



REVIEW

The evolution of teaching

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(Received 9 August 2007; initial acceptance 19 September 2007;
final acceptance 4 December 2007; published online 22 April 2008; MS. number: RV-75R)

Teaching has long been a neglected area in animal behaviour, despite its relevance for a wide range of topics. In light of recent evidence for teaching in nonhuman animals, research can begin to examine the conditions under which it may evolve. Here, we make the case for an evolutionary perspective that treats teaching as a form of cooperative behaviour which functions to promote learning in others. We outline its key characteristics and discuss the selection pressures that may favour its evolution. Teaching will be favoured by selection only where the costs to teachers of facilitating learning are outweighed by the long-term fitness benefits they accrue once pupils have learned, and these benefits will be scaled by the ease with which pupils could learn without teaching. This perspective allows us to make predictions as to the distribution of teaching, the forms it may take, and the relation between teaching in humans and other species. We conclude by considering how teaching may best be categorized. We suggest that natural selection is likely to favour different forms of teaching, depending on whether it serves to promote learning of procedural or declarative information.

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Keywords: cooperation; culture; evolution; parental care; social learning; teaching

Although debates on the topic of teaching in nonhuman animals first arose four decades ago (Barnett 1968; Ewer 1969), the first review of the topic was not published until 1992, when Caro & Hauser asked ‘is there teaching in non-human animals?’ (Caro & Hauser 1992, page 151). Despite suggestive evidence in a number of species (see Appendix), their question long remained unanswered. However, strong quantitative evidence for teaching has recently emerged from three distantly related species: tandem-running ants, *Temnothorax albipennis* (Franks & Richardson 2006), meerkats, *Suricata suricatta* (Thornton & McAuliffe 2006) and pied babblers, *Turdoides bicolor* (Raihani & Ridley 2008). This suggests that teaching has evolved independently in many unrelated taxa and challenges the assumption that teaching requires complex cognitive abilities (Pearson 1989; Tomasello et al.

1993; Premack & Premack 1996). As evidence for teaching in nonhuman animals emerges, research can begin to examine the conditions under which it is likely to evolve. This will be relevant for a wide range of fields. For example, teaching is often considered to underpin human culture (Boyd & Richerson 1985; Galef 1992; Tomasello 1994), yet studies of cultural transmission have ignored the evolution of teaching. Similarly, although teaching is a cooperative behaviour (Galef et al. 2005) and may often be manifested as a form of parental care (Maestripieri 1995a; Thornton 2007), studies of these key topics in behavioural biology have yet to consider its importance. Recent research on teaching has been dogged by debates over what precisely constitutes teaching (Premack & Premack 1996; Csibra 2007; Thornton et al. 2007) and what its key characteristics may be (Franks & Richardson 2006; Leadbeater et al. 2006). In this review, we aim to clarify the key characteristics of teaching and discuss the conditions under which it may evolve.

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THE EVOLUTIONARY PERSPECTIVE ON TEACHING

The debate over teaching has been polarized between those who favour a definition constrained by cognitive mechanisms (Tomasello et al. 1993; Premack & Premack 1996) and those who favour a broader, more inclusive approach (Caro & Hauser 1992; Maestripieri 1995a). Among researchers of behavioural evolution, the most commonly accepted definition is that proposed by Caro & Hauser (1992), which provides three criteria for teaching: (1) an individual, A, modifies its behaviour only in the presence of a naïve observer, B; (2) A incurs some cost, or derives no immediate benefit; and (3) as a result of A's behaviour, B acquires knowledge or skills more rapidly or efficiently than it would otherwise, or that it would not have learned at all. This definition differentiates teaching from other forms of social learning, in which naïve animals acquire information from other individuals engaging in their usual behaviour. Critically, it treats teaching as a functional category of behaviour and, through its use of testable criteria, has opened the door for rigorous investigation of teaching from an evolutionary perspective.

Evidence for teaching under Caro & Hauser's (1992) definition has been equivocal (Caro & Hauser 1992; Maestripieri 1995a; Rendell & Whitehead 2001; Galef et al. 2005), although this may be largely the result of the difficulties in providing support for all three criteria, rather than the absence of teaching per se (Thornton & McAuliffe 2006). To date, only three studies have satisfied all three criteria. In *T. albipennis*, knowledgeable ants modify their runs to food when accompanied by a naïve follower, continuing the run only when tapped frequently by the follower's antennae. This causes a fourfold reduction in the leader's speed relative to that when alone, but followers in tandem pairs can subsequently become leaders themselves and may learn the route faster than they would have done alone (Franks & Richardson 2006). In meerkats, older group members gradually introduce pups to live, mobile prey. Adults incur costs through giving pups mobile prey that might escape, but pups' handling skills improve as a result of practising handling live prey (Thornton & McAuliffe 2006). Finally, in pied babblers, cooperatively breeding passerines from southern Africa, adults often give specific 'purr' calls during feeding visits at the nest. This behaviour appears to be costly to adults, but it causes nestlings to learn to associate purr calls with food delivery (Raihani & Ridley 2008). Adults give purr calls most frequently in the few days before fledging (days 12–16) and playback experiments showed that the nestling response to purr calls emerges at around day 14 after hatching. However, when purr calls were experimentally played during feeding visits on days 9–11, nestlings responded by day 11. In contrast, playbacks of purr calls outside feeding visits during the same period did not cause nestling responses to emerge sooner. These experiments show that nestlings learn to respond to purr calls, and that calls must be reliably paired with food delivery in order for learning to occur. The benefits of this teaching arise postfledging, when adults use purr calls to lead offspring away from danger (Raihani & Ridley 2007).

Cognitive Perspectives on the Definition of Teaching

Whether these three species are considered to teach is largely a question of perspective. Some researchers consider teaching to be a flexible, generalizable ability facilitated by the ability to make assumptions as to what others know (Olson & Bruner 1996; Premack & Premack 1996). On this premise, teaching in ants, meerkats and babblers is highly unlikely. Indeed, given that evidence for theory of mind and the attribution of mental states is limited and contentious, even among the great apes (Heyes 1998; Penn & Povinelli 2007), the study of teaching would necessarily be restricted to humans.

