

ARE ANIMALS CAPABLE OF DECEPTION OR EMPATHY? IMPLICATIONS FOR ANIMAL CONSCIOUSNESS AND ANIMAL WELFARE

S Kuczaj[†], K Tranel, M Trone and H Hill

Department of Psychology, University of Southern Mississippi, Hattiesburg,
MS 39406-5025, USA

[†] Contact for correspondence and requests for reprints

Abstract

Animal Welfare 2001, 10: S161-173

Awareness of the self and awareness of others are difficult faculties to define. Part of the problem lies in the wide range of abilities that involve various aspects of awareness. Some of the most commonly studied abilities focus on the self-awareness of the individual. These abilities range from the capacity to distinguish self from non-self to the competency to reflect on one's past, present or future condition. Another set of abilities that is relevant to the study of awareness involves the interactions of individuals, and includes behaviours such as deception and empathy. We explore the possibility that species other than humans engage in deception and empathy, and consider the implications of such behaviours for self-awareness and other-awareness in these species. Although examples from a variety of species are provided, many examples come from dolphins and whales. This reflects both the authors' interest in these animals and the possibility that large-brained creatures are more likely to engage in deliberate deception and/or true empathy.

Keywords: *animal welfare, consciousness, deception, dolphin, empathy, theory of mind*

Introduction

Consciousness is a notoriously difficult faculty to define, let alone demonstrate. This is particularly true for non-human species. One aspect of consciousness that has received considerable attention in both human and non-human species is self-awareness. The most commonly studied aspects of self-awareness focus on individual abilities ranging from the capacity to distinguish self from non-self to the competency to reflect on one's past, present or future condition (Parker *et al* 1994; Lea 2001). Another set of abilities that is relevant to the study of consciousness involves the interactions of individuals, and includes behaviours such as deception and empathy. In this paper, we explore the possibility that species other than humans engage in deception and empathy, and consider the implications of such behaviours for self-awareness and other-awareness in these species.

Our examination of deception and empathy is complicated by the fact that it is often difficult to determine if a behaviour that looks like deception is in fact deception or if a behaviour that indicates empathy actually involves empathy. At one extreme, animals produce behaviours that look like instances of deception or empathy, but the behaviours are actually either innately specified or automatically elicited by external stimuli. At the other

extreme, animals' behaviours appear to involve deliberate decisions to act in a particular manner, decisions that may involve the ability to recognize another's conditions or needs. If these extremes are the endpoints of continua (one continuum for deception and another for empathy), then the problem is one of determining the extent to which behaviours reflect deception or empathy, not simply deciding whether or not a behaviour is an instance of deception or an instance of empathy.

Although we will consider examples from a variety of species, many of the examples considered in this paper come from cetaceans (dolphins and whales). This reflects both the authors' interest in these animals and the possibility that large-brained creatures may be more likely to exhibit deliberate deception and/or true empathy. The relative brain sizes of different species are often compared using the encephalization quotient (EQ), which is a ratio of brain size to body size (Jerison 1973). The EQ is high for many species of dolphin and whale (Ridgway 1986, 1990; Marino 1998), although it is unclear exactly how this large relative brain size corresponds to general or specific intellectual abilities (Ridgway 1990). Nonetheless, bottlenose dolphins (*Tursiops truncatus*) have demonstrated significant cognitive abilities. In the remainder of this paper, the term dolphin will refer to this species unless otherwise noted. For example, dolphins respond appropriately when asked to 'perform a novel behavior' (Pryor *et al* 1969) or 'repeat your last action' (Mercado *et al* 1998). They are also able to plan their behaviour when confronted with novel situations (Gory & Kuczaj 1999). The capacity to learn from experience and the ability to invent novel solutions to problems have been suggested as important components for deception (Hauser 1997). The dolphin's capacity in both areas increases the likelihood that it may attempt to deceive others and perhaps even understand others' attempts to deceive them.

