’s culture, respectively, transmitted by the kind of ISL evoked above. These behaviours follow the traditional pattern of cultural behaviours. Only certain populations of babies feed from baby bottles, it is not entirely a genetic behaviour, it requires SL and the presence of a baby feeding from a bottle increases the likelihood of observing the same behaviour in other babies. The behaviour spreads because parents share information between them and because other parents who see a baby feeding from a bottle are more likely to feed their baby from a bottle too. The traits “playing with plasticine”, or “feeding from a bottle”, for instance, goes from a baby B1 to a baby B2 by ISL through a chain of social interactions that connect step by step B1, B1’s parents, B2’s parents and B2.

Finally, note that for simplicity and clarity we have limited ourselves to cases with only two populations interacting but clearly, in theory, we can extend the case of ISL to more than two populations. Sheep for instance can learn new behaviours from dogs which have learned to interact with sheep from humans. The propagation of new behaviours in sheep in this case could be linked to two levels of ISL.

In summary, ISL mediated by behaviour could be an important part of SL and cultural transmission.

**Discussion**

**Guide dog learning from humans is social.** One could object that despite the fact that dogs are social animals, guide dog learning is not “social”, since it is training based on conditioning (associative learning by positive reinforcement). Therefore, guide dogs’ specific traits should not be considered as “cultural”.

However, firstly, numerous SL processes are based on conditioning. Many traits considered as socially learned, and then cultural, in animals and in humans, are learned by associative learning by positive reinforcement, as in the blue tits or black rats’ cases, or in children learning alphabet or table manners.

Secondly, the possibility and the efficiency of dog conditioning by human trainers rely on dog capacities to create social bonds with humans. The strength and specificities of dog–human social bond explains why it is so easy to train dogs in general, and so difficult to train wolves (see Coppinger and Coppinger, 2002). And within dogs, the degree of affiliation—i.e. a social variable—determines the efficiency of the training (Topál et al., 2005).

Thirdly, social bond is not only a variable that makes possible or enhances dog training: dog social behaviour patterns are part of the causal mechanism of conditioning itself, since it depends on rewarding by food. Relying on the observations made by Howard Liddel, an American psychologist invited to Pavlov’s research centre, Konrad Lorenz points out the following: “[When freed] from its harness a dog that had been conditioned to salivate at the acceleration in the beat of a metronome [...] ran to the machine, wagged its tail at it, tried to jump up to it, barked, and so on; in other words, it showed as clearly as possible the whole system of behaviour patterns serving, in a number of *Canidae*, to beg food from a conspecific. It is, in fact, this whole system that is being conditioned in the classical experiment (Lorenz, quoted in Jenkins et al., 1978; on dogs’ exhibition of social behaviours during conditioning experiments, see also Miklósi, 2014, p. 5). Some canine ethologists even suggest that the reward, which plays a key role in conditioning (training), can provoke a form of “aversion for lack of equity” in dogs (McGettrick and Range, 2018).

Therefore, since culture is classically defined as a set of traits widespread in a population and transmitted by SL, on one hand, and since dogs’ training by conditioning must be considered as SL, on the other hand, guiding dogs specific traits must be considered as cultural.

**Is ISL mediated by behaviour necessarily based on teaching? “Faire faire” and asymmetrical social relationships.** ISL mediated by behaviours is a chain of sequences of DSL. One of these DSL is crucial: DSL between two *different* individuals—between a dog and his owner, for instance. This kind of DSL could be

colloquially referred to as teaching. A human teaches a dog to guide a blind person for instance, a parent teaches a child to drink from a bottle. However, teaching in the evolutionary and animal behaviour literature has a very specific and somewhat different meaning. The most accepted definition of teaching, proposed by Caro and Hauser (1992), is the following: “An individual actor A can be said to teach if it modifies its behaviour only in the presence of a naive observer, B, at some cost or at least without obtaining an immediate benefit for itself. A’s behaviour thereby encourages or punishes B’s behaviour, or provides B with experience, or sets an example for B. As a result, B acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all.” For instance, adult meerkats disable scorpions before giving them to young pups that can then interact with them. Thornton and McAuliffe (2006) showed that depending on the developmental stage of the pup, adults will leave the prey more or less intact. Furthermore, as a result of these interactions with more or less disabled scorpions, meerkat pups more quickly learn to kill them. Another well-established example of teaching in animals comes from tandem running ants *Temnothorax albipennis* (Franks and Richardson, 2006). This example illustrates the fact that animal teaching, as defined above, is a form of cooperation (Thornton and Raihani, 2008) in which the teacher facilitates the learning of the pupil at a cost (or with no immediate benefit) in order to gain direct or indirect fitness benefits after the learning has occurred. Accordingly, and even if in theory this is not necessarily the case, examples of teaching in animals often involve high-relatedness between the teacher and the pupil.

