# Is There Teaching in Nonhuman Animals?

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# IS THERE TEACHING IN NONHUMAN ANIMALS?

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ABSTRACT

*We derive a simple operational definition of teaching that distinguishes it from other forms of social learning where there is no active participation of instructors, and then discuss the constituent parts of the definition in detail. From a functional perspective, it is argued that the instructor's sensitivity to the pupil's changing skills or knowledge, and the instructor's ability to attribute mental states to others, are not necessary conditions of teaching in nonhuman animals, as assumed by previous work, because guided instruction without these prerequisites could still be favored by natural selection. A number of cases of social interaction in several orders of mammals and birds that have been interpreted as evidence of teaching are then reviewed. These cases fall into two categories: situations where offspring are provided with opportunities to practice skills ("opportunity teaching"), and instances where the behavior of young is either encouraged or punished by adults ("coaching"). Although certain taxonomic orders appear to use one form of teaching more often than the other, this may have more to do with the quality of the current data set than with inherent species-specific constraints.*

*We suggest several directions for future research on teaching in nonhuman animals that will lead to a more thorough understanding of this poorly documented phenomenon. We argue throughout that adherence to conventional, narrow definitions of teaching, generally derived from observations of human adult-infant interactions, has caused many related but simpler phenomena in other species to go unstudied or unrecorded, and severely limits further exploration of this topic.*

## INTRODUCTION

INDIVIDUALS living in social groups often acquire information through interactions with other conspecifics and, in some cases, from cohabiting heterospecifics (e.g., waggle dance in *Apis* spp., Gould, 1982; central-place foraging in *Rattus norvegicus*, Galef and Wigmore, 1983; mixed species flocks of birds, Munn, 1986; see Galef, 1976 for an early review). Information is normally transmitted between individuals as a result of some form of social learning such as social facilita-

tion or local enhancement, although other mechanisms such as imitation have also been proposed (reviewed in Galef, 1988a). Teaching, normally understood as directed instruction of one individual by another, is yet another mechanism for the transmission of information, but it has received little attention with regard to observations of nonhuman animals (Barnett, 1969, 1973). This is surprising since one might expect directed instruction to allow for an even faster and more efficient means of transmitting information than other, less directed types of social learn-

ing. Models incorporating both vertical and horizontal transmission of information suggest that directed instruction would be a powerful force in the spread of skills or knowledge (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985, 1988).

The primary goal of this paper is to reevaluate the concept of teaching in nonhumans, using a functional and mechanistic perspective to examine a broad comparative data set. This review is timely for four reasons. First, comparative observations suggest that there are rudimentary forms of teaching in a variety of species, but because teaching has been characterized by stringent and mechanistic operational definitions (e.g., Barnett, 1969; Pearson, 1989), many putative examples of teaching may have gone unnoticed.

Second, despite increasing evidence for the role of social interaction in the acquisition of different types of skills and knowledge about the environment (see Zentall and Galef, 1988 for reviews), it is as yet unclear to what extent forms of teaching may also be operating within the general social context to guide the acquisition of such knowledge (e.g., see ten Cate, 1986; West and King, 1988).

Third, studies of the dynamics of cultural transmission in animal populations have recently increased due to both theoretical advances (e.g., Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1988) and a more rigorously collected set of observations from the laboratory (e.g., Galef, 1988b; Mineka and Cook, 1988; Pepperberg, 1988; Zentall, 1988) and the field (Curio, 1988; Hauser, 1988; Lefebvre and Palameta, 1988; Visalbierghi and Fragaszy, 1990). Yet evidence for some form of teaching is almost never referred to in any of these areas.

Fourth, there has recently been a resurgence of interest in the area of animal cognition (Griffin, 1981; Byrne and Whiten, 1988; Cheney and Seyfarth, 1990; Ristau, 1991; Whiten, 1991), and both theoretical analyses (e.g., Dennett, 1983, 1987) and empirical observations (e.g., Menzel and Halperin 1975; Premack and Woodruff, 1978; de Waal, 1982, 1989; Cheney and Seyfarth, 1988, 1990) now suggest the possibility of complex mental processes relevant to investigations of teaching.

Our position on teaching can be summa-rized as follows. Unlike most previous investigators, we do not think that teaching depends crucially on evidence of complex intentionality or attribution of mental states. This is not to say that intentionality plays no role in some *forms* of teaching. Given this theoretical stance, we are convinced that the only way to make progress in this area is to first provide a definition of teaching which can, and undoubtedly will, be modified as empirical data accumulate and then to present a rich description of existing data so that researchers can make more informed assessments of where, taxonomically, to look for evidence of teaching.

The paper is organized as follows. First, a working definition of teaching is provided that attempts to unify both functional and mechanistic considerations; its advantage is that it encompasses a diverse set of observations while excluding cases that are more appropriately described within other areas of social learning theory. Next we review studies that present both anecdotal observations and more detailed descriptive and experimental data on social interactions that have been or could be interpreted as forms of teaching. Finally, we raise theoretical issues regarding more complex forms of teaching and point out new directions for future research.

## A WORKING DEFINITION OF TEACHING

According to Webster's International Dictionary (1971:2346), teaching is "a general term for causing one to acquire knowledge or skill, usually with the imparting of necessary incidental information and the giving of incidental help and encouragement." Many different facets of teaching are emphasized in everyday usage: the behavior of the teacher shows, guides, or instructs the pupil. Instruction occurs by means of precept, example, or experience. And the pupil comes to know a subject, to become accustomed to some action or attitude, or to know the disagreeable or agreeable consequences of some action as a result of instruction. Nowhere in these colloquial usages is there discussion of teachers modulating their behavior for the benefit of the pupil, nor is there recognition of the pupil's ignorance, although arguably these are implicit. Moreover, the issue of intentionality on the part of the teacher is not explicitly dis-

cussed. It is unclear whether the intentions of the putative instructor are assumed to be present, given the anthropocentricity of dictionaries, or whether it is irrelevant to the definition.

The issues raised by such standard dictionary definitions suggest that a biologically relevant definition of teaching will have to incorporate the behavior of the actor and the pupil, and the type of information that is imparted between them. The following working definition has been constructed on the basis of our own empirical work (see below) and from our understanding of evolutionary theory:

> An individual actor **A** can be said to teach if it modifies its behavior only in the presence of a naive observer, **B**, at some cost or at least without obtaining an immediate benefit for itself. **A**'s behavior thereby encourages or punishes **B**'s behavior, or provides **B** with experience, or sets an example for **B**. As a result, **B** acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do, or that it would not learn at all.

Several terms in this definition require careful clarification. First, if teaching can be said to occur, then it will be necessary for actors to modify their behavior. By this we mean that there must be a change in behavior from what would otherwise take place under the same conditions if the naive observer was not present. This distinguishes teaching from instances where an individual engages in normal behavior that is incidentally learned by a naive observer (e.g., social facilitation and imitation). Obviously, what constitutes modified behavior is open to debate. As this review will show, however, instances of purported teaching that have repeatedly attracted the attention of researchers are behaviors that stand out markedly against the species' background repertoire and are not simply rare occurrences of normal behavior.

The phrase "only in the presence of a naive observer, **B**" is required to distinguish between cases where an actor behaves in a way that is only rarely seen in its repertoire, regardless of whether a naive observer (conspecific) is present. By making this distinction explicit, cases where novel behavioral patterns emerged, such as potato washing by Japanese macaques (*Macaca fuscata*) (reviewed in Nishida, 1987) and milk bottle-top opening by blue tits (*Parus caeruleus*) (Fisher and Hinde, 1949; Hinde and Fisher, 1951), can be excluded. In these situations, although behaviors were arguably copied by conspecifics, they were nevertheless performed by actors irrespective of whether other individuals were with them. The distinction also enables us to exclude cases of observational learning where individuals come to prefer or avoid foods as a result of observing conspecifics or heterospecifics feeding or avoiding noxious foods. These behaviors would have occurred without the naive observer being present (e.g., Mason et al., 1984). "Naive" in the definition simply indicates that **B** has not yet acquired the skill or knowledge in question.

An important component of our definition is that the actor incurs a cost, or at least does not obtain an immediate benefit, from its modified behavior; the extent of cost differs among species, behaviors and ecological circumstances. This restriction allows exclusion of instances of intraspecific aggression that might be included as teaching. While there is no doubt that winners of fights do teach the losers to avoid them in the future, this appears to be a secondary consequence of obtaining the direct benefit of a resource or position in the hierarchy. A similar example is that of weaning because it appears, superficially perhaps, to share many of the features of teaching that are highlighted in the definition. During weaning, a mother alters her current behavior (nursing) by rejecting her infant's attempts to suckle. As a result of this interaction or, more likely, repeated interactions, the infant will learn when the "appropriate" times for suckling are or will learn not to suckle (see Altmann, 1980). Moreover, a mother's rejection of suckling attempts is sensitive to the infant's changing physiological needs (see below). What distinguishes a case such as this from teaching is that the mother obtains an immediate benefit from not having to produce more milk.