In addition to their intelligence, the social behaviour of many cetaceans indicates that they may be sensitive to the conditions and needs of other members of their species. At the very least, many cetaceans behave as if they value social relationships. Long, stable patterns of association have been found between related female dolphins (Wells *et al* 1987), unrelated adult female dolphins (Wells *et al* 1987; Smolker *et al* 1992), adult male dolphins (Connor *et al* 1992), and mother and infant dolphins (eg Essapian [1953]; Tavalga & Essapian [1957]; Wells *et al* [1987]; Gubbins *et al* [1999]; Kuczaj *et al* [1999]; Mann & Smuts [1999]). These associations serve many functions. For example, dolphin calves use their mothers as a secure base from which to explore their world (Kuczaj *et al* 1999). When male dolphins form alliances, the members of the alliance may work together in isolating a female from her pod and mating with her (eg Connor *et al* [1992]). Another example of cooperation is found in the foraging behaviour of dusky dolphins (*Lagenorhynchus obscurus*). Groups of these dolphins cooperate to herd fish into a ball. Members of the group then take turns eating the fish or maintaining the ball (Connor & Peterson 1994). All in all, then, to the extent that social organization and intelligence are important components in the evolution of deception and empathy, dolphins and whales should be good candidates for one or the other of these abilities, if not both of them.

Deception

As a mantis shrimp (*Gonodactylus bredini*) grows, it must seek new homes that can accommodate its increasing size. Many of the available homes are already occupied by other shrimp. The occupants vigorously defend their homes from intruders, a feat made easier by their hard exoskeleton and powerful claw (Caldwell & Dingle 1975). When one of the shrimp moults, it is vulnerable to attack because it now lacks its exoskeleton. One might

expect such a shrimp to adopt a meek defence strategy, but just the opposite occurs (Adams & Caldwell 1990). The relatively defenceless shrimp behaves more aggressively towards smaller or same-size intruders in an attempt to 'bluff' the intruder. These aggressive behaviours could result in harm to the intruder if the defending shrimp had its exoskeleton, and so the relatively infrequent bluff behaviours often suffice to deter the intruder.

Many definitions of deception posit that in order for behaviours to be considered deceptive at least one animal must misinterpret another animal's behaviour. In addition, the animal that produces the misinterpreted behaviour must benefit from the misinterpretation (eg Byrne & Whiten [1992]; Hauser [1997]). According to these criteria, the moulting shrimp's bluff counts as deception. However, did the shrimp produce the threat with the intent to deceive the intruder? The shrimp's bluff behaviour seems to depend more on the state of the defender (moulted or not) and the nature of the stimulus (the size of the intruder relative to the defender) than on the outcome of an intentional deliberation by the defender. In his distinction between functional and intentional deception, Hauser (1997) noted that functional deception requires that the agent *know that* particular behaviours result in certain responses by others, but that intentional deception requires that the agent also *know why* others respond the way they do. In this framework, the shrimp's bluff could certainly be classified as functional deception, but is unlikely to be intentional deception.

Knowing why one's behaviours affect the behaviours of others requires that one have a 'theory of mind'. Specifically, one must be able to consider the mental states, perspectives, and intentions of others. In addition, for intentional deception to occur, the agent must understand how the deceptive behaviour will affect the receiver's beliefs and thereby the receiver's behaviour. However, it is often difficult to determine whether an apparently deceptive behaviour is intended to fool others, let alone whether the agent understands the effect of the deceptive behaviour on the receiver's beliefs. To illustrate, we will consider two examples of animal behaviour that could be instances of deception.

In the first example, an adult baboon (*Papio ursinus*) was observed digging and eating plant bulbs. An unrelated young baboon that was close to the foraging adult produced a yell that brought the youngster's mother to the area. The mother chased the foraging adult female away and then returned to her original location. When both adults were gone, the young baboon foraged for the bulbs (Byrne & Whiten 1985). Did the young baboon intentionally produce a distress call in the hope that his mother would believe that the foraging adult was bothering the youngster and consequently chase the adult away from the food supply? Or was the yell a vocalization that the young baboon normally used to indicate a need for help in foraging? If so, the mother's behaviour was not manipulated by a purposefully deceptive call, but instead was a response to her offspring's honest indication that it needed help in obtaining access to a food source. Or perhaps the young baboon screamed simply because he wanted to eat some of the bulbs, and was frustrated because he had none.

Another example concerns a young baboon that was being chased by older baboons (Byrne & Whiten 1985). At one point the baboon stopped, stood on his hind legs, and stared at a spot on the horizon, a behaviour that is commonly produced when a baboon spies a predator in the distance. The other baboons were distracted by this behaviour and the attack ceased. Did the young baboon intend to deceive its pursuers by pretending to look at a predator in the hope that they would be distracted? Or did the youngster actually think that it had seen a predator even though one never appeared? Alternatively, is it possible that the animal simply happened to look at the horizon for some unknown reason?