Teaching, as defined in the animal behaviour literature, can, under the right circumstances, result in ISL and the type of cultural spread we have described above. For instance, domesticated animals often benefit from their capacity to learn new behaviour from humans, either immediately by being rewarded or more generally by being cared for. Conversely, humans can benefit from the behaviour learned by domesticated animals, as in the case of dogs guiding behaviour. In such cases, the benefits are mutual and results from cooperation. In other cases, however, the costs and benefits of ‘teaching’ are either difficult to estimate (as is often the case when we consider human fitness) or one-sided. For instance, humans have trained various animals for warfare, a clear form of direct exploitation with a very high cost for the learner (death). More mundane examples in which the learner does not clearly benefit include the fact that we train pets to do their toilet outside for instance. Animals can also train humans for their own benefit, for example, when a dog imposes behaviours on his owner, like sleeping on a sofa.

These different examples reveal a broad category of DSL processes that are characterised by the fact that one individual makes another individual learn to do something new. In this article, we will use the term “*faire-faire*” (pronounced ‘fare-fare’), meaning “to make somebody do something” in French, to refer to cases of DSL in which one individual (the source) changes his or her behaviour in order to make another individual (the recipient) socially learn something. *Faire-faire* includes teaching, when the source and the recipient benefits from the learning, but also other cost–benefit relationships, such as when only the source or only the recipient benefit (Thornton and Raihani, 2008). An alternative to using the term *faire-faire* would be to develop an extended notion of teaching that would more closely approximate the colloquial use of the term. However, given that teaching has a well-established definition in the animal behaviour literature and is considered a form of cooperation, we think it is more fruitful to have two different terms. *Faire-faire* then is a broad category and can be linked to various forms of asymmetry between humans and animals, animals from distinct species or humans from different groups, including asymmetry in strength, habits, skills, resources and information for instance.

**Gene/culture coevolution, ISL and domestication.** ISL can help us fully understand certain co-evolutionary processes, and in particular domestication. The emergence and development of SL in humans with the mental capacities and social organisation that created the cultural explosion has given rise to new opportunities for humans but also for other animals. The behaviour of dogs, horses and other domesticated animals has evolved exploiting the SL capacities of humans: traits in domesticated species that could increase the cultural spread of corresponding behaviours in humans have flourished in the domesticated species as a consequence of their effects on human culture. For instance, the fact that horses, but not zebras, had the capacity to accept humans on their back has led to the spread of horse training practices in humans and “being ridden upon” behaviour in horses (Diamond, 1997). This has given rise to further cultural adjustments in humans (evolution of the training practice) and to corresponding genetic evolution (evolution of the capacity to be trained) and cultural (ISL) evolution (the way they are trained, or dressed, depending on human cultures) in horses. Indirect social transmission in such a case is associated to natural selection, creating a co-evolutionary process between horse’s genes, horse cultural traits and human cultural practices.

Similarly, domestication in dogs most likely happened through natural selection of dogs that could benefit from the food remains left by humans (Coppinger and Coppinger, 2001; Miklósi, 2014). This process selected dogs that could further approach humans, interpret their behaviour and be trained by them (Trut, 2000). The fact that dogs were able not only to approach humans but to develop behaviours that gave rise to a cultural spread in humans is largely responsible for their success as a domesticated species. Imagine what would have happened if dog behaviour had not given rise to a cultural spread in humans. That is exactly what happens with non-domesticated animals such as certain birds for instance. From time to time a person finds a chick, raises it and maybe trains it but it never goes much further than that.

More broadly, if strong social bonds exist or evolve between a species that does not have a high degree of intra-specific SL and one that does, the exploitation of the SL capacity of the second species may be a less costly strategy for the first than to develop one’s own intra-specific SL capacity (if at all possible). Given that humans rely so heavily on SL, it is possible to imagine that domesticated species do not need to develop intra-specific SL to a great extent; they can use humans as an indirect mean to spread new behaviours.

