Opinion

Lessons from animal teaching

William J.E. Hoppitt[1], Gillian R. Brown[2], Rachel Kendal[3], Luke Rendell[1], Alex Thornton[4], Mike M. Webster[1] and Kevin N. Laland[1]

[1] Centre for Social Learning and Cognitive Evolution, School of Biology, University of St. Andrews, Bute Medical Building, St. Andrews, Fife KY16 9TS, UK
[2] Centre for Social Learning and Cognitive Evolution, School of Psychology, University of St. Andrews, St. Mary's College, South Street, St. Andrews, Fife KY16 9JP, UK
[3] Department of Anthropology, University of Durham, Durham DH1 3HN, UK
[4] Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

Many species are known to acquire valuable life skills and information from others, but until recently it was widely believed that animals did not actively facilitate learning in others. Teaching was regarded as a uniquely human faculty. However, recent studies suggest that teaching might be more common in animals than previously thought. Teaching is present in bees, ants, babblers, meerkats and other carnivores but is absent in chimpanzees, a bizarre taxonomic distribution that makes sense if teaching is treated as a form of altruism. Drawing on both mechanistic and functional arguments, we integrate teaching with the broader field of animal social learning, and show how this aids understanding of how and why teaching evolved, and the diversity of teaching mechanisms.

Introduction

Many animal species learn skills and acquire information from others, ranging from food-processing and predator-evasion techniques to calls and songs [1–3], but until recently it was widely believed that animals typically did not teach – that is, they did not actively facilitate learning in others. Any learned information transmitted between individuals was characterised as 'inadvertent social information' [4], with experienced individuals thought rarely to adjust their behaviour to educate the naïve. Indeed, teaching, together with imitation, has been lauded as the mental faculty that underlies complex human culture by promoting the high transmission fidelity deemed necessary for cumulative culture [5–8]. Recent research challenges these assumptions, revealing strong candidate cases of teaching in a diverse set of species (Table 1).

Early studies of animal teaching were hampered by an anthropocentric viewpoint. The 'type specimen' of a teacher was a traditional schoolteacher, and definitions of teaching stressed the intention of the tutor to educate [9], a stance that effectively restricted teaching to our own species because intentions are difficult to infer in non-humans. Progress was made when Caro and Hauser [10] adopted a functional perspective (see Box 1), defining teaching according to observable criteria:

> "An individual actor **A** [the *tutor*] can be said to teach if it modifies its behaviour only in the presence of a naïve observer, **B** [the *pupil*], 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 so, or would not learn at all" (p. 153).

Caro and Hauser [10] were able to point to just two compelling examples of teaching, in cheetahs *Acinonyx jubatus* and domestic cats *Felis silvestris catus* [11–13] although, taken alone, neither unequivocally met their criteria. Mother cats with kittens, and cheetahs with young cubs, do not kill and eat their prey as felids without offspring do. Instead they bring the prey back to their offspring, in dead, disabled or intact form depending on the age of the young, seemingly so that the latter can practise hunting. Similar behaviour has been reported in a range of other carnivores [10]. Recent work has confirmed that, for meerkats *Suricata suricatta* at least, the behaviour satisfies Caro and Hauser's definition [14] (see Box 2). Other recent work in tandem-running ants *Temnothorax albipenni*, where an informed individual leads a naïve nest-mate to food, is also a strong case by these criteria [15] (see Box 3). This meerkat and ant research represents an empirical standard for work in this area. However, several other candidate cases have also recently come to light, summarised in Table 1 (for a review, see Ref. [14]). Taken together, these findings suggest a taxonomic distribution of animal teaching that is perhaps counterintuitive, with teaching not necessarily occurring in species closely related to humans (see Box 4), such as chimpanzees *Pan troglodytes*. Below we argue that application of Hamilton's rule to cases of teaching makes better sense of this distribution than the anthropocentric reasoning that pervades many discussions of animal teaching (see Box 4). However, we begin by reclassifying teaching mechanisms to reveal how they relate to other forms of social learning, and go on to show how this aids understanding of both how teaching could evolve and why different teaching mechanisms are observed in different animals.