These examples demonstrate the difficulty of reliably determining the motivational bases of individual behaviours, let alone whether an animal understands the effects its behaviour will have on another animal's beliefs. It is certainly possible that the baboons in each of the above examples were being deceptive and that they intended to be so. However, it is also possible that neither of the baboons intended to deceive another baboon. The observations themselves do not provide sufficient information to decide which possibility was correct. Keeping these difficulties in mind, we now consider other examples of animal behaviour that might involve deception.

As in the case of the above two examples involving baboons, members of a species may attempt to deceive other members of the same species. For example, a male chimpanzee (*Pan troglodytes*) that was courting a female chimpanzee noticed the presence of a higher-ranking male. The lower ranking male quickly positioned his hand over his erect penis, which concealed the erection from the higher-ranking male. Interestingly, the hand was positioned in such a manner that the female could see the penis even though it could not be seen by the more dominant male (de Waal 1998). If this result was intended by the courting male, he was able to consider the perspectives of both the other male and the female at the same time, suggesting that the courting male had at least some theory of mind.

At a zoological park in which we conduct some of our research, the lowest ranking member of a group of spotted hyenas (*Crocuta crocuta*) arrived at one of the outdoor areas before any of the other hyenas. For enrichment purposes, the keepers had placed a cow head in this area. The early arriving hyena picked up the cow head and ran into a pool of water. He then dropped the cow head into the water, submerging and sitting on it just before the other hyenas arrived. The arriving hyenas immediately began searching for the treat that they could sense had been there. During this search, the low-ranking male remained seated in the pool (still on top of the cow head) until the dominant female entered the pool and submerged her head while looking at him. When the female resurfaced, she seized the male by the scruff of the neck, tossed him aside, and collected the cow head. As the meal was consumed, the female prevented the male from obtaining even the smallest amount. The male certainly appeared to have tried to deceive the other hyenas, and suffered the consequences for his unsuccessful attempt.

Some of the dolphins that we have studied participate in shows in which trained behaviours are performed. At one of the facilities, the dolphins are always sent to retrieve all the objects that are in the pool before each show begins. The dolphins are rewarded with fish for retrieving these objects. On some occasions, after all the objects had been found and brought back to the trainers, one adult female, Kelly, left to 'search' for other objects. When she returned, Kelly typically brought back some small foreign object that had not been floating in the pool prior to the show. As a result, she received another fish from the trainers. We later discovered that Kelly kept an 'object box' at the bottom of the pool under the drain cover. She used this box to store foreign objects that visitors accidentally dropped in the pool (eg plastic beads, pieces of paper and sunglasses), and retrieved these cached items when it was to her advantage to do so. These behaviours may have involved deception because Kelly appeared to hide these objects from the other dolphins, and only retrieved them when she alone was able to capitalize by trading the retrieved object for a fish. Kelly has only been observed to put objects in her 'toy box' when no other dolphins were in the immediate vicinity. In addition, her retrieval of objects from this location has only been observed when the other dolphins were occupied by human trainers. Although these observations are far from proof that Kelly was deliberately deceiving the other dolphins, such behaviour is consistent with such an interpretation.

On other occasions, Kelly has tucked a miniature basketball (one of her typical toys) beneath one of her pectoral fins while all other objects in the pool were retrieved by herself and other dolphins. On each occasion, after all the objects in the pool had been given to the trainers and each of the other dolphins had returned to the dock, Kelly swam to the dock and presented the ball that had been hidden under her pectoral fin. As was the case when Kelly retrieved objects from her object box, presenting the hidden ball typically resulted in Kelly receiving the last fish given by the trainers for retrievals. Kelly appeared to hide the ball from the other dolphins until they had ceased to search for objects. Moreover, it is possible that she only used the 'hidden ball' ploy when her object box was empty, but we lack conclusive data for this possibility.

Although Kelly's behaviour seems to involve attempts to deceive other dolphins, we cannot state with certainty that such was the case. Kelly may have simply learned to 'save' objects that could later be traded for fish, and her caching of the objects when other dolphins were not present might reflect nothing more than coincidence. The other dolphins never behaved aggressively toward Kelly when she traded one of her objects for a fish, and so it is not immediately apparent why Kelly would need to hide objects from other dolphins. However, dolphins commonly play with objects that they find, and Kelly may have hidden the objects in order to ensure that other dolphins did not lose her treasures. At present, we lack sufficient data to unravel these possibilities.