Although the distinction between the cognitivist and evolutionary perspectives appears merely semantic, it has important implications. Definitions based on unobservable cognitive processes are of little use to researchers in recognizing teaching behaviour when it occurs. Moreover, they create confusion by interweaving proximate and ultimate causation. Like other common terms in biology, such as 'kin recognition' (Hepper 1991), we advocate defining teaching as a functional category, which may occur through different proximate mechanisms.

Some forms of teaching, variously referred to as 'active teaching' (Caro & Hauser 1992), 'intentional teaching' (Byrne 1995) and 'instructive learning' (Tomasello et al. 1993) may require mental state attribution. This may alter the nature of teaching in humans, for example, by allowing greater flexibility, but simpler mechanisms based on responses to behavioural cues from pupils may suffice in many contexts (Thornton & McAuliffe 2006). Indeed, many forms of human tuition do not require teachers to impute mental states to pupils. Parents, for example, promote learning of motor skills in children by encouraging and supporting infants' attempts, modifying their behaviour in response to behavioural cues from the child rather than an awareness of the child's changing knowledge about the world (Whiten & Milner 1984). Similarly, as Barnett (1968) pointed out, university lecturers may simply use one set of lectures for first-year undergraduates and another for advanced classes without being aware of what individual students know. From the perspective of the pupil, the 'pedagogical stance' concept (Csibra & Gergely 2006) suggests that humans may be particularly adept at extracting generalizable information from the behaviour of others. However, as decades of research into social learning have shown that animals across a whole range of taxa are able to learn (albeit in more limited contexts) from others (Heyes & Galef 1996; Galef & Laland 2005), there is no a priori need to assume that the capacity to benefit from teaching is dependent on sophisticated mental faculties.

KEY CHARACTERISTICS OF TEACHING

Caro & Hauser's (1992) definition outlines the criteria necessary to identify teaching, but does not provide a functional basis for understanding what teaching actually is. By clarifying the principal characteristics of teaching we

hope to aid researchers in predicting whether it may evolve in a given species or context. The key characteristics of teaching are threefold: (1) it is a form of cooperative behaviour with response-dependent fitness payoffs; (2) its function is to facilitate learning in others; and (3) it involves the coordinated interaction of a donor and a receiver of information.

(1) Teaching is a cooperative behaviour (Galef et al. 2005) in that one individual engages in an activity that benefits another, at some cost, or with no immediate benefit to itself (West et al. 2007). Ultimately, for such behaviour to be favoured by selection, it must result in positive net fitness payoffs to both parties. In teaching, these payoffs are response dependent and are entirely contingent on learning: teachers gain no benefit unless pupils learn, and the delayed benefits of teaching depend on both the teacher's efficacy and the pupil's aptitude. Since high relatedness may favour the evolution of cooperation (Hamilton 1964), teaching may be most common between closely related individuals, such as workers in eusocial insects or parents and offspring. Teaching may be particularly common as a form of parental care because the large discrepancy in knowledge between adults and infants means that parents can raise their offspring's potential fitness by helping them to learn critical skills or information (Thornton 2007). Specific fitness benefits to teachers may include increased offspring survival, reductions in the period of offspring dependence, communal recruitment to food sources and recruitment of future teachers to the population. Future studies should take inspiration from projects investigating the costs and benefits of other cooperative behaviours (reviewed in Heinsohn & Legge 1999; Dickinson & Hatchwell 2004; see Thornton, in press for discussion of the costs of teaching in meerkats) and begin to generate data on the net fitness consequences of teaching.

(2) In teaching, an individual modifies its behaviour to facilitate learning in another, and not for some other purpose (Maestriperieri 1995a; Thornton et al. 2007). Teaching need not involve higher-order cognitive intentionality (Dennett 1983), but is designed by natural selection to fulfil the 'goal' of promoting learning. Some authors argue that behaviour involved in the transfer of declarative information is better described as 'telling', and that the word 'teaching' should be reserved for skill transfer (Leadbeater et al. 2006). While all teaching is a form of communication in that senders influence the behaviour of receivers (Dawkins & Krebs 1978), we believe that it is worth retaining the term 'teaching' for all behaviour that evolved for the function of promoting learning in others. This clearly distinguishes fixed teaching from other forms of 'telling' or communication.

Restricting the term 'teaching' to behaviour that functions only to promote learning in others is operationally conservative. There may be instances in which behaviour with another function comes under additional positive selection because it also helps others learn. However, we would argue that such cases are better understood under the umbrella of standard social learning, and that classifying them as 'teaching' would merely confuse a nascent field of study. For example, functionally referential alarm

calls (Seyfarth et al. 1980) have an immediate function: alerting conspecifics to the presence of a particular type of predator, so that they may respond accordingly. Although infants may learn associations between given call types and predators simply by hearing the calls in context, learning here is an incidental by-product.

Researchers should consider alternative functions for observed behaviour before invoking teaching. Where there is evidence that behaviour has a clear function other than promoting learning, reference to teaching may be unwarranted (Thornton et al. 2007). In certain cases, however, teaching may be the most parsimonious explanation for behaviour. For example, widespread reports show that mothers in various felid species gradually allow their offspring opportunities to handle live prey (reviewed in Caro & Hauser 1992; Kitchener 1999). Caro (1994) documented costly changes in maternal provisioning behaviour in cheetahs, *Acinonyx jubatus*, as cubs grew older but, owing to the inherent difficulties of studying large carnivores in the wild, failed to detect any effect on the development of cub predatory behaviour. In laboratory studies of domestic cats, *Felis catus*, however, kittens that were consistently exposed to live prey in the presence of their mother showed improved hunting skills compared to kittens that were only exposed to prey alone (Caro 1980a), although the costs of maternal behaviour were not examined. Although neither study completely fulfils all of Caro & Hauser's (1992) criteria, the combined results are highly suggestive of teaching. Furthermore, it seems likely that selection would eliminate seemingly wasteful behaviour such as giving young live prey that might escape unless it serves a function. The most plausible adaptive alternative to teaching is that changes in provisioning behaviour optimize the efficiency of prey transfer from mothers to offspring. However, if this were the case, one would expect mothers to delay releasing live prey until cubs are old enough to have a high probability of catching it. The fact that mothers often release prey to young cubs, which then subsequently lose it, strongly suggests that the optimization hypothesis is unlikely. The most parsimonious explanation for the striking changes in provisioning behaviour in felids is that adults give their young opportunities to handle live prey, thus facilitating learning.