**Culture beyond intraspecific copying.** Looking at the literature on SL and culture in animals today, what we see is a discipline that has focused largely on the details of SL by DSL—copying—between individuals of the same species but maybe not enough on what culture and social influence is in general. Time and effort has been spent on organising and classifying the different forms that SL can take (Heyes, 1994; Whiten et al., 2004) and on designing new methodologies to document the use of these mechanisms in captivity (e.g. Alem et al., 2016; Claidière et al., 2014; Whiten et al., 2005) and in the field (e.g. Aplin et al., 2012; Thornton and McAuliffe, 2006; van de Waal et al., 2013). Field studies have also documented the spread of new behaviours in groups of wild animals (Aisner and Terkel, 1992; Fisher and Hinde, 1949; Garland et al., 2011; Kawai, 1965) and the existence of group-specific behaviours that cannot be readily explained by genetic differences or differences in the physical environment and that are most likely due to SL (e.g. Rendell and Whitehead, 2001; van Schaik et al., 2003; Whiten et al., 1999). ISL has also received some attention but only when mediated by chemicals or objects (e.g. Brown, 2003; Lefebvre, 1995; Terkel, 1996). Interspecific SL

has started to be investigated more thoroughly, but mostly within the copying paradigm (Dawson and Chittka, 2012; Lefebvre et al., 1997; Seppänen and Forsman, 2007). Finally, when interspecific SL is considered, as for some behaviour socially learned by dogs described previously for instance, but does not consist in copying, *the consequences at the populational level—i.e. regarding culture—* are not fully explored. All these efforts have served to firmly establish the existence of animal culture, but a narrow focus on SL can only be a first step in developing a comparative science of culture and cultural evolution.

In this article, our aim is to draw attention to these limitations and to start opening the field to a broader view of SL and animal culture.

By examining the spread of guiding behaviour in dogs we were able to show through this example, first, that such behaviours fulfil all the criterions that are traditionally needed for culture.

Second, that complex set of behaviours can spread by SL in species with relatively low intraspecific copying capacities (although recent research shows that dogs seem to have these capacities to some extent (Range and Virányi, 2013; Huber et al., 2018, 2020)).

And third, that research on SL and its cultural consequences should be more systematically extended, beyond DSL by copying, to *all the behaviours that emerge and spread through the complete network of the social interactions—*intraspecific and interspecific—that individuals have in a given ecological niche; and to *all the mechanisms—*direct as indirect—through which a behaviour can socially spread within this network.

Focusing on social interaction, its conditions and its effects, and on asymmetrical relationships between species or groups, this view also invites one to take into account knowledge accumulated by interactionist sociology (see in particular Goffman, 1961) and pragmatist inspired sociology (Jerolmack, 2009) and to anchor them in an evolutionary perspective. The view we propose in this article could therefore shed some light—and find some support and justification—in a field of research that aims to closely articulate the cognitive sciences and the social sciences around the study of social interaction (Claidière and Guillo, 2016; Enfield and Levinson, 2006; Rossano, 2013).

We believe that this broad view of SL and culture can lead to productive experiments involving new paradigms. For instance, and drawing on the example of human–dogs interactions, let us describe a possible adaptation of the standard transmission chain experiment to a case in which there is no contact between individuals of the same species and no copying of behaviour. This requires, for example, creating an experimental situation in which a human participant must perform a cooperative task with a dog to reach a certain resource, for example a dog toy. To accomplish this co-operative task, the human participant has two available options—e.g. using a key to open a red or a blue box mounted on a wall and containing one reward each. The key however is hidden and cannot be retrieved by the human participant, only a dog can. Retrieving the key can be done by the dog by, for instance, accessing a puzzle box by going through a tunnel and using one of two alternative means (action A or B). In this putative experiment, at least two human–dog groups are used. In one group, the first human participant is explained that action A can be used to retrieve the key to open the blue box in which a dog toy is. In the other group, the alternative option is explained to the first human participant (action B—red box; other combinations are of course possible). After this initial stage, one naïve dog is introduced to the first human participant in each group and the participants have to teach the dogs to do their part of the action (i.e. retrieve the key with action A or B). When the first participant–dog pair is proficient, the human participant is removed and a second completely naïve participant is introduced.