Deception does not always involve attempts to fool members of one's own species. For example, dolphin attempts to 'trick' their human trainers are not uncommon. A colleague told the following story (Turner personal communication): one morning a female dolphin brought a small piece of paper to him. As a reward for bringing him the foreign object, the dolphin was given a fish. A few minutes later the dolphin returned with another small piece of paper, and once again was rewarded. The dolphin swam away, but quickly returned with another piece of paper. At this point, our colleague became suspicious. A subsequent search of the pool revealed a large paper bag in one of the grates on the bottom of the pool. Apparently, the dolphin had intended to bring this bag to the trainers one small piece at a time in order to obtain as many extra fish as possible. Of course, it is not certain that the dolphin intended to deceive the human. The bag could have been sucked into the grate without any effort on the dolphin's part, although dolphins are known to play with objects in the water flow created by movement of water in and out of their pools. Regardless of how the bag came to be in the grate, it is clear that the dolphin was choosing to bring one small piece at a time. When the trainer signalled that the dolphin should retrieve the bag, she immediately brought him the entire remainder of the bag.

In two different facilities in which we have conducted observations, dolphins attempted to 'trick' the trainers into feeding them a fish that was not 'earned'. At one facility, each of the four dolphins was assigned a station where it received its fish reward after performing a requested behaviour. Occasionally, after an individual dolphin had completed its requested behaviour, a different dolphin would surface at the performing dolphin's station seconds before the arrival of the performing dolphin. The 'impostor' dolphin sometimes received a fish before the human realized that a different dolphin had appeared at the station. Each of the dolphins engaged in such behaviour, but not in a random manner. On the contrary, the dolphins were more likely to appear at another dolphin's station if a novice trainer was manning the station, indicating that they recognized that they were more likely to 'trick' the unfamiliar humans into giving them another dolphin's fish. Moreover, the 'impostor' dolphins never surfaced at the wrong station before the performing dolphin had completed the requested behaviour or after the performing dolphin had already received its fish and left

the station. The 'impostor' dolphins surfaced in front of the trainer just before the arrival of the 'performing' dolphin. The precise timing of their arrival increased the chances that they would fool the trainer into believing that they were the performing dolphin and thus receive the fish reward. In addition, at another facility the dolphin that engaged in this behaviour was a 2-year-old calf. She only attempted to trick trainers when another calf of similar size was being trained. These self-imposed restrictions on their own behaviour indicate that the dolphins were able to discriminate situations that might result in success from those that were more likely to fail. Once again, we cannot state with absolute certainty that the dolphins intended to deceive their human trainers, but the dolphins' behaviour is consistent with such an interpretation.

Empathy

What does it mean to say that an individual or a species has the capacity for empathy? Merriam Webster's Collegiate Dictionary (Merriam-Webster Inc 1997) defined empathy as:

the action of understanding, being aware of, being sensitive to, and vicariously experiencing the feelings, thoughts, and experiences of another of either the past or present without having the feelings, thoughts, and experiences fully communicated in an objectively explicit manner.

By this definition, empathy involves an awareness of the condition of others and in some cases also requires that the empathic being possess some 'theory of mind' (ie some understanding of the mental lives of other beings; see Connor & Norris [1982]).

The 'understanding' and 'vicarious experience' of the condition of others that characterize empathy make it difficult to study, since such aspects of the phenomenon are not open to objective observation. Thus, just as problems of interpretation are rife in the literature on deception, it is often unclear whether instances of helping behaviour are instances of empathy. For example, three Amazon ants (*Poleergus rufescens*) were observed pulling a wood splinter from a fourth ant (Leland 1997). This behaviour appears to be altruistic, in that the behaviour of the three ants could be interpreted as an attempt to improve the welfare of the impaled ant by removing the splinter. However, the division of labour in ant colonies is often based on age or morphological differences among the colony members. The behaviour of individual ants depends on their status in the colony and is typically automatically elicited by particular types of external stimuli (Sudd & Franks 1987). Therefore, the behaviour of the 'physician' ants was most likely not empathic, but instead automatically produced in response to the environmental context.