A point of clarification is necessary here. Although our definition demands that the teacher gains no benefits during the process of instruction, in theory the teacher might benefit from the pupil's new skill soon after instruction has ceased.

Implicit in the idea of a change in behavior

is a notion of short-term cost, because performing a different behavior will, at minimum, result in an opportunity cost, and may also involve a change in metabolic rate. Costs of teaching, however, may be much greater than a lost opportunity to behave in another way, and may ultimately constrain the frequency with which an individual can use instruction to transfer information to naive group members (see below). As a result, any careful documentation of teaching will rely upon a detailed description of the individual's time budget constraints.

Several mechanisms of instruction have been included in our definition in order to allow for a number of possible forms of teaching; these mechanisms are by no means mutually exclusive nor necessarily representative of all possible mechanisms that may be operating in situations that have yet to be uncovered. The first mechanism is concerned with encouragement or punishment, the second with giving an individual more opportunities to learn (Ewer, 1969) than if teaching did not occur, and the third is associated with more classic forms of social learning such as imitation or social facilitation. In this last case, the critical difference between our definition of teaching and normative models of social learning is that actor **A** has considerably modified its behavior specifically in the presence of naive pupil **B**. In contrast, social learning theory does not stipulate these conditions.

The definition requires that the naive observer acquire knowledge or a skill as a result of teaching in order to exclude more commonly observed social interactions. If, for example, a dominant adult monkey repeatedly chases a subordinate away from a favored food source, this might be considered to fall within our definition of teaching because **A** (the dominant) modifies its behavior (e.g., goes from resting to chasing) specifically in the presence of **B** (the subordinate) and punishes **B**'s behavior (i.e., sitting and eating). Two points rule out this and comparable examples from our definition of teaching. First, the dominant reaps benefits directly and immediately from chasing the subordinate away, rather than from the benefit of having the subordinate learn that it should move away from food when a dominant approaches. Second, subordinates clearly recognize their position in the hierarchy and in most cases will abandon a food source upon seeing a dominant animal, unless this is happening for the first time before a juvenile learns its rank. Thus the dominant's chase is not normally imparting new knowledge or a skill to the subordinate, but is promoting a previously practiced behavior.

In studies of nonhumans, it is assumed that acquisition of knowledge or a skill through teaching would often enhance the reproduction and survival of the pupil. Indeed, the costs of teaching to the instructor must be more than compensated, at some point, by benefits accrued by the pupil (through, for example, kin selection or reciprocal altruism) for teaching to have evolved; theoretical models of teaching have successfully relaxed this stipulation for humans (Boyd and Richerson, 1985). In theory, the teacher might manipulate the pupil's behavior only for its own subsequent benefit, but we are unaware of any case where this has been demonstrated. In this paper, we will not discuss in detail the problem of delayed benefits to the instructor from the pupil's acquisition of a skill or knowledge, although we recognize the importance of this problem for understanding the origins of teaching and its maintenance in the population as a stable form of transmission (see Cavalli-Sforza and Feldman, 1983; Boyd, 1988; Cheney and Seyfarth, 1990, for similar issues in behavioral ecology).

## STRINGENT DEFINITIONS OF TEACHING

To many, our working definition of teaching will fall far short of existing conceptions of teaching. We have not, for example, included some of the subtle distinctions in learning theory that are based on rigorous experiments and observations, because the data set on putative cases of teaching is of insufficient detail to warrant this as yet (see below). Nevertheless, we hope that insights from learning theory, and other areas of psychology, can be applied when observations with greater resolution are obtained.

More stringent definitions, derived primarily from observations of human adult-infant interactions, claim that instruction, to qualify as teaching, must be sensitive to the pupil's changing competence (e.g., Pearson, 1989). That is, the timing and quality of the

changes in the instructor's behavior may range from being acutely sensitive to somewhat insensitive to the pupil's changing skills or knowledge, and could even involve using alternative means to bring about a change in the pupil's performance if this became necessary. While some of the social interactions described below are characterized by a degree of sensitivity, our working definition would also encompass cases of a mother altering her behavior on a relatively stereotyped time course (e.g., geared to her own changing hormonal profile following cessation of suckling). It must be admitted, however, that modifying behavior only in the presence of a naive observer but not an experienced one already demands some sensitivity! The whole issue of sensitivity is concerned with a mechanism of teaching, but from an evolutionary perspective that focuses on the effects of teaching, there is no a priori reason why one should necessarily expect more or less sensitive mechanisms to have a greater or lesser effect on the reproduction and survival of the pupil. If the time available for teaching is limited, or if social and ecological environments are relatively stable, a stereotyped time course for teaching may be the most effective means of transmitting information, in that it presumably involves less cost in sensory processing to the teacher. In more fluctuating environments or social conditions faced by other species, however, a more malleable time course for instruction may be necessary to enable pupils to acquire skills, despite the increased cost incurred by the instructor of monitoring the pupil's progress. Thus, from an evolutionary standpoint, the interesting questions lie in determining the extent of different forms of teaching across species, the ecological and social circumstances that favor one form of teaching over another, and the costs and benefits of different types of teaching to both instructor and pupil. With this perspective, it would be much less fruitful to compare each case of putative teaching in nonhumans to teaching in humans.

It is commonly suggested that intentionality or the ability to attribute different mental states to others is at the foundation of any concept of teaching (e.g., Cheney and Seyfarth, 1990). For example, in a recent philosophical treatment of teaching in humans, Pearson (1989:66) states, "When faced with the question of determining whether an action is a teaching action, as opposed to some other kind of action such as reciting, talking or acting in a play, it is the intention of bringing about learning that is the basis for distinguishing teaching from other activities. The intention the activity serves, then, is a part of the meaning of the concept, and not a factual discovery one makes about the activity." This perspective suggests that the instructor attributes a set of beliefs to a pupil (where beliefs are discerned by the pupil's behavioral competence in confronting a given problem) and then sets out to modify these beliefs in order to improve the pupil's level of competence in solving a given task.

In nonhumans, there is only weak evidence that animals can attribute complex mental states to others (Premack and Woodruff, 1978; Cheney and Seyfarth, 1990). A number of studies, however, have provided evidence (1) that nonhuman animals, ranging from domestic chickens to chimpanzees, modify their behavior on the basis of the social contexts in which they find themselves (e.g., Cheney and Seyfarth, 1985; Gyger and Marler, 1988; see reviews in Cheney and Seyfarth, 1990; Hauser and Nelson, 1991), and (2) that their behavior is intentional in the weak sense of being purposive (e.g., Menzel and Halperin, 1975). This opens up the possibility of investigating teaching within the context of new theoretical and empirical developments in the area of cognitive ethology (e.g., Dennett, 1983, 1987; Griffin, 1984; Premack, 1986; Cheney and Seyfarth, 1990; Allen and Hauser, 1991).

From a functional perspective, the problem of the instructor's motives is not paramount because cognizant or noncognizant instructors may be equally accomplished at training and hence, at furthering their pupil's reproductive and survival interests (and hence usually their own). Without detracting from the importance of investigating intentions in nonhumans, we feel there is no a priori reason for using intentionality as a criterion to arrest investigation into evolutionary, ecological and causal aspects of teaching.

In the following section, we present a review of putative cases of teaching, dividing the comparative data set into anecdotal and quantitative accounts. While anecdotal observations cannot provide supporting evidence

for teaching, they lead one to consider intriguing behavioral interactions which, through further observation and experimentation, may prove to be cases of teaching as we have defined it. In contrast, more quantitative descriptions, though by no means definitive, force one to lay out explicitly some of the necessary experimental controls that need to be present in order to provide strong support for teaching. Lastly, by presenting a relatively complete review, we provide a synthesis of the current comparative database, thereby indicating where, taxonomically, possible forms of teaching may be most prevalent.

POSSIBLE EVIDENCE OF TEACHING

*Data on Felids and Other Carnivores*

Anecdotal Data

Observations of felids and other carnivores show that mothers modify their predatory behavior in a series of stages (Leyhausen, 1979). This has best been described in the domestic cat (*Felis catus*). Adult females in this species normally pursue, capture, kill and eat prey in a smooth sequence with little hesitation between acts. At a certain time after parturition, however, when kittens start to become mobile and walk out of the nest, mothers alter their behavior and carry prey to their kittens, eating it in front of them instead of consuming it away from the den where they caught it. Next, they carry live prey directly to their offspring and allow them to play with it, but recapture it if it escapes. Finally, they take little part in prey catching at all, merely moving toward prey initially while their young chase, capture and dispatch it efficiently (Baerends-van Roon and Baerends, 1979). Mothers give characteristic mewing calls to their kittens in all of these situations (Ewer, 1969; Caro, 1980a). In contrast, these interactions do not take place between adult animals.