The first dog now has to direct the human participant so that he/she completes his/her part of the action (take the key provided by the dog and open a box). Once completed, the first dog can be replaced by a second, naïve, dog and so on and so forth. If ISL mediated by behaviour is possible, then we expect to find persisting differences between transmission chains with different initial conditions, as in other transmission chains experiment.

## Conclusion

Cultural transmission is not always direct, it sometimes happens through products left in the environment such as scent marks or processed food but it also happens through the consequences of one individual's actions on another. ISL explains how behaviour can spread in a population with limited opportunities for intraspecific or intragroup DSL (in dogs for instance), through the spread of complementary behaviour in another population.

Overall, it is as if two strategies were possible for a cultural trait to spread in a population. It can spread through direct intraspecific social transmission between individuals: this strategy requires developed DSL abilities, as in humans. Alternatively, a behaviour can also spread by ISL: if individuals of a certain species lacking direct intraspecific SL dispositions have strong social bonds with individuals from another species or another group that have these abilities.

Such cultures force us to consider cases in which the recurrence we see in culture does not result from copying mechanisms but from complementarity or non-symmetrical relations between individuals. The non-symmetrical nature of many interactions creates a progressive behavioural adjustment between individuals that repeatedly interact, and thus create cultures in each group. Therefore, this view integrates the diffusion of behaviours that are consequences of power, constraints, inequality or differences between groups, which is not easily explained in a perspective based mainly on copying mechanism: power, for instance, is typically a relation in which an individual makes others do for his/her own benefit things that he/she does not do, does not want to do, even sometimes does not know how to do, what we have called *faire faire* here.

Finally, our goal is not simply to show that we must call “cultural” traits that are usually called otherwise, like guide dogs' behaviours. It is not a question of labelling. It is to show that we need to change the way we look at culture. Currently, this look is focused on one type of process: by simplifying, intraspecific copying. Our paper invites us to have a broader theory of what has to be studied: we need to extend the theoretical and empirical research to *all* the behaviours emerging and spreading in the *complete* network—*intraspecific and interspecific—*of social interactions, directly as well as indirectly.

## Data availability

No data were generated to write this article. All data evoked in this paper are taken from papers or chapter of books listed above. Data sharing is not applicable to this article as no datasets were generated or analysed during the current study.

Received: 30 January 2020; Accepted: 12 June 2020;

Published online: 14 July 2020

## References

- Aisner R, Terkel J (1992) Ontogeny of pine cone opening behaviour in the black rat, *Rattus rattus*. *Anim Behav* 44(2):327–336
- Akita S, Wada Y, Wada K, Torii H (2016) Variation and social influence of bowing behavior by sika deer (*Cervus nippon*). *J Ethol* 34(1):89–96. <https://doi.org/10.1007/s10164-015-0451-7>