Connor and Norris (1982) suggested that only animals that possess some 'theory of mind' are capable of reciprocal altruism, which in turn could be considered a form of empathy. In order to examine the notion that a theory of mind is necessary for reciprocal altruism, we will consider the food sharing behaviour of vampire bats (*Desmodus rotundus*). Both wild and captive populations of vampire bats practice a form of food sharing that appears to involve reciprocal altruism (Wilkinson 1984). Individual bats are not always successful in their search for blood and will sometimes beg for and obtain food from one of their roost mates. Wilkinson suggested that vampire bats are able to recognize individuals that ignore their begging behaviour, and subsequently refuse to regurgitate blood meals to these 'stingy' bats.

Given that the bats' behaviour is governed at least in part by their past experiences with their roost mates, it seems unlikely that the donating bats are producing some sort of automatic response to the begging behaviour of their hungry companions. Is it the case, then,

that despite their bloodthirsty reputation vampire bats are empathic animals that both recognize hunger in roost mates and strive to alleviate this condition? Perhaps not, for the donor bats could be prone to respond to begging roost mates by regurgitating food. However, their ability to recognize and remember roost mates allows them to withhold food from those bats that have not given them food on previous occasions. If bats can in fact recognize one another, it is curious that begging bats attempt to obtain food from other bats that they have slighted in the past. A more efficient strategy would involve only asking bats with which one has shared food or bats with which one has had no food seeking or food sharing interactions. Of course, we do not know that bats only withhold food from others that have denied them in the past (if this is the case, then one must wonder what caused the first bat to withhold food from a begging roost mate), but denying food to begging roost mates certainly decreases one's chances of obtaining food by begging if a subsequent hunt is unsuccessful. Perhaps bats learn to respond to the begging behaviour of other bats with food because it increases their chances of being rewarded during times when they must beg. Although it is not clear which of these possibilities is correct, the number of possibilities illustrates that reciprocal altruism need not always involve some form of theory of mind and thus need not always denote some form of empathy.

We offer the following examples of behaviour that might involve empathy. However, we acknowledge the difficulty of reliably determining whether a behaviour that seems to be empathic actually reflects an empathic response on the animal's part. Thus, the following examples are intended to illustrate the types of behaviour that might be empathic in species other than humans.

At one of the facilities with which we collaborate, we observed a dolphin calf tossing a ball up into the air as he swam about in a pool that he shared with nine other dolphins of varying ages and sexes. Following one of these tosses, the ball landed on top of a dock such that it was not possible for the calf to retrieve the ball. After spending several minutes in front of the dock looking at the ball, the calf swam away. A short time later, the calf returned to the dock with his mother. The mother retrieved the ball from the dock by nudging it into the water while the calf watched. The mother did not play with this ball, but left it in the water for her calf, which immediately retrieved the ball and began tossing it. Although we cannot state why the mother retrieved the ball, her behaviour indicates that she was aware that her son could not obtain the ball on his own. As a result, she helped him by relocating the ball to a position in the water where he could obtain it.

The alloparenting behaviour of cetaceans may reflect a form of empathy that some females experience when confronted with a motherless calf. In such cases, some female dolphins adopt the orphaned calves. If the females do not already have a nursing calf, they begin to lactate. This is essential for the orphaned calves' survival (Smolders 1988; Ridgway *et al* 1995). Although it is unclear why female dolphins adopt orphaned calves, such alloparenting behaviour may be triggered by an empathic response to the orphaned calves. Alternatively, alloparenting behaviour may be triggered by the calf nuzzling an available female, sometimes referred to as 'bumping' (Cockcroft & Ross 1990). Bumping may trigger a hormonal response in the female that results in lactation and subsequent alloparenting behaviour. In such a case, alloparenting would be epimeletic, but not empathic. However, even if the onset of alloparenting is not empathic, alloparenting does result in some sort of bond between the alloparenting female and her adopted calf. In one case that we followed for 4 years (Kuczaj & Solangi unpublished data), a female estimated to be over 30 years old adopted an orphaned calf. This female had never given birth during her preceding 23 years of captivity. Nor had she ever adopted another calf or even allowed a calf to attempt to nurse