Snapshots of mother-prey interactions have also been reported in free-living tigers (*Panthera tigris*) where Schaller (1967) saw a tigress pull down a buffalo (*Bubalus bubalus*), but then leave it for her cubs to kill. They failed to do this and when it stood up, she toppled it again for them. Schenkel (1966) interpreted lion (*P. leo*) mothers' unsuccessful hunts as allowing their cubs to practice stalking; and Kruuk and Turner (1967) reported cheetah (*Acinonyx jubatus*) mothers bringing back live prey to their cubs and allowing them to run after and knock it over. In meerkats (*Suricata suricatta*), mothers approach their pups and incite them to snatch morsels of insect from her (Ewer, 1963). The same sort of behavior has been seen in mongooses (*Helogale* spp.), but here both the mother and a male were involved (Jacobsen, cited in Ewer, 1973). Finally, Canadian otter (*Lutra canadensis*) mothers have been seen to bring back prey to their young and release it in front of them (Liers, 1951).

Although the examples described above are not exhaustive, it is a common theme that the mother gives her young the opportunity to interact with prey by presenting it to them and preventing it from escaping. Observational learning in the sense of the young watching their mother perform a specific act and then attempting it themselves is not a salient feature of any of these incidents (Ewer, 1969).

Quantitative Data

A more comprehensive study of the acquisition of predatory skills in cheetahs has documented both the change in mother's behavior and some of the costs to her. Cheetah cubs leave their den between six and eight weeks of age when they are introduced to solid food; cubs accompany their mother until they are between 16 and 21 months old (Laurenson et al., 1992). Caro (in press) carried out behavioral observations on free-living cheetah mothers and cubs from 1.5 months of age to independence in the Serengeti National Park, Tanzania. Over 2500 hours of data on 54 families were collected over a four-year period recording, among other variables, the hunting and feeding behavior of individual family members. Figure 1 (upper panel) shows the proportion of prey that mothers released for their cubs and (lower panel) who was responsible for killing prey, plotted against cub age. When cubs were 1.5 months old, mothers rarely released prey and usually killed it themselves either by suffocation, if it was a Thomson's gazelle (*Gazella thomsoni*), or by biting it through the skull, if it was a hare (*Lepus* spp.). This is the normal form of predation in females living alone without cubs. When cubs were 2.5 to 3.5 months old, mothers began to refrain from killing prey themselves and let it go in the presence of the cubs, sometimes after
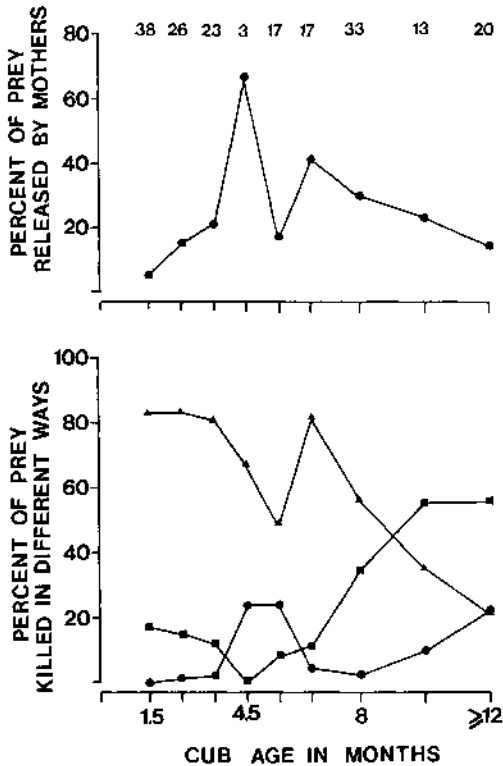
FIG. 1 (upper panel). PERCENT OF PREY CAUGHT BY CHEETAH MOTHERS THAT THEY RELEASED FOR THEIR CUBS, PLOTTED AGAINST CUB AGE. (NUMBERS AT THE TOP OF THE FIGURE DENOTE NUMBER OF KILLS.)

Mothers of cubs less than four months of age released 9.2 percent ($n = 87$) of prey, mothers of cubs greater than four but less than seven months released 32.4 percent of prey ($n = 37$), mothers of cubs eight or more months old released 24.2 percent ($n = 66$) of prey; G-test, $G_2 = 11.32$, $p = 0.004$.

FIG. 1 (lower panel). MEAN PERCENT OF KILLS MADE BY MOTHERS (TRIANGLES), BY CUBS (CIRCLES), OR THAT DIED BEING EATEN ALIVE (SQUARES) PLOTTED AGAINST CUB AGE.

carrying it to them; cubs then ran after it, repeatedly knocking it over. Mothers would normally intervene after 5 to 15 minutes and kill the prey; cubs very rarely killed prey at

this age [Fig. 1 (lower panel)]. Between the age of 4.5 and 6.5 months, mothers released almost one third of the prey that they caught, and cubs now started to suffocate prey, so the proportion of kills made by mothers declined. This pattern remained more or less unchanged up to the time cubs reached eight months, with mothers still releasing 30 percent of their kills, except that cubs would now disembowel prey alive or tear it apart while a family member held on to the esophagus. By ten months, more than half the prey were dispatched in this way; the proportion of prey released for the cubs declined during this period. This case study clearly demonstrates a change in mothers' prey-handling technique with cub age.

The cheetah study also demonstrates that the mother's change in behavior was costly, aside from the costs incurred in prolonging the time before the family would eat, and in running after the prey. Releasing prey for cubs increased the chances that it would escape. For example, whereas mothers captured and killed hares on 84.8 percent ($n = 33$) of occasions they pursued them, cubs only managed this on 46.2 percent ($n = 13$) of instances they chased hares that had been released for them, or that they had flushed themselves (Fisher exact probability test, $P = 0.01$). Released Thomson's gazelle fawns also escaped from the cubs occasionally. It is interesting to note that of the hares that were released by mothers, two out of five were maimed and ran erratically or in small circles, whereas none of the easier-to-catch neonate Thomson's gazelles ($n = 23$) was disabled (Fisher test, $P = 0.04$).

Further data suggest that mothers may have tried to ameliorate these costs (i.e., increased latency to eat, energetic expenditure and greater probability of losing a meal) because there was a tendency for hungrier mothers to be less likely to release prey for cubs. The average belly sizes of mothers when prey were released ($\bar{x} = 4.9$, $n = 35$) was slightly greater than when prey were killed outright ($\bar{x} = 4.3$, $n = 154$; Mann-Whitney U-test: $z = -1.71$, $P = 0.09$; see Caro, 1987 for details of scoring belly sizes). Mothers were also more likely to refrain from killing certain prey types than others (Table 1). In particular, they allowed cubs access to 30.9 percent ($n = 81$) of the live neonate gazelles they caught, but only

TABLE 1

*Number of kills separated according to whether cheetah mothers released prey for their cubs*

| Species | Released | Killed | Percent released |
|---|---|---|---|
| Hare | 5 | 28 | 15.2 |
| Neonate Thomson's gazelle | 23 | 55 | 29.5 |
| Neonate Grant's gazelle | 2 | 1 | 66.7 |
| Half-grown Thomson's gazelle | 3 | 17 | 15.0 |
| Subadult Thomson's gazelle | 0 | 9 | 0.0 |
| Adult Thomson's gazelle | 2 | 39 | 4.9 |
| Other* | 1 | 5 | 16.7 |

* Other consisted of three neonate wildebeests (*Connochaetes taurinus*), an adult female reedbuck (*Redunca redunca*), a subadult male Grant's gazelle (*Gazella granti*), and an adult dik-dik (*Madoqua kirki*), which was released.

4.0 percent ($n = 50$) of the adult and subadult gazelles (*G*-test, $G_1 = 16.38$, $P < 0.001$). Neonates were much easier to recapture than were older gazelles because they ran more slowly, could not turn as sharply (FitzGibbon, 1990), were unsteady on their feet, and sometimes even failed to recognize cheetahs as predators (Caro, in press).