(3) The behavioural coordination of individuals is a critical characteristic of teaching that serves to distinguish it from other forms of social learning and may help in understanding its evolutionary history. In standard social learning, naïve animals attend to knowledgeable individuals, but not vice versa. Indeed, in rats, *Rattus norvegicus*, even the presence of an anaesthetized conspecific or excretory deposits is sufficient to cause naïve individuals to approach a food patch and acquire information (Laland & Plotkin 1991; Galef & Giraldeau 2001). In contrast, teaching is characterized by the interaction of a donor and a receiver of information that attend to each other and engage in different, but coordinated behaviours (Coussi-Korbel & Fragaszy 1995). Teachers must modify their behaviour to produce learning in pupils. However, if pupils are unresponsive, no learning will occur. At the very least, therefore, pupils must attend to teachers. Pied babbler nestlings, for example, respond to the sight of

approaching adults by begging. The subsequent provision of food by adults, accompanied by purr calls, causes nestlings to learn to beg in response to purr calls (Raihani & Ridley 2008). In other cases, coordination may be more intricate. *Temnothorax albipennis* ants in a tandem run, for example, are sensitive to each other's actions, accelerating or decelerating in response to their partner's behaviour (Franks & Richardson 2006; Richardson et al. 2007). In cats and meerkats, adults make contact with prey if the offspring have lost interest in it. This causes the offspring to resume prey handling and often results in precise interdigitation of prey-handling bouts (Caro 1980b; Thornton & McAuliffe 2006).

Efficient behavioural coordination is likely to arise through the coevolution of teacher and pupil strategies. Such coevolution will result in mechanisms whereby each party responds to cues from the other. As some degree of bidirectional feedback between teachers and pupils is likely to be an inevitable characteristic of most teaching interactions, the addition of bidirectionality as an additional criterion to Caro & Hauser's (1992) definition, as proposed by Franks & Richardson (2006), may not be necessary. Moreover, the additional criterion is not necessary to distinguish teaching from other forms of behaviour such as signalling (Leadbeater et al. 2006). However, the behavioural coordination and feedback between individuals does have important implications for the debate over sensitivity and evaluation in teaching. Stringent definitions of teaching require that teachers respond sensitively to pupils' changing competence (Pearson 1989). From a cognitivist perspective, this involves attributing knowledge to pupils and responding flexibly to changes in pupils' knowledge (Pearson 1989; Premack & Premack 1996). However, teachers may show sensitivity simply by adjusting their behaviour in response to cues representing pupils' age or competence level. The degree of sensitivity may vary according to the costs involved and the cognitive abilities of the species. Adult meerkats, for example, do not treat individual pups differently according to their skill level, but are sensitive to age-related changes in pup begging calls and modify their pup-provisioning behaviour accordingly. Furthermore, adults monitor pups handling prey and may respond if pups struggle, for example, by further modifying the prey and returning it to the pups (Thornton & McAuliffe 2006). Similarly, in *T. albipennis*, tandem leaders evaluate their investment in teaching interactions by taking account of the time already invested, the value of the goal (e.g. a good or a poor quality nest site) and the rate of progress of their pupil (Richardson et al. 2007). Teachers may show a greater ability to track improvements in the abilities of individual pupils when there are fewer pupils to monitor and/or when the costs of a failure to learn are greater. For example, among felids, incompetent attempts at handling large prey may put infants in danger, but an infant that does not rapidly learn to hunt will not survive for long once parental care has ceased. One might, therefore, speculate that mothers would benefit from adjusting their behaviour according to improvements in the competence of individual offspring. This suggestion receives some support from work on domestic cats, which found that mothers varied in

their prey-provisioning behaviour towards different kittens of the same age (Caro 1980b).

Teaching, Punishment and Training

Considering the key characteristics of teaching allows us to differentiate teaching from other categories of behaviour such as punishment. In contrast to teaching, where benefits to teachers are contingent on pupils learning, punishment can produce immediate, direct benefits for the aggressor. For example, female elephant seals, *Mirounga angustirostris*, often attack unrelated young that attempt to suckle (Reiter et al. 1978). This has a clear, immediate benefit as it causes the infant to stop suckling. Although infants may consequently learn not to approach that female, aggressors gain a direct energetic benefit that is not dependent on infants learning, so this interaction cannot be considered a form of teaching. In contrast, certain forms of punishment, which we refer to as 'training', do result in delayed benefits to the aggressor that are contingent on learning by the victim. For example, in some altricial birds, elder brood members regularly attack smaller broodmates, often when no resource is being contested (Drummond 2006). This behaviour appears to fulfil Caro & Hauser's (1992) criteria: attackers modify their behaviour with no immediate benefit and at some cost to themselves, but broodmates learn to be submissive in future interactions. As in teaching, the aggressor gains positive fitness payoffs from promoting learning in another individual. However, unlike teaching, the victim incurs negative payoffs from training, relative to the payoffs it would obtain if it could carry out its desired behaviour without persecution (Table 1).

THE EVOLUTION OF TEACHING

Teaching will evolve only where the costs to teachers of facilitating learning in others are outweighed by the long-term fitness benefits they accrue once pupils have learned. However, if naïve individuals can easily acquire information or skills without assistance, teaching is unlikely to be favoured by selection. Teachers' fitness payoffs must therefore be scaled by the ease with which pupils could learn without teaching. Teachers' behaviour results in a change in the probability that pupils will learn during a given time period. We refer to this as the utility of

Table 1. Differing net fitness payoffs of teaching, punishment and training

	Fitness payoffs	
	Teacher/Aggressor	Pupil/Victim
Teaching	+D	+D
Punishment	+I	-I
Training	+D	-I/D

I = immediate payoffs; D = delayed payoffs contingent on learning by the pupil or victim.

teaching. Utility will be highest where there are few opportunities for pupils to learn alone, or where costs are prohibitively high, for example, if learning alone entails considerable risk. Although quantitative values of fitness costs, benefits and utility are unlikely to be available, knowledge of the natural history of a species may allow us to estimate their relative importance and make predictions as to whether teaching is likely to occur in a given species or context.