from her. The orphaned calf did not approach this female and 'bump' her. Instead, the female initiated the first interaction by lightly touching the calf's head with the parts of her body that contained her nipples. This in turn stimulated the calf to attempt to nurse from this female. Although we cannot be certain when the female began to lactate, the calf survived infancy and thrived until he succumbed to a bacterial infection at the age of 4 years. When the dead animal was discovered, none of the other five dolphins in the pool (including the alloparenting female) approached the animal or reacted to humans removing the body. However, once the body was out of the pool and therefore out of sight, the alloparenting female began vigorous high jumps out of the water that were accompanied by loud vocalizations. She continued to do this for over 10min. Although there are many possible interpretations of this behaviour, the female seemed to be disturbed by the removal of her adopted son from her sight. This interpretation gains some credence from the fact that the female refused to eat for 3 days after this incident. Dolphins often reject food after another dolphin dies or is moved to another pool, but do so selectively (Bel'kovich *et al* 1969). This sort of reaction is most likely to occur when the dead or missing animal is either an offspring or a member of the fasting animal's social group.

Many cetaceans have been observed to lift and hold injured or ill companions to the surface of the water, a helping behaviour that may involve empathy. Norris and Prescott (1961) reported the opposite behaviour from several pilot whales (*Globicephala melana*) whose companion had been shot and killed. Rather than lifting it to the surface, the whales kept the dead animal submerged and swam away from the boat that contained the whale's killers. The whales' behaviour indicates that they understood that the dead whale had been harmed by something associated with the boat, and that they were keeping their companion away from this harmful thing. Of course, we do not know if the whales believed their companion to be alive or dead. Nor can we be certain why the whales behaved as they did.

Empathy may also have been involved in the stranding-like behaviour of a group of false killer whales (*Pseudorca crassidens*) reported by Porter (1977). A large group of whales remained in very shallow water for approximately 3 days. Only one of the stranded whales was obviously ill. The other whales appeared to stay with the whale until he died, after which they departed. The healthy whales seemed to have chosen to stay with their ailing companion despite the risks associated with being in shallow water. This behaviour indicates that a form of empathy exists in these creatures, but it is also possible that the whales were hovering close to their distressed companion because it was producing distress calls that caused the other whales to maintain close proximity. Many species of cetaceans thrive in social groups (Connor 2000), and distress calls may trigger automatic responses by members of the group. It is not clear whether or not the ailing whale produced distress calls during this period, and so it is impossible to determine the role that distress calls may have played in this incident.

There is some evidence that indicates that cetaceans do not respond automatically to the distress calls of all conspecifics. Bel'kovich *et al* (1969) reported that captive dolphins were more likely to respond to the distress calls of some conspecifics than others. In one case, a sick dolphin's calls were ignored by the other dolphins in the pool for a period of 3 days, at the end of which the distressed dolphin died. The dolphins in this pool had provided assistance to other animals, including physical support for a female that could not keep herself afloat. Although we do not know why dolphins assist some dolphins but not others, the fact that they do so indicates that their helping behaviour is intentional rather than some sort of instinctive response.

Connor and Peterson (1994) reported an event that occurred in Shark Bay, Australia, that may have involved empathy. As mentioned earlier, dolphins sometimes form alliances with other males, often in order to gain access to specific females. On one occasion, a male alliance was observed pursuing a mother-calf pair. A group of females appeared to intervene and hide the pair amongst themselves, which allowed the mother and calf to escape the alliance. Once again, however, it is unclear if the intervening dolphins intended to intervene or if the mother and calf simply took advantage of the presence of the female pod to hide themselves.

Empathic behaviour does seem to have occurred in a setting where Diana monkeys (*Cercopithecus diana*) were conditioned to exchange tokens for food (Markowitz 1982). For some reason, the oldest female failed to learn to insert the tokens in the slot in order to obtain her food reward. During one 12h period during which the animals were continually observed, the female's mate watched her unsuccessful attempts to insert the tokens into the machine. On three separate occasions during this period, the male approached the female, picked up her dropped tokens, inserted them into the machine, and let her have the food that appeared. The male was behaving altruistically by helping his mate obtain her food reward. It is possible that he was doing so because he was empathic. The evidence for empathy, although not conclusive, is suggestive. Firstly, the male appeared to assess the situation before he acted. He only helped the female after she had failed. Secondly, he seemed to understand that the female wanted food, but was unable to get it herself. Thirdly, although the male could easily have eaten the food that he had obtained with the tokens, he let the female consume it. Finally, the male and female did not engage in any form of sexual activity during this period, indicating that the male's behaviour had nothing to do with courtship. All in all, then, the male's behaviour did not benefit him in any obvious way.