- Alem S, Perry CJ, Zhu X, Loukola OJ, Ingraham T, Søvik E, Chittka L (2016) Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect. *PLoS Biol* 14(10):e1002564. <https://doi.org/10.1371/journal.pbio.1002564>
- Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC (2012) Social networks predict patch discovery in a wild population of songbirds. *Proc R Soc B* 279(1745):4199–4205. <https://doi.org/10.1098/rspb.2012.1591>
- Brown GE (2003) Learning about danger: chemical alarm cues and local risk assessment in prey fishes. *Fish and Fisheries* 4(3):227–234
- Caldwell C, Millen A (2008) Studying cumulative cultural evolution in the laboratory. *Philos Trans B* 363(1509):3529
- Caldwell CA, Schillinger K, Evans CL, Hopper LM (2012) End state copying by humans (*Homo sapiens*): implications for a comparative perspective on cumulative culture. *J Comp Psychol* 126(2):161
- Caro T, Hauser M (1992) Teaching in nonhuman animals. *Q Rev Biol* 67(151):74
- Castro L, Toro MA (2004) The evolution of culture: from primate social learning to human culture. *Proc Natl Acad Sci USA* 101(27):10235–10240. <https://doi.org/10.1073/pnas.0400156101>
- Claidière N, Guillo D (2016) Comment articuler les sciences de la vie et les sciences sociales. *Année Sociol* 66(2):385–419
- Claidière N, Smith K, Kirby S, Fagot J (2014) Cultural evolution of systematically structured behaviour in a non-human primate. *Proc R Soc B* 281(1797). <https://doi.org/10.1098/rspb.2014.1541>
- Coppinger R, Coppinger L (2001) Dogs: a startling new understanding of canine origin, behavior & evolution. Simon and Schuster
- Coppinger R, Coppinger L (2002) Dogs: a new understanding of canine origin, behavior and evolution. University of Chicago Press
- Curio E, Ernst U, Vieth W (1978) Cultural transmission of enemy recognition: one function of mobbing. *Science* 202(4370):899–901
- Dawson EH, Chittka L (2012) Conspecific and heterospecific information use in bumblebees. *PLoS ONE* 7(2):e31444
- Diamond J (1997) Guns, germs, and steel: the fates of human societies. W.W. Norton & Co
- Enfield NJ, Levinson SC (2006) Roots of human sociality. New York, Berg
- Fisher J, Hinde RA (1949) The opening of milk bottles by birds. *Br Birds* 42(11):347–357
- Fishman GA (2003) When your eyes have a wet nose: the evolution of the use of guide dogs and establishing the seeing eye. *Survey Ophthalmol* 48(4):452–458
- Franks N, Richardson T (2006) Teaching in tandem-running ants. *Nature* 439(7073):153
- Freeberg TM (1998) The cultural transmission of courtship patterns in cowbirds, *Molothrus ater*. *Anim Behav* 56:1063–1073
- Garland EC, Goldizen AW, Rekdahl ML, Constantine R, Garrigue C, Hauser ND, Noad MJ (2011) Dynamic horizontal cultural transmission of Humpback Whale Song at the Ocean Basin Scale. *Curr Biol* 21(8):687–691. <https://doi.org/10.1016/j.cub.2011.03.019>
- Goffman E (1961) Encounters: two studies in the sociology of interaction. Bobbs-Merrill, New York
- Hetrick SA, Sieving KE (2012) Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. *Behav Ecol* 23(1):83–92
- Heyes CM (1994) Social learning in animals: categories and mechanisms. *Biol Rev* 69(2):207–231. <https://doi.org/10.1111/j.1469-185X.1994.tb01506.x>
- Hopper LM, Spiteri A, Lambeth SP, Schapiro SJ, Horner V, Whiten A (2007) Experimental studies of traditions and underlying transmission processes in chimpanzees. *Anim Behav* 73:1021–1032
- Hoppitt W, Laland, KN (2013) Social learning: an introduction to mechanisms, methods, and models. Princeton University Press
- Huber L, Popovová N, Riener S, Salobir K, Cimarelli G (2018) Would dogs copy irrelevant actions from their human caregiver? *Learn Behav* 46(4):387–397
- Huber L, Salobir K, Mundry R, Cimarelli G (2020) Selective overimitation in dogs. *Learn Behav* 23:1–11
- Jackson DE, Ratnieks FLW (2006) Communication in ants. *Curr Biol* 16(15):R570–R574. <https://doi.org/10.1016/j.cub.2006.07.015>
- Jenkins HM, Barrera FJ, Ireland C, Woodside B (1978) Signal-centered action patterns of dogs in appetitive classical conditioning. *Learn Motiv* 9:212–296
- Jerolmack C (2009) Humans, animals, and play: theorizing interaction when intersubjectivity is problematic. *Social Theory* 27(4):371–389
- Kaminski J, Tempelmann S, Call J, Tomasello M (2009) Domestic dogs comprehend human communication with iconic signs. *Dev Sci* 12(6):831–837
- Kawai M (1965) Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates* 6(1):1–30
- Krutzen M, Mann J, Heithaus MR, Connor RC, Bejder L, Sherwin WB (2005) Cultural transmission of tool use in bottlenose dolphins. *Proc Natl Acad Sci* 102(25):8939–8943
- Kupán K, Miklósi Á, Gergely G, Topál J (2011) Why do dogs (*Canis familiaris*) select the empty container in an observational learning task? *Anim Cogn* 14(2):259–268