To illustrate these concepts, consider teaching in meerkats. Here, repeated interaction with live prey promotes the development of handling skills, so simply observing experienced individuals with prey is unlikely to promote skill acquisition. Pups rarely find mobile prey themselves, so the opportunities for trial and error learning are limited, and incompetent attempts by young pups at handling dangerous prey such as scorpions may be risky. As the probability that pups will acquire hunting skills alone is low, helpers can significantly raise this probability by providing pups with opportunities to learn, so the utility of teaching is high. Mobile prey account for over 50% of items in the meerkat diet (Doolan & Macdonald 1996), so the development of handling skills is critical for pup survival. For helpers, the development of competent handling skills in pups may provide multiple delayed benefits including a reduction in the period of pup dependence, kin-selected benefits of increased pup survival and direct benefits of increased group size (Clutton-Brock et al. 1999; Kokko et al. 2001). Under these conditions, the product of utility and the fitness benefits to helpers is high, and outweighs the costs of teaching, which are divided among multiple helpers (Thornton, *in press*).

Consideration of utility allows us to make predictions as to the distribution of teaching. For example, in large ant societies, recruitment to food or nest sites occurs through broadcasting using chemical cues (Hölldobler & Wilson 1990), so there is little need for knowledgeable individuals to teach routes to others. In species with small colony sizes, however, pheromone trails would degrade rapidly, as there are insufficient colony members to maintain them (Franks & Richardson 2006). Individuals can learn routes through solitary exploration, but this takes longer than following an experienced leader and presumably carries an increased predation risk. As tandem leaders can significantly increase the rate at which new leaders are recruited, utility is high and teaching is favoured by selection. Once an individual has learned a route, it can then teach others, and when a threshold number of individuals in the colony know the route, they can then carry remaining colony members, promoting rapid recruitment.

The utility of teaching also varies in carnivores. Here, reproductive fitness is heavily dependent on young learning to hunt effectively. In pack-hunting species, young may gain valuable experience from joining the hunt (Ginsberg & Macdonald 1990), so the utility of teaching is relatively low. In contrast, young solitary hunters have few opportunities to interact with live prey unless provisioned by adults, so teaching utility is high. This may explain the distribution of putative examples of teaching of hunting skills in the literature (Appendix).

Among felids, which typically hunt alone, behaviour suggestive of teaching has been reported in tigers, *Panthera tigris* (Schaller 1967), cheetahs (Kruuk & Turner 1967; Caro 1994), caracals, *Caracal caracal* (Ewer 1969), black-footed cats, *Felis nigripes* (Leyhausen 1979) and domestic cats (Leyhausen 1979; Caro 1980a, b). In contrast, there are no records of adult pack-hunting canids modifying their behaviour in such a way as to promote learning when young are present at a hunt (Ewer 1973; Ginsberg & Macdonald 1990; Nel 1999). The only anecdotal examples of teaching in canids are in bat-eared foxes, *Otocyon megalotis* (Nel 1999), which, like meerkats, forage individually for invertebrate and small vertebrate prey, and between a mother red fox, *Vulpes vulpes*, and her cub hunting for earthworms (Macdonald 1980). Further suggestive evidence of teaching in river otters, *Lutra canadensis* (Liers 1951), dwarf mongooses, *Helogale parvula* (Ewer 1973) and raptors (Newton 1979; Caro & Hauser 1992), all of which hunt individually, supports this trend.

Hunting utility may also depend on the degree to which prey capture requires dangerous or specialized techniques, the potential danger posed by prey and the prevalence of difficult prey in the diet. For example, Patagonian killer whales, *Orcinus orca*, strand themselves on beaches to capture pinnipeds (Guinet & Bouvier 1995). As this behaviour is risky, it has been suggested that adults help young to learn the techniques of intentional stranding by pushing them up and down the beach and directing them towards prey (Guinet & Bouvier 1995; Rendell & Whitehead 2001). Similarly, felids commonly kill prey through precise bites to the skull or nape of the neck (Ewer 1968), and meerkats handle scorpions using a stereotyped sequence to avoid being stung (A. Thornton, personal observation). In contrast, canids possess less specialized canines and killing bites are less accurately oriented (Ewer 1968). African wild dogs, *Lycaon pictus*, for example, run prey down, biting at their flanks until they collapse (Ewer 1973). As young animals can practise this relatively imprecise technique by joining the hunting pack, adults have no need to teach young and can feed them with regurgitated meat rather than having to release live prey. Low utility might also explain the lack of teaching of mouse-killing techniques in rats. Galef (1996) found no effect of the presence of the mother on the efficiency of pups' muricidal attempts. Given that rats rarely eat mice, parents do not actively provision young, mice cannot cause injury to rats and the location of the killing bite is highly variable (Karli 1956), it is not surprising that selection has not favoured teaching in this context. Similarly, Galef et al. (2005) found that rat dams do not teach offspring to eat safe foods. This is, perhaps, to be expected given that pups are easily capable of picking up information about food through asocial and simple social learning without the need for teaching (Galef 2003), so the utility of teaching in this context is low.

Teaching in Humans and Other Primates

Although anthropocentric biases have resulted in a focus on our closest relatives, consideration of potential costs

and benefits suggests that teaching is unlikely among great apes. All reported examples of teaching among apes are qualitative, anecdotal and open to alternative interpretation (Caro & Hauser 1992; Galef 1992; Maestripieri 1995a; Whiten 1999 review putative examples). Moreover, in contexts where teaching is necessary to promote learning in naïve individuals it should be ubiquitous, yet reported instances of teaching in apes are rare: the most widely cited example of teaching in apes, a report of a chimpanzee, *Pan troglodytes*, mother apparently aiding her offspring to crack nuts using a stone (Boesch 1991), has been observed only twice in over 50 years of chimpanzee research. Furthermore, young apes are adept at gathering information from older individuals without their elders modifying their behaviour (King 1994; Hirata & Celli 2003; Lonsdorf 2006), and may even be capable of imitation (Horner & Whiten 2005), so the utility of teaching is low. One possible exception may be in the context of promoting infant motor skills (Appendix). Several descriptive reports suggest gorilla, *Gorilla gorilla*, and chimpanzee mothers facilitate the development of independent locomotion by assisting their infants' early movements (Maestripieri 1995a; Whiten 1999; Maestripieri et al. 2002). More quantitative data are available in monkeys, although conclusive evidence for teaching is lacking (Caro & Hauser 1992; Maestripieri 1995a; Visalberghi & Fragazy 1996). Among the most suggestive studies are those by Maestripieri (1995b, 1996), who reported that macaque (*Macaca* spp.) mothers occasionally break contact with young infants, move away from them and give retrieval signals to lure the offspring back. These data from monkeys and apes are reminiscent of methods used by human parents to promote motor skill development in children (Whiten & Milner 1984; Maestripieri 1995a; Whiten 1999), suggesting that teaching of basic skills to infants may share important similarities between humans and other animals.