Mechanisms of teaching

Caro and Hauser [10] proposed two categories of teaching in animals, 'opportunity teaching,' where the teacher puts

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Corresponding author: Laland, K.N. (knl1@st-andrews.ac.uk).

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Table 1. Potential evidence for teaching in non-human animals[a]

Species	Tutor modifies behaviour in presence of pupil	Cost or no immediate benefit to tutor	Evidence that pupil learns useful skills or knowledge earlier or more efficiently	Possible additional immediate benefits to pupil	Refs
Ants	S: Knowledgeable ants guide naïve workers to food by 'tandem running.' Tutor sensitive to feedback from pupil.	S: Fourfold increase in time taken to get to the food.	M: Some evidence that the route to food is learned, but has not been directly demonstrated (see Box 3).	Results in immediate access to food source for the pupil. But less effective than carrying (see Box 3).	[15,48]
Bees	S: *Apis*: Knowledgeable workers perform waggle dance, informing naïve individuals of direction and quality of food. *Melipona*: Knowledgeable workers produce sound pulses to transmit foraging information.	S: Increased competition for food. Increased latency to next foraging expedition.	S: Route to food and characteristics of food (e.g. odor) learned.	None obvious: immediate access to food source is only possible through the pupil's learning.	[45,47,64,65]
Callitrichid monkeys	S: In the presence of infants, adults emit 'food-offering' vocalisations when in possession of food or when they have located a hidden prey item.	L: Increased competition for food and increased foraging time. Potential attraction of predators.	L: Access to otherwise unobtainable animal prey or difficult-to-process fruits. Possible improvement in foraging skills.	Nutritional benefits.	[66–68]
Cheetahs	S: Caught prey not killed but transported and released to cubs.	S: Increased latency to eat. Potential loss of prey.	L: Purported increase in hunting skills due to opportunity to practise on caught prey; not proven but likely.	None obvious.	[13]
Domestic cats	S: Caught prey not killed but transported and released to kittens.	L: Plausibly as for cheetahs, but not yet demonstrated.	S: Laboratory experimental evidence that predatory skills are acquired earlier in life owing to opportunity to practise on caught prey.	None obvious.	[11,12]
Domestic fowl	S: Mothers peck at ground and call chicks to draw attention to palatable food. Call intensity increases when chicks consume unpalatable food.	W: Increased latency to eat. Increased competition for food.	W: Purported increase in foraging skills due to opportunity to identify appropriate food. Indirectly supported by transmission of arbitrary maternal food preferences to offspring.	Prevents feeding on poisonous/unpalatable food.	[24]
Meerkats	S: Caught prey not killed but transported to and released to pups. Scorpions can be disabled before presentation to younger (less experienced) pups.	S: Potential loss of prey. Increased latency to eat, while monitoring the performance of the pup.	S: Increase in hunting ability due to opportunity to practise skills on otherwise unobtainable/dangerous prey. Pups experimentally exposed to live scorpions learned to handle them at an earlier age.	None obvious.	[14]
Pied babblers	S: Adults give 'purr' calls to nestlings before food presentation.	S: Evidence that 'purr' calls are energetically costly.	S: Nestlings experimentally exposed to additional 'purr' call-food contingencies learned the appropriate response earlier. Later used to recruit the pupil to food patches, and to lure them away from dangerous situations.	Other functions to calling at the nest?	[20,21]

[a] Columns 2–4 each correspond to a criterion in the definition by Caro and Hauser [10]. We include cases where the first criterion of teaching (first column) appears to be adequately met by the data and the second and third criteria (second and third columns) are at least plausible. We give our interpretation of the strength of the evidence in each case: S = strong evidence; M = moderate evidence; W = weak evidence; L = not proven but highly plausible. The fifth column gives possible benefits to the pupil that are unrelated to teaching (see Box 1), signifying the tutor's behaviour might have an alternative function, with learning as an inadvertent byproduct. Note that whereas in virtually all cases experimental evidence is currently observed in just a single species, the candidate teaching behaviour is reported in multiple, closely related species. We include only cases where the sample size is reasonable (>5 instances/individuals involved).