- Lakatos G, Soproni K, Dóka A, Miklósi Á (2009) A comparative approach to dogs' (*Canis familiaris*) and human infants' comprehension of various forms of pointing gestures. *Anim Cogn* 12(4):621–631
- Laland K, Galef B (Eds.) (2009) The question of animal culture. Harvard University Press, Cambridge
- Laland K, Hoppitt W (2003) Do animals have culture. *Evol Anthropol* 12(3):150–159
- Leadbeater E, Raine NE, Chittka L (2006) Social learning: ants and the meaning of teaching. *Curr Biol* 16(9):R323–R325. <https://doi.org/10.1016/j.cub.2006.03.078>
- 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. *Behav Processes* 34(1):43–53
- Lefebvre L, Templeton J, Brown K, Koelle M (1997) Carib grackles imitate conspecific and Zenaida dove tutors. *Behaviour* 134(13):1003–1017
- Lycett SJ, Collard M, McGrew WC (2007) Phylogenetic analyses of behavior support existence of culture among wild chimpanzees. *Proc Natl Acad Sci USA* 104(45):17588–17592
- McGettrick J, Range F (2018) Inequity aversion in dogs: a review. *Learn Behav* 46:479–500. <https://doi.org/10.3758/s13420-018-0338-x>
- Mery F, Varela SAM, Danchin E, Blanchet S, Parejo D, Coolen I, Wagner RH (2009) Public versus personal information for mate copying in an invertebrate. *Curr Biol* 19(9):730–734
- Miklósi Á (2014) Dog behaviour, evolution, and cognition. Oxford University Press, Oxford
- Miklósi Á, Kubinyi E, Topál J, Gácsi M, Virányi Z, Csányi V (2003) A simple reason for a big difference. *Curr Biol* 13(9):763–766. [https://doi.org/10.1016/S0969-9822\(03\)00263-X](https://doi.org/10.1016/S0969-9822(03)00263-X)
- Miklósi Á, Topál J (2012) The evolution of canine cognition. In: Vonk J, Shackelford TK (eds) The Oxford handbook of comparative evolutionary psychology. Oxford University Press, Oxford, pp. 194–213
- Mondémé C (2019) La socialité interspécifique: Une analyse multimodale des interactions hommes/chiens. Lambert-Lucas, Limoges
- Naderi S, Miklósi Á, Dóka A, Csányi V (2001) Co-operative interactions between blind persons and their dogs. *Appl Anim Behav Sci* 74(1):59–80
- Odendaal JS, Meintjes RA (2003) Neurophysiological correlates of affiliative behaviour between humans and dogs. *Vet J* 165(3):296–301
- Osiurak F, De Oliveira E, Navarro J, Lesourd M, Claudière N, Reynaud E (2016) Physical intelligence does matter to cumulative technological culture. *J Exp Psychol* 145(8):941–948. <https://doi.org/10.1037/xge0000189>
- Ostermeier M (2010) History of guide dog use by veterans. *Mil Med* 175(8):587–593
- Otoni EB, Mannu M (2001) Semifree-ranging tufted capuchins (*Cebus apella*) spontaneously use tools to crack open nuts. *Int J Primatol* 22(3):347–358. <https://doi.org/10.1023/a:1010747426841>
- Pike TW, Kendal JR, Rendell LE, Laland KN (2010) Learning by proportional observation in a species of fish. *Behav Ecol* 21(3):570–575. <https://doi.org/10.1093/beheco/arq025>
- Pongracz P, Miklósi Á, Kubinyi E, Gurobi K, Topál J, Csányi V (2001) Social learning in dogs: the effect of a human demonstrator on the performance of dogs in a detour task. *Anim Behav* 62(6):1109–1117
- Putnam P (1997) Love in the lead: the miracle of the seeing eye dog. University Press of America, Lanham
- Range F, Virányi Z (2013) Social learning from humans or conspecifics: differences and similarities between wolves and dogs. *Front Psychol* 3(4):868
- Rendell L, Whitehead H (2001) Culture in whales and dolphins. *Behav Brain Sci* 24(2):309–324. discussion 324–382
- Richardson TO, Sleeman PA, McNamara JM, Houston AI, Franks NR (2007) Teaching with evaluation in ants. *Curr Biol* 17(17):1520–1526. <https://doi.org/10.1016/j.cub.2007.08.032>
- Rossano F (2013) Sequence organization and timing of bonobo mother–infant interactions. *Interact Stud* 14(2):160–189
- Seppänen J-T, Forsman JT (2007) Interspecific social learning: novel preference can be acquired from a competing species. *Curr Biol* 17(14):1248–1252
- Sherry DF, Galef BG (1990) Social learning without imitation: more about milk bottle opening by birds. *Anim Behav* 40(5):987–989
- Shettleworth SJ (2009) Cognition, evolution, and behavior. Oxford University Press
- Sperber D (2006) Why a deep understanding of cultural evolution is incompatible with shallow psychology. In: Enfield NJ, Levinson S (eds) Roots of human sociality. Berg, Oxford, New York
- Sperber D, Claudière N (2008) Defining and explaining culture. *Biol Philos* 23(2):283–292
- Terkel J (1996) Cultural transmission of feeding behaviour in the black rat (*Rattus rattus*). In: Heyes CM, Galef BG (eds) Social learning in animals: the roots of culture. Academic Press, London, UK, pp. 17–47
- Thornton A, McAuliffe K (2006) Teaching in wild meerkats. *Science* 313(5784):227–229
- Thornton A, Raihani N (2008) The evolution of teaching. *Anim Behav* 75(6):1823–1836