Although this study provides the first quantitative documentation of changes in maternal hunting behavior in a wild mammal, it is unclear whether changes in females' hunting behavior are due to changes in cub age or improvement in cub hunting skills, since individual families were not followed for periods longer than a week. Moreover, because data on families were collected over a short interval of time, they cannot show whether changes in maternal behavior directly affected cub hunting skills. Indeed, cubs' hunting skills remained poor up to, and beyond, independence from their mother, showing surprisingly little improvement in the ten months after first being introduced to prey (Caro, in press). Thus, although a cub's skills may have improved as a result of maternal hunting behavior, we can only tentatively suggest this possibility.

Under more controlled laboratory conditions, Caro (1980b) examined the development of predatory behavior in domestic cats. In that study, kittens between the ages of 4 and 12 weeks were exposed to live prey (e.g., *Mus domesticus*) on 17 occasions for 40 minutes in the presence of their mother and for 30 minutes when she was absent. Control kittens received identical exposure, but without their mother ever being present in the training situation. This experiment yielded a number of results: (1) During the period of exposure,

young kittens in the experimental group under eight weeks of age showed higher mean rates of interaction with the prey when their mother was present than when she was absent, and were more likely to monitor visually the prey when their mother did so (Caro, 1980a); (2) By the time the experimental procedure had terminated at 12 weeks, significantly more experimental kittens had killed mice more than five times in total than had control kittens, and they had killed significantly more mice by this age (Caro, 1980b); (3) When six-month-old kittens were tested on their predatory abilities, experimental subjects delivered significantly more bites to the nape, but not to other regions of the mouse, than did control kittens (Caro, 1980b). This is the method by which adult cats dispatch rodent prey.

Behavior of mothers was carefully recorded during the experimental protocol and mothers did indeed show the characteristic sequence of encouraging their kittens to interact with prey. Moreover, many measures of kittens' predatory skills were correlated with the predatory behavior of their mothers. This strongly suggests that the mother's interaction with her kittens enhanced the development of predatory skills and goes some way in ruling out the possibility that the mother's presence alone was sufficient to change the kitten's behavior (Caro, 1980a). Taken together, these findings suggest that maternal behavior reduces the age at which kittens acquire predatory skills.

Despite the observation that domestic cats appear to provide circumstances for their kittens to show predatory behavior, it is unclear whether such maternal behavior is sensitive

to developmental changes in kitten behavior. That is, the timing of each step in the mother's predatory sequence (bringing dead prey back, letting it go, and so on) might not be contingent upon improvements in her cubs' predatory skills, but rather change according to a relatively stereotyped time course (e.g., yoked to parturition or aspects of lactation). Some evidence, however, militates against an invariant time course for the sequence of predatory behaviors in this species. (1) Certain mothers started to leave dead prey for their kittens very early on in the tests at four weeks, while others did not start until kittens were six weeks old (Caro, 1980a). (2) Many aspects of mothers' predatory behavior were significantly negatively correlated with increasing skills of their offspring (Caro, 1980a). (3) More subtly, between weeks four and eight of development, mothers in six out of seven litters were significantly more likely to initiate a bout of interaction with prey when none of their kittens was interacting with it than when one was doing so. Mothers did not interrupt their kittens' bouts, but rather contacted the prey when kittens had lost interest (Caro, 1980a). The interdigitation of mothers' bouts with those of offspring suggests that they were responsive to their kittens' shortcomings. Observations show that individual mothers respond differentially to differences in prey-catching skills of kittens of the same age, but the definitive experiment has yet to be carried out.

### Data on Pinnipeds and Cetaceans
#### Anecdotal Data

We found only two examples of instruction-like behavior in these orders, and suspect the paucity of data reflects the difficulty of observing aquatic mammals; there are few papers on these taxa when compared to those on other orders of mammals (May, 1988). California sea lion (*Zalophus californianus*) mothers give birth on beaches. When disturbed by humans, they have been observed running down the beach into the sea carrying their newborn pups in their mouths. Once at sea, the pup is forced to swim on and off its mother's back and to return to the shore (B. Le Boeuf, pers. commun.). While the behavior could simply be interpreted as a form of maternal defense, one of the consequences would certainly be to encourage young to practice their swimming techniques, possibly

for the first time. More observations are necessary to determine whether offspring have begun to swim on their own before they are thrown out, and whether mothers show the same behavior in less dangerous circumstances.

Killer whales (*Orcinus orca*) off the southern Argentinian coast hunt southern elephant seals (*Mirounga leonina*) and southern sea lions (*Otaria flavescens*) by rushing toward these species when they are on shore or in the surf zone. Lopez and Lopez (1985) observed 17 sessions where an adult killer whale floated 50–100 m off the shoreline, while an immature killer whale had beached itself pursuing the prey. In 7 of the 17 instances, the adult also charged toward the beach in a manner similar to the cooperative hunting of pinnipeds observed between adults, but did not make a capture; the adult then returned to its former position before repeating the process again. It was noted that these were areas where an adult killer whale could have been successful in trapping a pinniped. On six occasions, when an adult and juvenile were both seen stranded at the same time approximately four meters from each other, the adult killer whale flung a captured live sea lion toward the juvenile, whether it had caught a victim or not, the juvenile then pushed the prey with its head or body or captured it in its mouth. These observations suggest that some adults were not completely sensitive to the situation because they gave juveniles opportunities to capture prey when they had already captured one. Killer whales have also been observed to take prey out to sea and play with it, including flipping it out of the water using their tail (reported in Caro, 1989); whether this occurs in the presence of juveniles and provides them with further opportunities is unknown. Nor is it known whether killer whales that have not received such opportunities are able to learn how to capture sea lions as effectively or as early in life as those who have received instruction.

### Data on Nonhuman Primates
#### Anecdotal Data

Primatologists have claimed that evidence of instruction or teaching is better documented in nonhuman primates than in other mammalian orders (e.g., Nishida, 1987). While purported cases of teaching in nonhuman pri-

mates, like those in other mammalian orders, can often be more parsimoniously described as situations where one individual provides the opportunity for a naive individual to learn (Ewer, 1969; Jolly, 1972; Nishida, 1987), there are some intriguing observations among monkeys and apes that conceptually appear to involve different sorts of transmission mechanisms than those described for carnivores, pinnipeds and cetaceans.

In reviewing cultural transmission, Nishida (1987) suggests that nonhuman primate data on instruction can be divided into two forms, encouragement and discouragement. We found five reports of encouragement, although there may be more. In captive chimpanzees (Yerkes and Tomlin, 1935), gorillas (*Gorilla gorilla*, A. Whiten, cited in Passingham, 1982), rhesus macaques (*Macaca mulatta*, Hinde and Simpson, 1975), free-living yellow baboons (*Papio cynocephalus*, Altmann, 1980), and spider monkeys (*Ateles geoffroyi*, Milton, 1988), mothers have been observed encouraging their young to walk and follow them, typically in the context of group movement or foraging. Altmann's description (p. 130) is representative of the reported phenomena: "A mother began to take a few steps away from her infant, paused, and looked back at the infant. As soon as the infant began to move toward her, she again moved slowly away. At first, this sequence was repeated every few steps, but soon a mother seemed to be able to initiate a long bout of following, by just one such pause." Although this example could be interpreted as a mother wanting to leave with the troop but not wanting her infant to remain behind, it is at least suggestive of teaching.

Cases of discouragement are apparently more widespread. In captive macaques (*Macaca fuscata* and *M. mulatta*), mothers pull their infants away from explorations of novel objects (Kawamura, 1959; Menzel, 1966); free-living chimpanzees remove food from their infants if the food item is not part of the group's diet (Goodall, 1973; Wrangham, 1977; Nishida, 1983).

In an experimental study with captive chacma baboons (*Papio ursinus*), Fletemeyer (1978) has shown that when a high-ranking male knows (as a result of experience) that experimentally presented fruits are poisonous

(i.e., because they have been treated with cyanalin), he will aggressively threaten naive juveniles and subadults who approach and show interest in the fruit. As a result, group members rapidly learn to avoid the poisonous fruit. A similar example concerns a captive group of squirrel monkeys (*Saimiri sciureus*), where one animal accidentally died as a result of being choked by a chain. When young and presumably naive squirrel monkeys approached the chain, adults actively discouraged their approach, which resulted in other group members avoiding the chain (Leger et al., 1981).

Although these studies imply some form of teaching, there are several problems. First, cases where food is apparently taken away from younger individuals are difficult to interpret because such events could have been accidental; moreover, it is unclear whether such behavior had an effect on the infant's subsequent selection of food from the environment. One would need to know whether infants who picked poisonous foods and were reprimanded had a lower probability of picking such foods up again in contrast to infants who were not reprimanded. Furthermore, no data are presented on the frequency with which adults knock food away from older individuals, and thus it is unclear whether naive individuals (infants) receive *special* attention. Second, in situations where objects are avoided, one needs to rule out the possibility that individuals learn to avoid certain objects simply because other individuals also do so. In the chacma baboon situation, it is unclear whether the alpha male's aggression (which might imply teaching), in contrast to his active avoidance of the poisonous fruits, was primary or secondary to the acquisition of avoidance behavior in other group members.