Box 1. Defining 'teaching'

Conceptually, we view 'teaching' as a class of behaviour patterns that are adaptations for transmitting knowledge and skills to others. Caro and Hauser's widely adopted operational definition [10] is designed to minimise the probability of a false report of animal teaching by ruling out behaviour that might be adapted for a different function. It is important to keep this distinction between a conceptual definition (what teaching is) and an operational definition (how we detect it) in mind; behaviour is always subject to multiple selection pressures, and this operational definition will miss out on potentially numerous cases where a teaching function modifies the selection favouring a behaviour that already benefits the performer. Accordingly, we endorse Caro and Hauser's definition with one caveat. Their requirement that there be a cost or no immediate benefit to the tutor is only partially successful in ruling out behaviour with alternative functions. For instance, parental provisioning is costly and can transmit dietary preferences to offspring, but it might have evolved because selection benefits parents that provide nutrition to their young, rather than because provisioning functions to teach. Consequently, for cases where behaviour increases the inclusive fitness of the tutor irrespective of whether knowledge is transmitted to the pupil to be regarded as teaching, we would require evidence that the tutor's behaviour has been modified by selection to promote learning.

One means by which behaviour could be so modified is if the tutor responds to feedback from the pupil, such as in tandem-running ants (see Box 2). Some have suggested that feedback should even be considered diagnostic of teaching [15,48]. However, there are other ways in which modified behaviour could promote learning. For instance, meerkat helpers, although they do monitor their pupil to some degree, do not directly assess the hunting ability of a pup to give it an appropriately processed scorpion. However, the helpers have evolved a differential response to the call of the pup, which ensures that, as pups get older, they are given scorpions of increasing difficulty (Box 2).

Leadbeater *et al.* [46] argue that 'teaching' should be restricted to the passing on of 'skills, concepts, rules and strategies,' differentiating this from 'telling' another individual a fact, such as the location of a particular food source. Csibra [49] makes a similar argument. However, this distinction would require much of human teaching to be recategorised as telling, or we risk imposing stricter criteria for animals than humans [50]. Moreover, the distinction between teaching and telling is often unclear: if an individual tells another about the location of a food, and the recipient consequently learns that food of that type is good to eat, it could be said to have acquired a general rule.

Box 2. Teaching in meerkats

Young meerkat *Suricata suricatta* pups (Figure I) are almost entirely reliant on food provisioned by older group members, including both parents and helpers [51], yet by 3 months of age they are nutritionally independent and can handle a variety of difficult prey, including lizards, spiders and potentially dangerous scorpions. Recent work shows that adults facilitate this transition by gradually introducing pups to live prey [14]. This process meets all the criteria of Caro and Hauser's definition of teaching [10]. Adults normally consume prey immediately upon catching it, but when young pups are present, they typically kill or disable mobile prey before carrying it to a begging pup. Scorpions are often disabled by removing the sting, allowing pups to interact safely with the live prey. As pups grow older, they are increasingly given intact prey. The decision to modify prey before provisioning does not depend on a tutor's capacity to gauge the level of skill of the pupil, but on responses to changes in pup begging calls with age. Playbacks of the begging calls of old pups to groups with young pups caused adults to bring live prey, even though the pups were too young to handle it. Conversely, playing back the calls of young pups to groups with old pups caused an increase in the proportion of prey provisioned dead. Nevertheless, adult behaviour is not inflexible, but shows some sensitivity to the performance of pups, including nudging prey items if pups ignore them, retrieving escaped prey and further modifying it if pups struggle. This provisioning strategy incurs costs, because time is spent monitoring pups handling live prey and there is a risk that pups will lose the item. Finally, unlike previous studies describing similar patterns of provisioning in felids, there is strong experimental evidence that the behaviour of adult meerkats promotes skill acquisition by pups. Pups that were artificially given additional opportunities to handle live, stingless scorpions subsequently outperformed siblings that were given dead scorpions, showing that the opportunity to practise on disabled scorpions facilitates skill acquisition. As pups very rarely find mobile prey items themselves, helpers can actively facilitate the acquisition of handling skills by giving them otherwise unavailable opportunities to handle difficult prey. In the long term, this offsets the costs of teaching by providing adults with multiple potential benefits including a reduction in the costs of provisioning by hastening the acquisition of independence, kin-selected benefits of increased pup survival and benefits of increased group size [52].