Unlike other animals, however, humans are able to teach flexibly, and in many different contexts. We propose three main reasons for this difference. First, language allows the transmission of limitless information, abstract concepts and knowledge relating to past and future events (Hauser et al. 2002). Second, in addition to placing pupils in situations conducive to learning and reinforcing or punishing pupils' behaviour, humans are inclined to manifest their knowledge and can demonstrate actions (Gergely & Csibra 2006). For demonstration to be useful, it requires a capacity on the part of the observer to imitate, which is rare among nonhuman animals (Galef 1988; Heyes 1993; Heyes & Galef 1996). Finally, humans can attribute knowledge to others and can use knowledge gained in different circumstances to respond flexibly to novel problems (Byrne 1995). This allows human teachers to generalize across contexts, to recognize ignorance in their pupils and to alter their techniques according to individual pupils' current knowledge, rather than simply responding to behavioural cues. Although some authors have argued that great apes may possess similar cognitive abilities and therefore have a capacity for flexible or 'insightful' teaching (Boesch & Tomasello 1998; Boesch 2003), this currently seems unlikely, given the

equivocal evidence for mental state attribution (Povinelli & Vonk 2003; Penn & Povinelli 2007; but see Tomasello et al. 2003) and unconvincing anecdotal reports of teaching.

CATEGORIES OF TEACHING

Caro & Hauser (1992) suggested that teaching in nonhuman animals is likely to fit within one of two categories: opportunity teaching or coaching. Opportunity teaching is defined as the 'teacher put[ting] pupil in a situation conducive to learning a new skill or acquiring knowledge' (page 166; see also Ewer 1969), whereas in coaching, the teacher 'directly alters the behaviour of [the] pupil by encouragement or punishment' (page 167). However, these categories may not always be mutually exclusive and certain forms of behaviour may satisfy the three criteria for teaching, but not be fully consistent with either opportunity teaching or coaching (Appendix). For example, in pied babblers, adult behaviour is reminiscent of coaching in that adults encourage nestlings to respond to purr calls by providing food. On the other hand, one could argue that adults provide nestlings with opportunities to learn an association between purr calls and food (Raihani & Ridley 2008). We suggest that it may be more productive to categorize teaching according to the nature of the knowledge acquired. Educational psychologists distinguish between teaching to promote procedural knowledge (the knowledge exercised in performing tasks or skills, i.e. 'knowing how') and declarative knowledge (which refers to content and facts, i.e. 'knowing that'), and note that facilitation of these two forms of knowledge in pupils requires different actions by teachers (Dillon 1986; Ennis 1986). For example, teachers may promote the acquisition of procedural knowledge by working through progressively more difficult examples of a task with pupils, while declarative knowledge may be taught by encouraging repetition and recitation. Natural selection may therefore favour different forms of teaching behaviour depending on whether it functions to facilitate the acquisition of procedural or declarative knowledge. We refer to these two categories as 'progressive teaching' and 'fixed teaching'.

Progressive Teaching

Progressive teaching facilitates the acquisition of procedural knowledge required for the development of skills: knowing how to hunt or move independently, for example. It is therefore most likely to exist as a form of parental or alloparental care promoting infant development. The acquisition of procedural knowledge follows a continuum from incompetence to competence. Moreover, the costs of teaching and the requirements of pupils change as pupils mature and develop. The teaching of procedural knowledge must be progressive: teachers must modify their teaching behaviour in accordance with pupils' stage of skill development. For example, in carnivores, adults that bring live prey to young individuals risk injury to the young and the loss of the prey. Young must first learn to

recognize and consume dead prey; further learning is then facilitated by making the task progressively more difficult. Since this form of teaching is likely to require a relatively long time frame, it may be likely in species with extensive periods of parental care.

In nonhumans, progressive teaching aids in the development and refinement of skills that are, to some extent, already biologically specified in pupils. For example, basic motor abilities or rudimentary prey capture techniques may have a genetic basis, but teaching may build on these basic attributes to facilitate the rapid and efficient development of skills such as hunting or independent locomotion. The same may be true of some forms of teaching in humans. For example, although the ability to use language is widely considered to be underpinned by an evolved 'universal grammar' or 'faculty of language' (Chomsky 1965; Hauser et al. 2002), language acquisition in infants is heavily dependent on early exposure to speech, and infants who are profoundly deaf (Petitto 1993) or raised in isolation (Lane 1976) fail to acquire language. Adults may also play an active role in teaching infants about language through the use of child-directed speech: that is, syntactically and semantically simple speech with elevated pitch and exaggerated intonation (Kuhl et al. 1997; Burnham et al. 2002; Matychuk 2005). Unlike other species, humans also teach novel skills that may lack biological prespecification. For example, although the basic motor capacities involved in playing the piano may be genetically determined, the precise procedural knowledge involved in the performance of this skill would be unlikely to develop in the absence of social input. Human progressive teaching therefore allows the propagation of procedural knowledge involved in technological innovations.

Fixed Teaching

Fixed teaching is involved in facilitating the acquisition of declarative knowledge. Unlike procedural knowledge, declarative knowledge is binary: an individual either knows a fact, or it does not. Selection will not, therefore, act on teachers of declarative knowledge to modify their behaviour progressively in response to gradual changes in their pupils' current abilities. Rather, teachers are likely to perform a single type of action to promote learning of specific information.