Gardner et al. (1989) present an impressive data set on sign language acquisition in captive chimpanzees. The majority of signs appeared to have been learned through instruction by human signers or through observational learning and imitation of other chimpanzees. Observations by Fouts and his colleagues (1989) on Loulis, the female chimpanzee raised without instruction from humans, are most telling with regard to a phenomenon called molding. Molding occurs when an instructor takes the hands of a pupil

and "molds them into the sign while putting them through the movement" (Gardner et al., 1989:18). Loulis gradually acquired sign language even though she was prevented from seeing human trainers use signs with each other or with the other chimpanzees. Although Loulis clearly obtained some signs from watching other chimpanzees signing to each other, there were a few observations of Loulis' hand being shaped into an apparently appropriate configuration by her foster mother Washoe. For example, Fouts et al. (1989:286) describe one of several cases where Washoe was waiting for a candy bar from a friend and "signed FOOD repeatedly with much excitement and food-grunts. Loulis was sitting next to her, watching. Washoe stopped signing, took Loulis' hand, and molded it into the FOOD configuration, and put it through the FOOD movement several times." These data provide suggestive evidence that Washoe was sensitive to Loulis's signing deficiencies and was attempting to improve her signing skills directly through the use of "hands-on" experience.

## Quantitative Data

In free-living vervet monkeys, the predator alarm call system develops gradually over time (Seyfarth and Cheney, 1980, 1986). Initially, infants will call at inappropriate objects, such as falling leaves, but gradually different calls are given to particular species within three classes of predator (large cats, raptors and snakes) as observed among adults (Seyfarth et al., 1980). Observations on the production of eagle alarm calls by infants (Seyfarth and Cheney, 1986) reveal that if an infant has called to an appropriate aerial predator (e.g., martial eagle, *Polemaetus bellicosus*) as opposed to an inappropriate object (e.g., a falling leaf), adults will also produce eagle alarm calls (12 out of 17 cases versus 3 out of 60 cases, respectively). Although Seyfarth and Cheney (1986) state that this type of "reinforcement" may have an effect on the development of knowledge concerning correct usage of alarm calls, they caution that such vocal behavior by adults may not be targeted only at naive individuals and hence may not be relevant to the issue of instruction. Indeed, adults did not produce significantly more second alarm calls after correct alarm

calls by infants (70.6%) than after correct alarm calls by adults (51.6%).

Using the same vervet monkey study population, Hauser (1987) conducted a two-year developmental study that provided additional information on whether production of alarm calls by mature individuals, following the production of alarm calls by infants, had an effect on the infants' ability to produce such calls in appropriate contexts. Over 2,500 hours of focal observation on 32 infants suggested that not only encouragement but also punishment may be important for the development of alarm calls. Encouragement in this study was defined as the production of a same-type alarm call by a mature individual following, within five seconds, the production of an alarm call by the infant. Punishment was defined as physically aggressive contact by one individual toward another individual who had just produced a contextually inappropriate call in a given situation.

Based on 68 independent cases of alarm calls by 15 infants (under the age of one year), in circumstances where the infant was the first member of the group to call, 34 (50%) of the cases of encouragement were recorded [Table 2 (a)]. Twenty-six of these occurred when the infant produced an appropriate sounding alarm call in the appropriate context (i.e., to species such as large cats, raptors and snakes that predated all age classes of vervets in Amboseli National Park, Kenya); eight cases of encouragement occurred following the production of an alarm call in an inappropriate context.

What are the consequences of encouragement for the development of vervet alarm calls? In observations where the alarm call was given to an appropriate predator and encouragement occurred ($n = 26$ cases), there were eleven cases (42%) where the infant's production of the same-type alarm call was next heard (interval between consecutive alarm calls = 2–18 days, $\bar{x} = 11.2$ days) in the appropriate context and four (15%) cases where it was next heard in the inappropriate context [Table 2 (b)]; data on subsequent calls were unavailable for many of the original 68 cases. In cases where the alarm call was given in an inappropriate context and there was no encouragement ($n = 14$ cases), 21 percent of the infant's subsequent alarm calls (interval

TABLE 2

*Encouragement of infant alarm calls by adult vervet monkeys*

(a) Responses of adults to infants' encounters with a predator

| Infant's call | Number of instances adults did or did not call | |
| --- | --- | --- |
| | Encouragement | No encouragement |
| In an appropriate context | 26 | 20 |
| In an inappropriate context | 8 | 14 |

(b) Consequences of encouragement for subsequent alarm calls by infants

| Infant's initial call | Number of subsequent alarm calls by infants in | |
| --- | --- | --- |
| | Appropriate context | Inappropriate context |
| Appropriate context and encouragement | 11 | 4 |
| Inappropriate context and no encouragement | 3 | 11 |

between consecutive alarm calls = 1–22 days, $\bar{x} = 12.4$) were next heard in appropriate contexts, whereas 79 percent were heard in inappropriate contexts. These results could be interpreted as infants simply persisting in the way they called initially, either inappropriately or appropriately, regardless of whether adults had called at the same time. Nevertheless, an alternative explanation is that second alarm calls by mature individuals had at least some beneficial effect on the infant's knowledge of the association between call-type and predator-type. Because the interval of time between consecutive alarm call situations is long for some infants, and because of the potential confounding effects of individual differences, arguments concerning causality and the effectiveness of the second alarm call must be tempered.

Data presented thus far concern only those cases where adults called after an infant's alarm call in the appropriate context, or failed to respond when the infant called in an inappropriate situation. But what are the consequences of the adults' second calls in cases where the infant produces an inappropriate alarm call? There were only five cases of this, four involved punishment, whereas one interesting case involved encouragement. A five-month-old infant (WC) saw a herd of stampeding elephants (*Loxodonta africana*) and produced a leopard alarm call. By chance and at approximately the same time, the alpha male of this group spotted a leopard (*Panthera pardus*) in the opposite direction from the

elephants and produced a leopard alarm call. During the next four encounters that were observed when elephants were moving nearby (over a period of four months), WC uttered leopard alarm calls, even though no other group members called. Again, this might simply be an example of call persistence but the probability of the infant's calling behavior having been accidentally encouraged by the male cannot be excluded.

In the four other cases, which involved four other infants, an inappropriate alarm call was punished by the mother who, after initially responding with flight, returned and physically attacked (e.g., bit or slapped) her offspring; in three out of four of these cases, the infant's subsequent and same-type alarm call was next heard in the appropriate context. Such aggressive interactions were never observed following inappropriate alarm calls by adults which, though infrequent, nonetheless occurred. As far as we know, therefore, this is the only demonstration of direct punishment under field conditions. Because most of the infants died before one year, however, it was not possible to compare their rate of vocal development with infants whose calls were not punished.

These data only meet some of the conditions stated in our definition of teaching. In particular, because adults do not call more often after the correct alarm calls of infants than after the correct alarm calls of adults, it does not seem that such second alarm calls are necessarily directed at naive individuals.

Moreover, in playback experiments using predator alarm calls (Seyfarth and Cheney, 1986), there was no evidence that mothers attempted to modify the inappropriate behavioral responses of their young and vulnerable infants. In contrast, the few cases of punishment were obviously directed at the infant, and given the short time delay between inappropriate alarm call and maternal aggression, it seems likely that the mother's behavior was causally related to the infant's call. Moreover, although the instructor may eventually benefit from her act by not being misled again, the payoff is not likely to be immediate and thus conforms to our definition. Nonetheless, a claim that the behavior of adults is directed at infants, and has an effect on vocal development, needs to be strengthened by additional observations in a variety of social contexts and, for example, by playback experiments selectively shaping or not shaping the inappropriate and appropriate alarm calls of infants.

Chimpanzees living in the Tai National Park, Ivory Coast, use hammers and anvils to crack open nuts. Adult males and adult females tend to specialize on different nut species. One explanation for this sex difference is that males, who are stronger than females, crack open those species with the hardest shell (Boesch and Boesch, 1984). Based on almost ten years of observation, Boesch (1991) has recently reported on changes in nut-cracking behavior of mothers and offspring in the Tai chimpanzees. His data indicate that there are three different ways in which mothers can influence the development of nut cracking in young under the age of eight years. The first type of interaction, called "stimulation," was observed on 387 occasions and occurs when a mother leaves either a hammer, or a cache of nuts, or sometimes both, near or on top of an anvil while the infant remains at the anvil. This behavior is most commonly seen among mothers with young who are three years old or older, precisely the age at which young begin to show interest in nuts. Stimulation is interesting because a common behavioral pattern for adult chimpanzees in the Tai forest is to carry their hammers during nut collection and consume the nuts that they have placed on an anvil. Chimpanzees who leave their hammers behind risk losing them to

other community members. As a result, mothers often incurred a foraging cost by having to find more nuts and another tool for opening them. Nonetheless, hammers that were left behind were used by offspring in 46.2 percent of all observed cases.