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Figure I. Meerkat adult and pup. Picture by Katherine McAuliffe.

the pupil in 'a situation conducive to acquiring a new skill or knowledge,' and 'coaching,' where a tutor directly 'alters the behaviour of [a pupil] by encouragement or punishment.' However, recent cases do not easily fit into this scheme. Here we propose a more comprehensive categorisation, which has the additional benefit that it aligns teaching phenomena with 'inadvertent' social learning.

Researchers of animal social learning recognise several processes by which social learning can occur ('local enhancement,' 'observational conditioning,' 'imitation' etc.) [16,17], some of which are defined in Table 2. Currently, teaching is regarded as contributing additional mechanisms of information transfer to the list of social learning processes. Here we suggest an alternative way to think about teaching. Social learning mechanisms relate primarily to psychological processes in the observer (pupil), whereas teaching processes relate specifically to activities of the demonstrator (tutor): clearly, a full description of information transmission requires both. The presence or absence of 'active' demonstration (behaviour whose function is to facilitate learning in others) can be regarded as orthogonal to social learning processes, a scheme that has the advantage that it integrates teaching with research into social learning (see Table 2). Hence, it is possible to categorise instances of teaching as, for example, 'teaching

Box 3. Tandem-running ants

Tandem running by ants [53–55], where successful foragers guide nest-mates to newly discovered food sources or nest sites, provides another compelling example of teaching. Here, unlike with other cases where uninformed observers follow demonstrators to food (e.g. [56]), there is evidence that the behaviour is adapted to the function of teaching nest-mates the locations of food sources. Research using the species *Temnothorax albipennis* has demonstrated that informed leaders respond to feedback from followers: leaders ran rapidly only after being tapped by the antennae of a follower, enabling the follower to remain in close contact [15]. This resulted in a fourfold increase in the time leaders took to reach food, whereas the followers found food significantly sooner when tandem running than when searching alone. Learning on the part of the follower is inferred from the fact that followers take a more direct return route to the nest than that of the leader on its initial return, before the tandem-running event.

Tandem running does have an alternative benefit to a leader's inclusive fitness: another ant is available to help carry food back to the nest. However, there is strong evidence that tandem running has evolved for a teaching function. First, it is more efficient for leaders to carry naïve ants directly to the food, as they sometimes do; however, when this occurs, route learning almost certainly does not take place, because the ant is typically carried upside down, and facing backward [57]. Observations of other species of ants during nest emigration support this [54]. *Leptothorax* spp. use both tandem running and carrying to transport fellow workers to a new nest site. During the first phase of the move, the number of tandem runners stays constant, but the number of carriers increases, indicating that the number of workers with knowledge of the route is increasing. Once the population at the new nest site reaches a critical mass, tandem running ceases, and the remaining workers are carried. This suggests that the function of tandem running during nest emigration is to ensure that enough workers know the location of the new nest site to enable the move to occur. Although it has not yet been experimentally demonstrated that followers can find the target location more quickly than naïve individuals on subsequent visits, it is difficult to conceive of a plausible alternative function for tandem running.

Box 4. The anthropocentric view of teaching

Several authors have judged cases of animal teaching on mechanistic similarity with human teaching. For instance, Hauser [58] has emphasised the importance of the distinction between the reflexive teaching of animals and that teaching observed in humans that involves foresight and planning, the latter requiring 'mental tools' such as intentional instruction. Csibra and Gergely [59] argue that teaching evolved in a hominid lineage and is reliant on 'pedagogical cues' such as 'ostensive communication,' 'reference assignment' and linguistic priming. Premack [60] concludes that animal examples are fundamentally different from human teaching, as the latter is uniquely reliant on theory of mind, language competence and an aesthetic motivation to teach. This anthropocentric view sees teaching as an indicator of certain human-like cognitive abilities. The alternative approach that we favour is to consider as teaching any behaviour that is adapted to the purpose of transmitting knowledge and skills to other individuals, regardless of the proximate mechanisms involved. Our approach has the advantage that it both allows us to identify teaching (see Box 1) and provides a basis for analysing the circumstances under which teaching evolved.