The dichotomy between progressive and fixed teaching may be criticized on the grounds that learning of declarative information may facilitate the acquisition of procedural knowledge. For example, if an infant is taught that a particular food item is safe to eat, it will subsequently be more likely to handle food of that type, and may therefore acquire information on how best to process it. However, if we consider precisely what is taught, the dichotomy holds: in this example a teacher helps the infant to learn that food is safe. Further learning about how to eat the food is dependent only on the infant's behaviour, not the teacher's.

To date, the strongest evidence for fixed teaching comes from *T. albipennis* and pied babblers. In the former, pupils

learn the location of landmarks along a route, allowing them to navigate effectively (Franks & Richardson 2006). In the latter, adults actively condition nestlings to associate a neutral stimulus (purr calls) with an unconditioned stimulus (food; Raihani & Ridley 2008). Similar fixed teaching may be involved in promoting learning about the meaning or correct use of signals such as alarm calls and food calls in other species. In vervet monkeys, *Chlorocebus aethiops*, for example, there is anecdotal evidence that adults act aggressively towards infants that give alarm calls in the wrong context (Hauser 1987, cited in Caro & Hauser 1992). Although it is possible that this may promote infant learning, there is insufficient evidence at this stage to determine whether aggression is ever involved in teaching among nonhuman animals (Caro & Hauser 1992 discuss relevant anecdotes; see also the Appendix). There is stronger evidence suggesting that adult vervet monkeys use positive reinforcement to promote infant learning of alarm calls. Hauser (1987, cited in Caro & Hauser 1992) found that adults often produced same-type alarm calls when infants attended appropriate alarm calls and that infants were subsequently more likely to call in the correct context. However, the possibility that infants simply persisted in the way they called initially, regardless of whether adults called, was not ruled out. Furthermore, the function of reinforcing alarm calls by adults may equally be to reiterate potential danger, rather than to promote infant learning.

Fixed teaching may also facilitate learning of what to eat (Appendix). For example, Nicol & Pope (1996) showed that mother hens, *Gallus gallus domesticus*, that were trained to perceive one colour of food as unpalatable and another as palatable produced more intense feeding displays when observing chicks eating the 'unpalatable' rather than the 'palatable' food. Although this study does not provide evidence that chicks learn as a result of this interaction, it raises the possibility that hens may facilitate learning about palatable foods by chicks. Similarly, some authors have suggested that callitrichid monkeys teach by preferentially transferring novel foods to infants, sometimes in association with food calls, and that infants learn by sampling these items and incorporating them into their diet (Rapaport 1999; Roush & Snowdon 2001). However, other studies have found that novel items are less likely to be donated (Price & Feistner 1993; Brown et al. 2005) and currently available evidence suggests that patterns of food donation in primates are more consistent with infants seeking information than with adults actively engaging in fixed teaching (King 1994; Visalberghi & Fragaszy 1996; Brown et al. 2004; Voelkl et al. 2006). Nevertheless, the possibility that individuals in some species may actively facilitate learning about food deserves further examination.

Acknowledgments

We are grateful to Matthew Bell, Tim Clutton-Brock, Sinéad English, Sarah Hodge, Rufus Johnstone, Kevin Laland, Katherine McAuliffe, Bonnie Metherell, Kelly Moyes and Andrew Radford for comments and discussion.

Louise Barrett and three anonymous referees provided constructive criticism and useful suggestions. This work was funded by the Natural Environment Research Council (A.T. and N.J.R.), the Cambridge Philosophical Society (A.T.) and Pembroke College, Cambridge (A.T.).

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Appendix

Table A1. Species in which teaching has been suggested or investigated

Species	Context	Category of teaching		Type of study		Caro & Hauser criteria**				High costs/lack of opportunity for individual learning?††		Source
		Caro & Hauser*	P/F‡	A/Q‡	Data§	Teacher changes behaviour?	Costs to teacher?	Pupil learns?	Notes	Yes/No	Comments	
Communication												
Cowbird, <i>Molothrus ater</i>	Communication	C/O	F	Q	O	YS	N/NC††	YS	1	YW	a	West & King 1988
Pied babbler, <i>Turdoides bicolor</i>	Communication	C/O	F	Q	E	YS	YS	YS	2	YS	b	Raihani & Ridley 2008
Chimpanzee, <i>Pan troglodytes</i>	Communication (Human language acquisition)	C	F	A	O	YS	N	YW	3	YW	c	Fouts et al. 1989
Vervet monkey, <i>Chlorocebus aethiops</i>	Communication	C	F	Q	O	YS	N	YW	4	YW	d	Hauser 1987
Foraging												
Golden lion tamarin, <i>Leontopithecus rosalia</i>	Extractive foraging	C/O	P	A	O	YS	N	N	5	YW	e	Rapaport & Ruiz-Miranda 2002
Pied babbler, <i>Turdoides bicolor</i>	Foraging	C/O	P	Q	E	YS	N	N	5	N	f	Rapaport 2006 (Comment on Radford & Ridley 2006)
Bat-eared fox, <i>Otocyon megalotis</i>	Hunting	O	P	A	O	YS	N	N	6	YS	g	Nel 1999
Black-footed cat, <i>Felis nigripes</i>	Hunting	O	P	A	O	YS	N	N	6	YS	g	Leyhausen 1979
Canadian otter, <i>Lutra canadensis</i>	Hunting	O	P	A	O	YS	N	N	6	YS	g	Liers 1951
Cheetah, <i>Acinonyx jubatus</i>	Hunting	O	P	A	O	YS	YS	N	6	YS	g	Kruuk & Turner 1967; Caro 1994
Domestic cat, <i>Felis catus</i>	Hunting	O	P	Q	E	YS	N	YS	6	YS	g	Leyhausen 1979; Baerends-van Roon & Baerends 1979
Dwarf mongoose, <i>Helogale parvula</i>	Hunting	O	P	A	O	YS	N	N	6	YS	g	Ewer 1973
European fox, <i>Vulpes vulpes</i>	Hunting	O	P	A	O	YS	N	YW	7	YS	g	Macdonald 1980
Lion, <i>Panthera leo</i>	Hunting	O	P	A	O	YW	N	N	8	YW	h	Schenkel 1966
Meerkat, <i>Suricata suricatta</i>	Hunting	O	P	Q	E	YS	YS	YS	9	YS	g	Thornton & McAuliffe 2006
Tiger, <i>Panthera tigris</i>	Hunting	O	P	A	O	YS	N	N	6	YS	g	Schaller 1967
Killer whale, <i>Orcinus orca</i>	Hunting	O	P	A	O	YS	N	N	10	YS	i	Lopez & Lopez 1985; Guinet & Bouvier 1995
Cooper's hawk, <i>Accipiter cooperii</i>	Hunting	O	P	A	O	YS	N	N	11	YS	g	McElroy 1974