A second form of interaction, called "facilitation," occurred when a mother allowed her offspring to take a hammer or cache of nuts from her. Facilitation was observed on 272 occasions with hammers and 316 occasions with nuts. As in stimulation, facilitation also resulted in a cost to the mother and a benefit to her offspring. For example, in one case a mother allowed her son to take four consecutive hammers. After each hammer was taken, she was forced to search for another. Consequently, the mother's intake rate was reduced, whereas her offspring enjoyed an increase of 20 percent in the number of nuts eaten per minute.

Boesch's final case was called "active teaching," which occurred only twice and involved direct intervention on the part of the mother in her offspring's attempt to crack open a nut. In one example, a six-year-old male had taken a majority of his mother's nuts, as well as her stone hammer. After the young male placed a nut on the anvil, but prior to opening it, his mother approached, picked up the nut, cleaned the anvil, and put the nut back in a different position; the reoriented position more closely approximated that of adults preparing the same species of nut. The young male then pounded the nut open and ate the kernel inside. In the second example, a different mother reoriented the hammer for her five-year-old daughter who then succeeded in opening some nuts by maintaining the same grip on the hammer that her mother had used.

There are several features of these observations that fit our definition. The behaviors described occur only in the presence of offspring, and are associated with some cost to the mother (e.g., increased search time for another hammer or additional nuts) and have no immediate benefit. From the descriptions, it appears that the young benefit from some of these interactions, at least, in the short term since they gain access to the nuts. It is unclear, however, whether young who obtain some type of instruction learn to crack open nuts at an earlier age than those who do not obtain

instruction. If they did, one might have expected more cases of "active teaching" to have been observed during the long study.

## Data on Birds
### Anecdotal Data

In birds, there is some evidence of instruction-like behavior in relation to the acquisition of foraging skills. For example, juvenile yellow-eyed juncos (*Junco phaeonotus*) are inept foragers and, apparently as a result of this, appear to have low survivorship in contrast to adults (Sullivan, 1988). To determine how juveniles acquire the necessary skills to forage in their environment, Sullivan staged a series of observations where different food items were presented to flocks comprised of adults and juveniles (K. Sullivan, pers. commun.). When meal worms were presented, juveniles tended to pick them up with the inappropriate orientation and as a result, either dropped the worm or struggled to ingest it. During some observations, however, adults would intervene in the juvenile's eating bout and reorient the meal worm to its appropriate orientation in the juvenile's beak, thereby facilitating ingestion. Although the number of adults failing to make corrections is not known to us, such instances of intervention were apparently rare under natural conditions, despite adults being under relaxed time budget constraints and the benefits to the juveniles being potentially quite large.

Our literature search of avian species suggested that putative cases of teaching were most prevalent in raptors. Literature on falconry contains accounts of adults enticing their young away from the nest with food and subsequently teaching them to hunt and, like domestic cats, there is a characteristic sequence of events (see Newton, 1979). Adults initially take food to their young and pass it to them in a perched position or leave it on the nest. Once the young can fly, however, they begin to catch the prey that adults drop for them in the air, or fly to the parent and remove it from their beak or feet. Young kestrels (*Falco tinnunculus*, Tinbergen, 1940) and young European sparrow hawks (*Accipiter nisus*, Newton, 1986) can manage this two weeks after they leave the nest. Later still, adults may surrender the prey only after being chased by their offspring and may release live small birds for young to catch. This has been seen in the European sparrow hawk (Newton, 1986), Cooper's hawk (*A. cooperii*, McElroy, 1974), and peregrine (*F. peregrinus*, S. Sherrod cited in Newton, 1979). Adults of the latter species have been seen to capture and release prey several times before their young eventually caught it. Beebe (1960) describes cases of adult peregrines flying low over the ground to flush prey that were then caught in a steep dive, or stoop, by the young. Adults also dive at but miss birds they would easily catch, thereby leaving them for the young to capture during their stoops.

The best account of apparent instruction in raptors is provided by Meinertzhagen's (1954) rich description of adult ospreys (*Pandion haliaetus*) encouraging their fledglings to catch fish. At first, the adults perched away from the nest with fish in their talons, but would not feed the young (despite their screaming for food), repeatedly flying away with it in an apparent attempt to encourage the young to follow. On the first day the fledglings would not leave the nest, but on the next two days when the young flew off the nest to a rock, they were fed. On the following day, the young followed the parents hunting over a lake. Each caught a fish, carried it toward the young and then dropped it, but caught it again and secured it before it hit the water. After repeating this many times, one of the young finally caught the fish in a stoop and carried it to the rock to eat it. The less successful sibling now flew to the rock to share the catch, but after a fight the parent arrived and literally pushed this offspring off the rock forcing it to take wing again. The process of dropping a fish was repeated until the second fledgling finally caught it and went back to the rock to feed.

On day five the same procedure was observed with each fledgling following a parent around and unsuccessfully attempting to catch fish that were dropped for it in midair. When the fish reached the surface, the parents would retrieve it until eventually one youngster finally descended to the water and picked up the fish; by afternoon, both were doing this. The next day, all four ospreys were seen diving for fish. On day seven, the adults drove the offspring away from the lake and they

were not seen again. Thus, the period of education took only six days. Nevertheless, observations of hand-raised young ospreys successfully catching prey within three days to three weeks of being released into the wild, in the absence of parental instruction, question the importance of teaching in this species (Schaadt and Rymon, 1982).

These anecdotal accounts suggest that birds alter their behavior in the presence of naive fledglings. Meinertzhagen's detailed report is exemplary because it followed the same family on consecutive days, making it difficult to dismiss his observations as pathological behavior. Moreover, these longitudinal observations strongly suggest that changes in adult behavior (e.g., dropping prey and driving offspring away) were contingent on offspring behavior (e.g., leaving the nest and taking fish from the water, respectively). The report of an adult pushing its offspring off the rock suggests parental encouragement in raptors may be more forceful than previously envisaged.

### Quantitative Data

West and King (1988) studied the role of social factors in the ontogeny of male song in the cowbird (*Molothrus ater*). Their observations illustrate the difficulty in ascribing teaching to nonhumans when both parties are adult. In this species, when males are placed in cages with nonsinging females, they appear to modify the structure of their song based on the female's preferences for certain song types. Using video analyses of eight male-female pairs, West and King found that females produced a "wing stroke" display on approximately 1 out of every 79 songs on average, and upon seeing the display, males approached and inspected the subsequent behavior of females. Once the wing stroke display was given, males now sang the song type eliciting the display more often than song types that failed to elicit the display. In the second part of the study, one year later, females in breeding condition were tested with playback experiments for preferences to certain song types; in this species, preference by the female is shown by a copulatory posture. Analyses revealed that songs that elicited a wing stroke display in the previous year were consistently the most preferred songs. These results suggest that the female's wing stroke display encourages the male to sing the appropriate song, and that males benefit from doing this by being able to copulate with the female (but see Rothstein et al., 1989).

Although the cowbird study appears to fall under our definition of teaching, there are at least two problems with this example (D. Premack, pers. commun.). First, the female's display may simply serve as a reinforcer to increase the rate of production of her preferred song type. By this account, the female is like a wing-stroke machine, waiting for the appropriate input. There is no modification of behavior and from the original description of the phenomenon, it is unclear whether the display ever emerges under other conditions. Second, by giving the wing stroke display, the female appears to gain an immediate benefit by copulating with the male. Although these two problems must be taken seriously, we would rather remain skeptical about the strength of the cowbird example as a form of teaching. Specifically, more details are needed on (1) the social conditions eliciting the wing stroke display, (2) the costs to the female of waiting for males to produce the appropriate song, and (3) the latency between putative instruction (i.e., display) and benefit (i.e., copulation).

None of the examples described fits our definition of teaching exactly. The social interactions we have discussed, however, differ from the behaviors typically associated with social learning (e.g., local enhancement, social facilitation, contagious behavior, observational learning, or matched-dependent behavior) because the presumed teacher (**T**) modifies its behavior in the presence of a naive pupil (**P**). Social learning, in contrast, demands only that one individual pays attention to what another is normally doing. A weakness in some of the examples reviewed here is that it is rarely stated explicitly that **T** does *not* modify its behavior in the presence of experienced conspecifics. Nonetheless, the behavioral change exhibited by **T** involves no immediate benefit and usually incurs some cost in that **T** loses the opportunity to perform another behavior that is more appropriate to the given

situation. Occasionally, in the case of cheetahs for example, the cost is substantial: as a result of apparent tuition, prey had a higher probability of escaping.