Although it is clear that neither language-based nor institutionalised teaching have animal counterparts, recent research reveals a notion of human teaching quite different from the archetypical schoolteacher. Research on human infants has demonstrated specific sensitivity to the presence of cues that accompany the demonstration of behaviour, such as the direction of a mother's gaze. Experiments have shown that such 'pedagogical cuing' directs imitative learning in human children by helping the learner to identify what aspects of the manifested skill represent new and relevant information to be imitated [59]. Whereas pedagogical cuing is usually characterised as uniquely human [59], its reliance on subtle cues rather than direct instruction arguably leaves human teaching looking less distinct from that of animals.

Moreover, the nature of teaching in prehistoric and pre-industrial human societies is far from clear. Although some archaeologists have interpreted Paleolithic tool finds as signifying teaching [61], it is difficult to rule out a more passive form of information transfer. There is surprisingly little evidence of teaching among modern-day hunter-gatherers, in comparison to learning by imitation [62]. One study of !Kung infants noted that 'adult tuition related to object manipulation seems minimal' [62]. Even for complex cultural content, human 'instruction' can be very sparse. For example, the transmission of rug weave patterns in Iranian tribal populations occurs in virtual silence, and largely through inadvertent demonstration with occasional active intervention [63]. Human and animal teaching might be less distinct than implied by advocates of the anthropocentric viewpoint.

through local enhancement' or 'teaching through imitation.' From the perspective of the pupil, such phenomena would be identical to their inadvertent social learning equivalent, but here a tutor will have actively demonstrated a behaviour pattern or actively drawn attention to a location, with the specific function of transmitting information to the pupil. Potentially, cases could be categorised further on the teaching dimension by specific features of the tutor's teaching behaviour, such as response to feedback (see Box 1).

Some candidate cases of teaching can be accounted for by 'local enhancement' [18], which occurs when the behaviour of one individual draws the attention of another to a particular part of the environment, about which the observer learns after visiting that location. Many species of birds and mammals aggregate and follow other individuals, which can result in observers learning where to find food [19]. In most cases, there is no evidence that the experienced are actively leading the inexperienced to food; rather than teaching, they are providing an inadvertent cue as they go about their own business. Tandem running in ants (Box 3) can be viewed as an otherwise equivalent case, but one in which the behaviour of the tutor has been adapted to the function of leading the pupil to the food, with leader ants adjusting their behaviour to ensure they are followed [15].

Teaching can also occur when a tutor actively exposes the pupil to a relationship between stimuli, a case of 'observational conditioning' [16] (Table 2). A possible case is provided by pied babblers *Turdoides bicolor*, which give a 'purr' call before presenting food to nestlings, allowing the nestlings to learn the association between call and food [20]. The call, which is costly to produce and, when used at the nest, has no obvious benefit to the adult, is later used to lead fledglings away from danger and recruit them to food patches [21,22]. Adults might be teaching nestlings an association that is useful in later life.

'Opportunity teaching' and 'coaching' can also be incorporated into our scheme, even though there are no commonly used terms to describe their non-teaching equivalent. In carnivores such as meerkats, mothers and helpers provide young with the opportunity to interact with prey and engage in operant learning. Meerkat helpers do not merely give pups scorpions to practise on, but present first dead, then disabled, then intact scorpions,

Table 2. Parallel classification of processes involved in social learning based on 'inadvertent'[a] information and social learning based on teaching, with plausible examples