- Topál J, Gácsi M, Miklósi Á, Virányi Z, Kubinyi E, Csányi V (2005) Attachment to humans: a comparative study on hand-reared wolves and differently socialized dog puppies. *Anim Behav* 70(6):1367–1375
- Trut LN (2000) Early canid domestication: the farm-fox experiment. *Scientific* 24(2):124–124
- van de Waal E, Borgeaud C, Whiten A (2013) Potent social learning and conformity shape a wild primate's foraging decisions. *Science* 340(6131):483–485
- van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Merrill M (2003) Orangutan cultures and the evolution of material culture. *Science* 299(5603):102–105
- Virányi Z, Gácsi M, Kubinyi E, Topál J, Belényi B, Ujfalussy D, Miklósi Á (2008) Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Anim Cogn* 11(3):373
- Want SC, Harris PL (2002) How do children ape? Applying concepts from the study of non-human primates to the developmental study of 'imitation' in children. *Dev Sci* 5(1):1–14. <https://doi.org/10.1111/1467-7687.00194>
- Whiten A (2005) The second inheritance system of chimpanzees and humans. *Nature* 437(7055):52–55
- Whiten A, Caldwell CA, Mesoudi A (2016) Cultural diffusion in humans and other animals. *Curr Opin Psychol* 8:15–21. <https://doi.org/10.1016/j.copsyc.2015.09.002>
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Boesch C (1999) Cultures in chimpanzees. *Nature* 399(6737):682–685
- Whiten A, Hinde RA, Stringer CB, Laland KN (2011) Culture evolves. *Philos Trans R Soc Lond B* 366:938–948
- Whiten A, Horner V, de Waal FB (2005) Conformity to cultural norms of tool use in chimpanzees. *Nature* 437(7059):737–740
- Whiten A, Horner V, Litchfield CA, Marshall-Pescini S (2004) How do apes ape? *Learn Behav* 32(1):36–52
- Whiten A, McGuigan N, Marshall-Pescini S, Hopper LM (2009) Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philos Trans R Soc B* 364(1528):2417–2428. <https://doi.org/10.1098/rstb.2009.0069>
- Whiten A, Mesoudi A (2008) Establishing an experimental science of culture: animal social diffusion experiments. *Philos Trans R Soc B* 363(1509):3477–3488
- Wilkinson A, Kuenstner K, Mueller J, Huber L (2010) Social learning in a non-social reptile (*Geochelone carbonaria*). *Biol Lett* 6(5):614–616. <https://doi.org/10.1098/rsbl.2010.0092>
- Worden BD, Papaj DR (2005) Flower choice copying in bumblebees. *Biol Lett* 1(4):504–507. <https://doi.org/10.1098/rsbl.2005.0368>
- Zwirner E, Thornton A (2015) Cognitive requirements of cumulative culture: teaching is useful but not essential. *Sci Rep* 5:16781. <https://doi.org/10.1038/srep16781>

### Competing interests

The authors declare no competing interests.

### Additional information

Correspondence and requests for materials should be addressed to D.G.

Reprints and permission information is available at <http://www.nature.com/reprints>

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2020