(continued on next page)

Table A1. (continued)

Species	Context	Category of teaching		Type of study		Caro & Hauser criteria**				High costs/lack of opportunity for individual learning?††		Source
		Caro & Hauser*	P/F†	A/Q‡	Data§	Teacher changes behaviour?	Costs to teacher?	Pupil learns?	Notes	Yes/No	Comments	
European sparrowhawk, <i>Accipiter nisus</i>	Hunting	O	P	A	O	YS	N	N	11	YS	g	Newton 1986
Kestrel, <i>Falco tinnunculus</i>	Hunting	C/O	P	A	O	YS	N	N	12	YS	g	Tinbergen 1940
Peregrine, <i>Falco peregrinus</i>	Hunting	O	P	A	O	YS	N	N	13	YS	g	Beebe 1960; Newton 1979
Osprey, <i>Pandion haliaetus</i>	Hunting/motor skills	C/O	P	A	O	YS	N	YW	14	YS	g	Meinertzhagen 1954
Yellow-eyed junco, <i>Junco phaeotus</i>	Food handling	C	F	A	O	YW	N	N	15	YW	j	Caro & Hauser 1992
Cottontop tamarin, <i>Sanguinus oedipus</i>	What to eat/communication	C/O	F	Q	O	YW	N	YW	16	YW	k	Roush & Snowdon 2001
Golden lion tamarin, <i>Leontopithecus rosalia</i>	What to eat	O	F	Q	O	YS	N	YW	17	YW	k	Rapaport 1999
Marmoset, <i>Callithrix jacchus</i>	What to eat	C/O	F	Q	E	NC	N	YW	18	YW	k	Brown et al. 2005; Voelkl et al. 2006
Meerkat, <i>Suricata suricatta</i>	What to eat	O	F	A	O	YS	N	N	19	YW	k	Ewer 1963
Domestic chicken, <i>Gallus gallus domesticus</i>	What not to eat	C	F	Q	E	YS	N	N	20	YW	k	Nicol & Pope 1996
Norway rat, <i>Rattus norvegicus</i>	What not to eat	C/O	F	Q	E	NC	Y	N	21	N	l	Galef et al. 2005
Chimpanzee, <i>Pan troglodytes</i>	Tool use (nut cracking)	O	P	A	O	YW	N	N	22	N	m	Boesch 1991
Tandem-running ant, <i>Temnothorax albipennis</i>	Route to food	C/O	F	Q	E	YS	YS	YW	23	YS	n	Franks & Richardson 2006
Motor skills												
Barbary macaque, <i>Macaca sylvana</i>	Independent locomotion	C	P	A	O	YS	N	YW	24	YW	o	Burton 1972
California sealion, <i>Zalophus californianus</i>	Independent locomotion	C/O	P	A	O	YW	N	N	25	YW	p	Caro & Hauser 1992
Chimpanzee, <i>Pan troglodytes</i>	Independent locomotion	C	P	A	O	YS	N	N	26	YW	o	Yerkes & Tomilin 1935; Nicolson 1977; Van de Rijt-Plooi & Plooi 1987
Gorilla, <i>Gorilla gorilla</i>	Independent locomotion	C	P	A	O	YS	N	N	27	YW	o	Whiten 1999; Maestriperi et al. 2002
Hamadryas baboon, <i>Papio hamadryas</i>	Independent locomotion	C	P	A	O	YS	N	N	28	YW	o	Bolwig 1980
Olive baboon, <i>Papio anubis</i>	Independent locomotion	C	P	A	O	YS	N	YW	29	YW	o	Ransom & Rowell 1972
Pigtailed macaque, <i>Macaca nemestrina</i>	Independent locomotion	C	P	Q	O	YS	N	YW	28	YW	o	Maestriperi 1996

Rhesus macaque, <i>Macaca mulatta</i>	Independent locomotion	C	P	Q	O	YS	YS§§	YW	28	YW	o	Maestriperi 1995a, b
Spider monkey, <i>Ateles geoffroyi</i>	Independent locomotion	C	P	A	O	YS	N	N	30	YW	o	Milton 1988
Yellow baboon, <i>Papio cynocephalus</i>	Independent locomotion	C	P	A	O	YS	N	N	30	YW	o	Altmann 1980
Oystercatcher, <i>Haematopus ostralegus</i>	Independent locomotion	C	P	A	O	YS	YW	N	31	YW	o	Norton-Griffiths 1969
Avoidance of dangerous situations												
Chacma baboon, <i>Papio ursinus</i>	Remove harm	C	F	Q	E	YS	N/NC§§	YW	32	YW	q	Fletemeyer 1978
Chimpanzee, <i>Pan troglodytes</i>	Remove harm	C	F	A	O	YS	N/NC§§	N	33	YW	q	Goodall 1973; Wrangham 1977; Nishida 1983
Gorilla, <i>Gorilla gorilla</i>	Remove harm	C	F	A	O	YS	N/NC§§	N	34	YW	q	Schaller 1963; Fossey 1979; Watts 1985
Japanese macaque, <i>Macaca fuscata</i>	Remove harm	C	F	A	O	YS	N/NC§§	N	35	YW	q	Kawamura 1959; Menzel 1966
Squirrel monkey, <i>Saimiri oerstedii</i>	Remove harm	C	F	A	O	YS	N/NC***	YW	36	YW	q	Leger et al. 1981

*Category of teaching as per Caro & Hauser (1992): O = opportunity teaching: teacher puts pupil in a situation conducive to learning a new skill or acquiring knowledge; C = coaching: teacher directly alters behaviour of pupil by encouragement or punishment.