The examples also have a common theme in that **P** appears to benefit by acquiring new knowledge or a skill, as a result of **T**'s behavior. These examples, however, are weakened by the fact that we do not know whether individuals who were not taught failed to acquire the knowledge or skill at all, or whether they would have acquired it later by other means; only in the case of domestic cats, and perhaps vervet monkeys, has an attempt been made to demonstrate it.

Most of the examples appear to occur between kin, specifically with **T** being the parent of **P**. In species with biparental care, both parents have been seen to teach offspring (e.g., ospreys). Only two potential examples of teaching could be found that occurred between nonrelatives: the female cowbird reinforcing the male's production of an appropriate song type, and the chacma baboon's aggression toward naive individuals who were approaching poisonous fruits; the killer whale example was not clear as to whether parents were involved or not. Given the prevalence of kin selection in animals and the more limited opportunities for reciprocity, one might expect most examples of teaching in nonhuman animals to be between parents and their young.

### CATEGORIES OF TEACHING

Although there is a great need for additional empirical studies, inspection of the examples covered in our review (Table 3) suggest that there are at least two different mechanisms underlying teaching in nonhuman animals. In the first, **T** puts **P** in a situation conducive to learning a new skill or acquiring knowledge ("opportunity teaching"). In the second, **T** directly alters the behavior of **P** by encouragement or punishment ("coaching").

The majority of examples fall under opportunity teaching and as such, build on the issues elucidated by Ewer (1969) and supported by others (Jolly, 1972; Nishida, 1987). All of the descriptions of carnivores, including the domestic cats and cheetahs, involve giving **P** the opportunity to interact with prey that

TABLE 3
*Summary of putative cases of teaching described in the text. W denotes weak, S denotes strong evidence*

|  | Actor modifies its behavior in presence of naive observer | Demonstrated cost (or no benefit) to actor | Demonstrated benefit to naive observer |
|---|---|---|---|
| **Opportunity teaching** |  |  |  |
| Various carnivores | *W* |  |  |
| Cheetah | *S* | *S* |  |
| Domestic cat | *S* |  | *S* |
| California sea lion | *W* |  |  |
| Killer whale | *W* |  |  |
| Chimpanzee (wild) (*s&f*) | *S* | *S* | *W* |
| Yellow-eyed junco | *W* |  |  |
| Various raptors | *W* |  |  |
| Osprey | *S* |  | *W* |
| **Coaching** |  |  |  |
| Various nonhuman primates | *W* |  |  |
| Chimpanzee (laboratory) | *S* |  |  |
| Chimpanzee (wild) (*AT*) | *S* |  | *W* |
| Vervet monkey | *S\**, *W*ᵉ |  | *W\** |
| Cowbird | *W* |  | *W* |

Note: For wild chimpanzees, *s* refers to stimulation, *f* to facilitation, and *AT* to active teaching. For vervet monkeys, * refers to punishment, ᵉ refers to encouragement. For many species it was difficult to assign a particular notation due to lack of reported data; for example, in the costs column, implied costs based on descriptions alone were not assigned *W*.

would not otherwise be possible if **T** was not there. For instance, five-month-old cheetah cubs are almost never able to approach a gazelle undetected and contact it on their own (T. M. Caro, unpub.). It is clear that placing **P** in a new situation can take many forms depending on the species. With so few examples presently at hand, it seems premature to separate conceptually the forcefulness or directedness of **T**'s behavior toward **P**. In other words, allowing **P** access to an object or prey item, placing **P** in a novel situation, or making **P** perform an act, seem to differ only by degree. Some of the examples discussed, however, point to a role of **T** in directly causing a change in the development of **P**'s behavior, a role that has heretofore gone unnoticed or at least, has been poorly described (Ewer, 1969). In this sense, our perspective extends that of Ewer's in that **T** might not only provide **P** with the opportunity to learn a skill or some information, but might also directly interact with **P** in order to cause a change in **P**'s behavior.

In all of these situations, **P** may subsequently have acquired the skill through trial-and-error learning (seal pups will eventually enter the sea on their own accord, for instance), but **T**'s behavior probably caused this to happen earlier; such trial-and-error learning may either be random, or innately guided and triggered by specific contextual cues. In this sense, teaching serves as a facilitating influence in that it causes behavior to appear earlier than would normally occur during ontogeny (Bateson, 1976). Nevertheless, it is rarely known for certain whether teaching either facilitates development or initiates new forms of behavior as required by our definition. Thus it is crucial that the behavior of necessary control subjects that receive no instruction is carefully monitored in future field and laboratory studies.

Coaching involves direct modification of **P**'s behavior by **T**, either through encouragement or punishment. The chimpanzee molding another's hand into the FOOD configuration and the vervet mother slapping her infant are clear examples, which contrast with placing **P** in a novel situation as described above. While this class of interactions probably facilitates development of behavior, it also seems logically possible that **P** would never have ac-

quired the appropriate behavior without the intervention of **T**, as suggested by the vervet infant's reaction to elephants. If true, then teaching under these conditions may also initiate new forms of behavior or encourage existing behavior to be performed in a new context, as well as serve a facilitating influence; however, the necessary controls to demonstrate this are typically lacking. At present, there are rather few examples of **T** encouraging **P**'s behavior in an overt manner.

A third category of teaching, seen commonly in humans, is characterized by **P** directly imitating the behavior of **T** following **T**'s solicitation or encouragement to imitate. For example, **T** says to **P** "Now watch me hit the squash ball," **T** then hits the squash ball, passes the racquet over to **P** and then **P** hits the squash ball which, with any luck, represents some approximation of **T**'s demonstration. We can find no compelling evidence for this category in the nonhuman animal literature. The only potential cases are where nonhuman primate mothers use repeated stop-and-go movements in an attempt to solicit following behavior from their infants. Given that stronger examples may be found in the future, the possibility of "setting an example" was included in our working definition.

CONCLUSIONS AND DIRECTIONS FOR FUTURE
RESEARCH ON TEACHING

*Fixed versus Flexible Teaching Patterns*

From a theoretical standpoint, it does not seem necessary for **T** to alter its behavior in response to **P**'s behavior in opportunity teaching (by definition this must occur in coaching). Instruction that begins at a certain age after **P** is born (or during a particular season) will be more effective than no instruction at all and will hence be favored by natural selection. In nearly all such cases, relatively fixed teaching will be less effective than what we would call flexible teaching, where **T**'s behavior shows some sensitivity to **P**'s changing skills or knowledge. Nevertheless, there might be circumstances where fixed teaching could be as effective: in situations where **P** needs to be introduced to a situation only once to gain a skill, or in extremely stable social and ecological environments where **P**'s development follows an invariant time course. More so-

phisticated forms of teaching may also be costly in terms of time and effort to both T and P, and in terms of cognitive machinery, and might militate against flexible teaching. Formal modeling would provide one approach to determining the circumstances under which different degrees of flexibility would be favored. At present, however, the empirical evidence is of insufficient resolution to distinguish examples of relatively fixed from more flexible interactions. Clearly, in order to distinguish between these two, it will be necessary to obtain simultaneous observations of T and P and, to decouple P's age from its experience.

### Benefits of Teaching and Constraints on the Delay between Instruction and Performance

The vast majority of the examples did not attempt to measure the benefit that P derives from T's behavior, either capitalizing on variability in teaching or by comparison with controls. Current examples thus do not conform to our definition of teaching because no direct benefit has been demonstrated unequivocally, except perhaps in domestic cats, and possibly vervet monkeys, wild chimpanzees, ospreys and cowbirds. Nevertheless, arguments based on design strongly suggest that some forms of teaching, according to our definition, do occur in nature. Measuring the benefits of teaching is critical for assessing the strength of selection on teaching in nonhuman animals, for understanding the economics of teaching (i.e., the costs that T should be willing to incur given the benefits that P is likely to derive from interactions with T), and for developing quantitative models that attempt to show how one mechanism of transmission may be more effective, in an evolutionary sense, than another mechanism. To obtain data on the benefits to P, observational and experimental studies should focus on the question of whether specific knowledge of skills would normally be acquired in the absence of teaching and hence, whether it facilitates the learning of behavior currently in the repertoire, or aids in the transmission of novel behaviors. Here it will be important to determine whether mothers selectively encourage those offspring that are poor at mastering a skill, since this will confound comparisons between individuals that have received tuition

and those that have not. Experimental studies will also be useful in demonstrating the rate at which information is transmitted from one individual to another.