Type	Inadvertent social learning	Teaching
Local enhancement	A *demonstrator inadvertently attracts an observer to a specific location, leading to the observer learning.* Naïve guppies follow informed individuals to food [56].	*The behaviour of the tutor functions to attract a pupil to a specific location, leading to the observer learning.* Tandem running in ants [15], in which leader ants slow down to ensure followers keep in touch (Box 3).
Observational conditioning	*The behaviour of the demonstrator inadvertently exposes an observer to a relationship between stimuli, allowing the observer to form an association between them.* Blackbirds learn to recognise predators through observing birds mobbing unfamiliar objects [69].	*The behaviour of the tutor functions to expose a pupil to a relationship between stimuli, causing the pupil to form an association between them.* Adult babblers expose nestlings to the relationship between the 'purr' call and food [20].
Imitation	*After observing a demonstrator perform a novel action, an observer learns to reproduce that action.* Birds learn to produce novel sounds through vocal imitation [70].	*The behaviour of the tutor functions to demonstrate a novel action, causing the pupil to learn how to perform it.* A human tennis coach demonstrates a shot.
Opportunity providing	*The products of the behaviour of the demonstrator provide the observer with an opportunity to engage in operant learning that would otherwise be unlikely to arise, for example by providing an easier, less dangerous or more accessible version of the task.* Black rat pups in Israel steal semiprocessed pinecones from their mothers [23].	*The behaviour of the tutor functions to produce products which provide the pupil with an opportunity to engage in operant learning that would otherwise be unlikely to arise, for example by providing an easier, less dangerous or more accessible version of the task.* Adult meerkats provide pups with dead, disabled or live scorpions depending on the pups' age [14].
Coaching/inadvertent coaching	*The response of a demonstrator to the behaviour of the observer inadvertently acts to encourage or discourage that behaviour.* Female cowbirds respond to preferred male songs with 'wing stroking,' which acts to reinforce that song in the male [25].	*The response of the tutor to the behaviour of the pupil functions to encourage or discourage that behaviour.* Mother hens attract their chicks away from food the mother perceives to be unpalatable [24].

[a] Use of the term 'inadvertent' signifies that the demonstrator's behaviour is not adapted to the function of transmitting knowledge or skills to the observer, and does not imply that teaching requires any intentionality on the part of the tutor. Other social learning processes exist, which might also prove to have a teaching equivalent.

as the pups age. Here Caro and Hauser's term 'opportunity teaching' seems more appropriate than current social learning terms, but there are parallel cases of social learning where the behaviour of the demonstrator seems to have inadvertently provided the opportunity for an observer to engage in operant learning, which we call 'opportunity providing.' The mechanism by which black rats *Rattus rattus* in Israel learn how to strip pinecones for seeds is an example [23]. Although pups raised by a 'stripper' mother or foster mother learn to strip cones, naïve adult rats do not. However, adults can learn to strip if provided consecutively with pinecones with decreasing numbers of stripped scales [23]. It seems that rat pups learn to open cones through 'stealing' partially opened cones from their mother, providing them with the opportunity to learn the task backward, like the above adult rats.

The maternal display of the domestic fowl *Gallus gallus domesticus* is a candidate case of 'coaching.' The display includes food calls and pecks directed at food and at the ground, which act to attract chicks toward palatable, and away from unpalatable, food [24]. There are also cases, which we label 'inadvertent coaching,' where the demonstrator's response to the observer's behaviour acts to punish or reinforce that behaviour, even if the demonstrator's response is not obviously an adaptation for that purpose. For instance, when female brown-headed cowbirds *Molothrus ater* hear a preferred song from a male cowbird, they respond with a 'wing-stroking' display, which encourages performance of that song in the male [25]. Wing stroking has an alternative function related to courtship, and would not qualify as a case of teaching; rather, female cowbirds inadvertently shape male behaviour.

In summary, instead of being seen as a separate set of mechanisms for information transfer, teaching can usefully be regarded as introducing another dimension to social learning, corresponding to whether the role of the demonstrator is active or passive. Because many of the processes thought to underlie social learning in animals do not rely on human-like mechanisms, such as intentionality, the same should hold for teaching. This categorisation helps us to understand how teaching could evolve; teaching will often arise as signals, or responses, given by tutors that take advantage of pre-existing social learning mechanisms.