†Progressive (P) or fixed (F) teaching.

‡Anecdotal (A) or quantitative (Q) data.

§Experimental (E) or purely observational (O) data.

**NC = evidence to the contrary; N = no evidence reported; YW = weak positive evidence; YS = strong positive evidence. Notes: (1) females make wing strokes during attractive male songs.

This acts to reinforce these songs in males, but has additional courtship functions, so should not be considered a form of teaching. (2) Adults actively condition nestlings to associate purr calls with food. (3) Adult observed to mould infant's hand into a sign. (4) Adults may reinforce correct alarm call production by infants or act aggressively towards infants that call incorrectly. (5) Adults make food calls to attract young to foraging sites. Young subsequently extract food. No evidence that adult behaviour facilitates acquisition of foraging skills by infants. In pied babblers, food calling by adults increases fledglings' food intake. As this is the clear primary function of adult behaviour, it should not be considered a form of teaching (Thornton et al. 2007). (6) Adults provision young with live prey. (7) Mother allowed cub to complete capture of earthworms. (8) Interprets unsuccessful hunts by mothers as giving cubs opportunities to practise stalking prey. (9) Adults gradually introduce young to prey; nudge prey if young do not interact with it; retrieve and further modify prey if young struggle. (10) Adults push young up and down beach and towards prey. (11) Adults incite young to chase them before releasing prey; provision young with live prey. (12) Adults drop food for young to catch. (13) Adults drop food for young to catch; release prey only after young have chased them; provision young with live prey. (14) Adults observed inciting young to follow, pushing young off rocks to make them fly and dropping fish for young to catch. Adult behaviour changed progressively as fledglings grew older. (15) Adults occasionally reorient mealworms to facilitate ingestion by chicks. (16) Begging by infants is more successful if adults utter food calls. Infants who received food from adults when young began independent foraging earlier; infant food calls became more adult-like with age. No evidence that adults preferentially transfer novel food. (17) Adults preferentially transfer novel foods to infants. (18) Adults tolerate infants' presence, but do not modify their behaviour to promote learning. (19) Mothers incite pups to snatch food, which may promote learning about novel foods. However, Thornton (2007) presented data suggesting that allowing young to snatch food constitutes an efficient mode of food transfer to young pups, rather than a form of teaching. (20) Mothers produce intense feeding displays to attract young away from food perceived to be unpalatable. Study tests sensitivity, not teaching. (21) Mothers did not eat a less preferred food type to attract young away from toxic food. (22) Mothers leave tools, allow offspring to shape tools or assist offspring in nut cracking. (23) Knowledgeable individuals lead others to food, allowing followers to learn landmarks en route. (24) Father broke contact with infants and used gestures to lure offspring back. (25) Mothers force pups to swim on and off their back. Interpreted as mothers teaching pups swimming techniques. (26) Mothers break contact with infants and use gestures to lure offspring back. (27) Mothers break contact and encourage infants to follow; 'scaffolding' interactions include physical support of crawling and climbing, tugging, luring and dangling offspring. (28) Mothers break contact with infants and use gestures to lure offspring back. (29) Mothers place infants on ground and walk away to encourage infants to follow. (30) Mothers break contact with infants and move away as infants approach. (31) Adults invest considerable time using vocalizations to lure young out of the nest and present food just out of reach so that young must move in order to be fed. Luring is less efficient than simply donating food to young. Unclear whether adult behaviour is causally related to motor skill acquisition in young. (32) Adult threatened juveniles that approached toxic fruit. (33) Adults take food from infants if it is not part of the normal diet. (34) Mothers take nonfood items from infants. (35) Mothers prevent infants from interacting with novel objects. (36) Adults threatened young that approached a chain that had previously choked an adult group member.

††N = no evidence reported; YW = weak positive evidence; YS = strong positive evidence. Comments: (a) few obvious costs, but song development in males is influenced by female behaviour, so males might develop less sexually attractive song if females are not present. (b) Nestlings never hear purr calls unless adults make them. (c) No obvious costs of learning, but infant was prevented from seeing human trainers using signs with other chimpanzees, so opportunities for learning by observation were limited. (d) Incorrect alarm call responses may be dangerous, but infants can learn by simply observing adults. (e) Incompetent foraging attempts may be costly in terms of lost time and energy investment; risks of sampling poisonous items. However, young may simply learn by observing and interacting with adults without the need for teaching. (f) Adult food calls attract fledglings to divisible food patches (Radford & Ridley 2006). These

typically consist of common prey types such as ants and termites (N. Raihani, unpublished data). Groups move widely during foraging and are unlikely to revisit previously sampled patches. It is therefore unclear what, if anything, fledglings could learn as a result of adult behaviour. (g) Young rarely catch own prey so few opportunities for learning; incompetent handling attempts may be dangerous. (h) Young seldom catch own prey so few opportunities for learning; incompetent handling attempts are dangerous. However, may gain experience from joining adults on hunts. (i) Incompetent attempts at stranding may result in death. (j) Young are incompetent foragers, so may have limited opportunities to learn food-handling techniques. However, mealworms are not dangerous and consuming them does not require complicated techniques. (k) Learning by sampling unknown food may be costly to infants if there are poisonous items in the environment. However, infants may learn simply by eating what adults eat. (l) Rats are adept at picking up information about food through individual or social learning without the need for teaching. (m) Adults tolerate close presence of young; young are adept information gatherers, arguably capable of imitation. Numerous reports suggest adult chimpanzees do not actively facilitate infant learning about tool use (Matsuzawa et al. 2001; Hirata & Celli 2003; Lonsdorf 2006). (n) Individual exploration slow; high risk of predation. (o) Young may acquire skills through maturation, but at high risk of kidnapping, predation or being left behind if they do not learn rapidly. (p) Young may acquire swimming skills through maturation, but at high risk of drowning, predation or being left behind if they do not learn rapidly. (q) Individual learning about potentially toxic food or harmful objects may be dangerous.

‡‡No costs of female behaviour reported. Wing stroking may produce benefits by eliciting copulation.

§§Infants whose mothers broke contact with them were more likely to be kidnapped.

***Removing infants from dangerous situations may produce immediate benefits that are not contingent on learning.