The examples discussed also shed little light on the issue of different periods of delay between instruction and P's acquisition of knowledge or a skill, an issue that is central to many facets of learning theory. We would expect great variation in such latencies dependent on the skill and species in question. For example, skill acquisition in opportunity teaching will, in some species, be primarily influenced by variations in the strengths and skills of P's (e.g., knocking prey down or swimming). In others, the rate at which T provides P with appropriate opportunities to learn will affect variation in the timing of skill development and may thus depend on environmental constraints operating on T's ability to provide such opportunities. In yet other species, rate of acquisition may be determined by variation in T's sensitivity to P's developing skills.

### Intentionality

It has been our contention that, on a functional level, discussions of teaching can be divorced from discussions of higher mental processes such as intentionality. That is, by adopting a functional approach to the problem of teaching in nonhumans, it is unnecessary to make assumptions about what the instructor knows about the pupil's beliefs, desires, or motives. The same functional approach has been successfully applied to the problem of deception in nonhuman animals (for a review, see Cheney and Seyfarth, 1990). For teaching to be functionally useful, the instructor must observe that there are individuals whose current age or behavior indicates that they lack species-specific skills or knowledge; it is also necessary for instruction to provide a payoff both to the pupil and indirectly to the instructor.

The advantage of knowing the beliefs and motives of others is that one can generalize from one context or individual to another (Cummins, 1983; Dretske, 1989; for application of this idea to nonhumans, see Cheney and Seyfarth, 1990). In part, this claim relies upon a notion of conventions, with individuals having certain expectations about the ways

in which others behave (Lewis, 1969). An animal whose pedagogical interactions were limited to particular behavioral contingencies (e.g., "when my offspring sees an eagle and runs out into the open, rather than running under a bush, I should retrieve him"), might limit such interactions to certain individuals, or wait for certain cues to present themselves and then begin the instructional sequence. If, however, interactions are based on more general beliefs (e.g., most infants, genetically related or not, respond inappropriately to encounters with different kinds of predators), then pedagogical relations can be extended, perhaps more quickly and efficiently, to different contexts (e.g., not just swooping eagles but partially concealed leopards) and different individuals (e.g., unrelated infants whose mothers may reciprocate in the future by retrieving their offspring). In short, the ability to attribute mental states to others would almost certainly enhance the utility of teaching, as appears to be the case for humans and should, without question, be investigated empirically. There is still great utility, however, in teaching that is guided by a less complex mental calculator. As debate about intentionality is typically concerned with mechanisms of behaviors, few would disagree with these functional considerations.

Putting functional considerations aside, however, and considering the mechanisms involved in teaching, it seems more productive to investigate the scope of different mechanisms of teaching across species than to dismiss those that do not show sophisticated levels of intentionality as being uninteresting. This point is made with even greater force because the level of sophistication attributed to each example currently rests on our lack of investigation of case studies.

Current research on intentionality in nonhumans suggests that individuals do not know what others know (Cheney and Seyfarth, 1990). Rather, their interactions are founded on the predictability of another's behavior. Thus, based on Dennett's (1983, 1987) classification of intentional systems, nonhumans can be satisfactorily described by first-order intentions. From this review of the literature, however, we are confident that the current ceiling on levels of intentionality is more likely to reveal an impoverished experimental design than the absence of such complex mental processes. As in other areas of behavioral research on nonhumans, it has not been possible to design sufficiently clever experiments to rule out lower levels of intentionality unambiguously. One of the major stumbling blocks has been to overcome the possibility that seemingly rational, and in some cases devious behaviors, are simply based on one trial learning followed by the establishment of behavioral contingencies. For example, it has been shown experimentally that adult female vervet monkeys give more alarm calls to predators when they are in the presence of kin than nonkin, and that adult males produce more alarm calls in the presence of adult females than adult males (Cheney and Seyfarth, 1985). Similar results have been described for domestic chickens (Marler et al., 1986a,b; Karakashian et al., 1987). These experiments show that alarm call production is not an automatic response to predators and that individuals are sensitive to others that are nearby. As these researchers acknowledge, such experiments do not necessarily show that individuals intend to communicate to particular individuals alone, because one cannot rule out the possibility that alarm call production is based on a behavioral rule that incorporates such information as age-sex composition and number of animals nearby. When such conditions are met, calls are produced.

In summary, two issues argue in favor of decoupling current investigations of teaching from investigations of intentionality. First, if teaching facilitates skill acquisition, then it should be favored by natural selection irrespective of the extent of attribution of mental states. Second, although members of some species may attribute mental states to others in the context of teaching (what we will call "intentional teaching"), members of other species may not, and no experiments have yet been conducted to determine the extent to which animals do attribute mental states to others in the context of teaching. Clearly, this is a productive area for future research.

### Distribution of Teaching in Nonhuman Species

All of the forms of potential instruction that have been reviewed appear to allow offspring to learn important facets of their environment or to learn new skills more often or efficiently

than they would normally do in the absence of teaching. As a result, such interactions will be favored by natural selection, provided costs to the parent are less than half the net benefit to the offspring. Why has so little evidence of teaching accumulated thus far? Six possible answers to this question are briefly discussed, but it is not yet possible to determine the relative importance of each, due in part to the paucity of current data.

(1) The most probable explanation is that instruction is likely to be most highly favored and most easily observed in species where parental guidance is crucial for their young to learn difficult foraging skills. Hence, predators (e.g., felids, killer whales and raptors) and insectivorous mammals (e.g., meerkats) need to instruct their offspring about prey-catching techniques; to an ethologist such behaviors are often some of the most spectacular, and thus frequently recorded and reported. In contrast, herbivores and graminivores do not appear to instruct their offspring with respect to foraging techniques and, even if they did, such instruction might go undetected. If this hypothesis is correct, it is likely that other cases of teaching will be uncovered in those species using more specialized feeding techniques.

(2) Another possible explanation is that the costs of instruction are normally too high for parents. Certainly the apparent absence of instruction in ungulates and lagomorphs and its prevalence in carnivores would support this possibility, as adults in many carnivore species spend much of their time resting compared to herbivores, and thus may have extra time for teaching skills to offspring. In considering the wild chimpanzee example, however, it seems unlikely that time budget constraints would be sufficient to explain the extremely low rate at which "active teaching" occurs. In the case of mothers reorienting the nut or hammer on the anvil for their offspring, the time spent represents a trivial cost in relationship to the potential benefit obtained by the pupil from such tutelage.

(3) Alternatively, in many species, there normally may be rather few opportunities for mothers to introduce offspring to novel situations, or a one-trial introduction may be sufficient for skill acquisition. This might account for why most examples are currently restricted to situations where young animals are introduced to prey, in particular, since these are likely to arise quite frequently during development.

(4) There are advantages to parents instructing their offspring about sources of danger, as demonstrated by the vervet monkey example. Observations of baboons and macaques suggest that individuals may inform others about noxious foods or dangerous predators by threatening them away from such contexts. Similarly, in ungulates, mothers followed by their offspring will run after predators, monitoring them from a safe distance (Kruuk, 1972; C. FitzGibbon, pers. commun.). This "fascination" behavior may help offspring to learn about their predators. The fact that there are so few other examples of adults teaching their young about predators suggests that, in these species, predator recognition is, in part, mediated through innate predispositions or other learning mechanisms, as in fish-fry avoiding predators (e.g., Magurran, 1986) or in the context of failed predation attempts. The importance of predation as a selective agent suggests further examples of teaching offspring about predator avoidance may soon emerge.

(5) If the ability to teach is contingent upon complex mental processes, we might expect to find it in taxa with relatively large brains for a given body size, although brain size is admittedly a poor measure of cognitive ability. The fact that certain forms of teaching have been noted in carnivores, pinnipeds, cetaceans and primates is suggestive, but does not entirely fit data on brain-body size ratios in mammals (Jerison, 1983), given that the highest ratios are found in cetaceans and primates. In birds, parrots, not raptors, have the relatively largest brains. Circumstantial evidence suggests that all species of mammals and birds may be able to monitor the changing needs of offspring in contexts such as nursing and food begging, so there is no a priori reason to expect flexible teaching to be associated with large cranial capacity. Certainly fixed teaching (if it exists) might demand even less cognitive abilities. Thus, we expect ecological, rather than cognitive, differences to explain the distribution of teaching across species.

(6) Last, information on teaching may be

lacking because researchers have failed to recognize it or have not, perhaps, considered it worthwhile to record forms of teaching that did not meet their concept of teaching in humans. Realization that there are different forms of teaching, as we propose here, may stimulate renewed interests in this poorly understood aspect of animal behavior.

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