Evolution of teaching

We expect that specific forms of teaching will have evolved from the ancestral condition of the equivalent form of inadvertent social learning. For example, teaching by local enhancement is only likely to evolve in a population that exhibits inadvertent local enhancement. This is because, to teach in this way, a tutor need only evolve signals or other behaviour necessary to increase the likelihood or efficiency of local enhancement in the pupil. Further evolutionary modifications might enhance the effectiveness of those cues or selectivity in the circumstances in which they are produced. This recognition offers a plausible path by which teaching can evolve even in a wide range of taxa.

Take the display of the mother hen: it is known that the observation of another individual pecking will elicit pecking in chicks and attract them to a specific location [26–28]. The maternal display might have evolved as a superstimulus that takes advantage of this pre-existing response, and to have been further modified by selection to facilitate adaptive food choice in chicks. We suspect that many cases of animal teaching will prove to rely on signals that act to attract a pupil toward or away from a particular location.

Our hypothetical evolutionary pathway from inadvertent social learning to teaching leads us to predictions regarding the taxonomic distribution of different types of teaching: we expect teaching to have evolved only where the relevant social learning mechanism was already in place, a prediction that can be tested using comparative statistical methods. This reasoning provides a guide for future research. For instance, we would not expect to find teaching by imitation in meerkats or other carnivores, because imitation has not been found in the Carnivora, but we might expect teaching by imitation to occur in the parrot family (Psittacidae), where there is such evidence [29,30]. By contrast, teaching by observational conditioning, which is merely reliant on classical conditioning, is likely to be less taxonomically restricted.

We do not suggest that the transition from social learning through inadvertent cues to teaching by active signals is inevitable. Teaching must evolve in the tutor, but its immediate benefits, the learning of a skill or acquisition of information, are for the pupil. Because it is a costly behaviour that benefits others, teaching can be understood in a similar way to altruism. As with altruism, we would expect teaching behaviour ultimately to benefit the tutor's inclusive fitness, either through kin selection [31] or because the tutor benefits directly from the pupil learning [32]. In the case of kin selection, teaching will evolve according to Hamilton's rule: if the fitness cost to the tutor (c) is less than the fitness benefit to the pupil (b), multiplied by the degree of relatedness between them (r), or $c < br$ [31].

The benefits of teaching clearly depend on the resulting increase in the probability that pupil learning occurs, or increase in the rate or efficiency of learning [32]. This factor must be quantified relative to the probability that learning occurs asocially or via an inadvertent demonstrator, because such learning can occur in the absence of teaching. Therefore, we only expect teaching to evolve when the equivalent form of inadvertent social learning is relatively ineffective or when there are few opportunities for social or individual learning. This might help to explain why teaching is rare in chimpanzees and other non-human apes, species that are known to be extremely capable social learners [33]. Young chimpanzees generally feed alongside their mothers for extended periods of their life, which potentially provides youngsters with considerable opportunities for social learning [34,35], with little selective advantage to active information transfer. Conversely, in meerkats, where teaching is present, there are few opportunities for pups to acquire foraging skills by inadvertent social learning, because foraging adults will rapidly consume a fast-moving scorpion [14]. Unlike other apes, in humans, teaching could have been favoured by the requirement to transmit complicated skills and technology that are not easily acquired through inadvertent social learning.

Another potential benefit of teaching for the pupil is to reduce the costs of learning. This might be especially important when learning a dangerous skill, such as meerkats learning to deal with scorpions. Here, provisioning behaviour has been modified to increase the probability that pups will receive a scorpion in a form appropriate to their age [14] (see Box 2). If a pup encounters an intact scorpion before it is able to deal with it, the prey is likely to escape or, worse, sting the pup. Contrast this with the rat pup learning how to strip pinecones: there is little impact on fitness if the youngster steals pinecones that are beyond its ability to strip, because pinecones do not pose a threat.

Now consider the fitness costs of teaching to the tutor. These will effectively be reduced if the tutor benefits directly from the pupil learning [32]. Dependent infants are a burden to parents and alloparents, creating a selective advantage to adults who behave in ways that lead offspring to acquire relevant life skills early. In meerkats,

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Figure 1. The honeybee waggle dance. If teaching is defined according to the criteria of Caro and Hauser [10], then the waggle dance of honeybees *Apis mellifera* [45], historically not considered as teaching, could be seen in a similar light to tandem running in ants [46]. There is little doubt that the waggle dance is costly to perform, and experimental studies reveal evidence of learning in the pupil [47]. Honeybees will dance on an empty 'dance floor' [48], which might seem to contradict the requirement that a tutor modifies its behaviour only in the presence of the pupil. However, the waggle dance occurs only in a context in which it would reliably be observed by other workers, and so functions in the same way as behaviour that is conditional on the presence of a pupil. Consequently, we suggest that the waggle dance, and indeed other forms of communication in bees, constitute strong cases of teaching (Table 1). Picture copyright: Scott Camazine.

for instance, adult helpers are required to provision weaned offspring for several weeks before the offspring become competent, nutritionally independent foragers [14]. Teaching young animals foraging skills allows them to become independent earlier, which means they do not have to be provisioned as long [32]. This saving in the costs of provisioning is offset against the costs of teaching. Candidate cases of teaching appear to be disproportionately found in cooperative breeders – meerkats, tamarins *Saguinus* spp., babblers, ants, bees *Apis* spp. (see Figure 1) and even humans [36]. This could either be because cooperative breeding promotes teaching, or because some other factor, perhaps the high costs of rearing, generates selection for both cooperative breeding and teaching.

Finally, consider the degree of relatedness. Teaching is more likely to evolve in species where the average relatedness between interacting individuals is high, or to occur selectively between individuals of high relatedness. This could explain why teaching appears to be present in many eusocial insect colonies, where the average relatedness tends to be higher than in other animal populations. As relatedness varies considerably among the hymenoptera, there are opportunities here for comparative analyses that test to what extent teaching conforms to Hamilton's rule. In other species, when the costs of teaching are high, we would expect teaching to occur mainly between close kin, whereas less costly teaching might occur between more distant relatives. However, high relatedness is not obligate for the evolution of teaching: in meerkats, direct benefits seem more important (see Box 2).

In summary, we would expect teaching to evolve in the tutor when (i) the relevant social learning mechanism is already in place in the observer and (ii) the tutor benefits from the pupil learning, either directly or through kin selection. In time, these predictions could be tested using comparative statistical methods [37]. From this perspective, the most important task for researchers of animal teaching is to investigate more fully the taxonomic distribution of teaching. In light of the scheme presented here, many established cases of social learning could be re-examined from the demonstrator's perspective, with the above reasoning as a guide to plausible candidates for teaching. However, caution is needed in inferring the taxonomy of teaching, because the absence of evidence for teaching might reflect difficulties in studying the species concerned, rather than an absence of teaching. For instance, observational studies of killer whales *Orcinus orca* suggest that some adults might actively teach young to intentionally beach themselves, a technique used to capture pinniped prey [37–41]. In this case, it is implausible that researchers could ever make experimental manipulations similar to those used in studies of meerkats and ants, so 'hard' evidence of teaching is unlikely to be forthcoming.

In debates over whether animals exhibit culture [42], sceptics have argued that human and animal culture differ qualitatively, partly because the former uniquely relies on teaching [6,7], whereas advocates of animal culture have suggested that teaching in animals is currently underestimated and have defended comparative arguments [43]. In fact, both might be correct: teaching could be common in animals, yet reliant on completely different underlying mechanisms from human teaching. Indeed, we expect teaching in other animals not to resemble that in humans, because they will typically be unable to exploit the same learning processes. For instance, humans might be unique in their ability to teach by imitation, and teaching among non-relatives might have been favoured by additional processes such as reciprocity or cultural group selection [39]. Nonetheless, the evolution of human teaching will only be understood by consideration of the costs and benefits. Analogy can be as potent as homology in elucidating evolutionary history, allowing us to draw conclusions about the conditions under which specific traits evolve [44]. The study of animal teaching could provide valuable lessons on this aspect of human evolution.

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