Empathy need not always involve members of the same species. For example, a captive male orang-utan (*Pongo pygmaeus*) obtained a piece of wire and began chewing on it (Markowitz 1982). The zookeepers realized that the wire was a potential health hazard, and attempted to gain possession of the wire by bribing the orang-utan with food. Although the orang-utan accepted the food bribes, he never returned the wire. When the zookeepers offered a female orang-utan a piece of food, she took the food to the male, gave it to him, obtained the wire, and gave it to the zookeepers. Although it is impossible to determine what motivated the female orang-utan's behaviour, it is possible that she understood that the humans wanted the wire, and realized that she could obtain the wire from the male even though the humans could not. The female was certainly not motivated by food, since she was first given food, which she then gave to the male in exchange for the wire. If her behaviour had been caused by a desire for food, she should have kept the food she was given rather than exchanging it for the wire.

Two curious examples of interspecies altruistic behaviour involved hippopotamuses (*Hippopotamus amphibius*) and impalas (*Aepyceros melampus*). In one report, a hippopotamus charged a crocodile that held an impala in its jaws. After the crocodile released the impala, the hippopotamus was reported to have guarded the impala and even licked its wounds (Leland 1997). The other incident involved an impala that attempted to escape a pack of African wild dogs (*Lycaon pictus*) by swimming across a river. The impala tired as it swam across the river but was reportedly pushed to shore by a hippopotamus (Leland 1997). In both of these incidences the hippopotamuses gained nothing by their behaviour. It is difficult to say what motivated their actions, but perhaps the hippopotamuses recognized and responded to distress in the impalas. If so, this would certainly seem to be some form of empathy. However, it is also possible that the hippos' behaviour has nothing to

do with empathy. Although adult hippos are capable of killing crocodiles, baby hippos are sometimes killed by crocodiles (Guggisberg 1972; Pough *et al* 1998). Perhaps adult hippos are prone to attack crocodiles with hippo calf-size animals in their mouths and to remove all struggling or dead animals from the water so that crocodiles are not attracted to the vicinity. It is also possible that the first hippo licked the impala because blood attracts crocodiles, and lessening the amount of blood in the vicinity decreased the likelihood of attracting additional crocodiles (we thank an anonymous reviewer for bringing these possibilities to our attention).

Conclusions

We have described a number of observations that indicate that animals other than humans are capable of at least some forms of deception and empathy (for additional examples and discussion, see Byrne & Whiten [1988] and Whiten & Byrne [1997]). The observations are often anecdotal, and so it is often unclear exactly why the animals behaved the ways they did. For humans, intentionality is an essential component of both deception and empathy. Deception typically refers to some intentional act that deceives others for one's own benefit or for the benefit of one's relatives. Empathy often involves an intentionally helpful act, and may have no obvious benefit for the empathic being. In addition, the highest forms of deception and empathy require that the agent understand the mental states of others and the impact of the agent's actions on these states.

Although the concerns over intentionality and theory of mind issues may seem somewhat esoteric in the consideration of animal behaviour, the implications for animal consciousness are significant. The available evidence on animal deception indicates that animals are aware of their own situations, and that they can act in ways to improve these situations (if the deceptions are successful). However, we do not know if animals engage in deceptive behaviour with the intent to deceive because we do not know what they think about the beliefs of others, if they think about such things at all. The evidence for animal empathy is also open to a number of interpretations because we know so little about animal intentions and the extent to which animals have a theory of mind.

To sum up, there is evidence to indicate that at least some animals engage in deceptive and empathic behaviour. Although this evidence is far from unequivocal, it does indicate that these animals have some form of self-awareness, and that they may even have some awareness of the conditions of others. However, there is no conclusive evidence that animals intentionally engage in deceptive or empathic acts, or that they understand the mental lives of others and the ways in which their own actions might affect others' mental states.

Although this emphasis on self and other awareness may make it appear that deception and empathy depend solely on these cognitive abilities, both deception and empathy require a number of other cognitive skills. In order to successfully deceive another, the agent must be able to recognize the opportunity to benefit from an act of deception. Similarly, an agent must be able to recognize the need to assist another in order to be empathic. In both deception and empathy, the ability to plan one's behaviour by choosing a specific action plan and the ability to successfully execute the plan are important if the chosen behaviours are to accomplish their goals. Thus, deception and empathy rest on a foundation of sophisticated cognitive abilities. Both additional observation studies of spontaneous behaviour and additional experimental studies that focus on specific abilities are needed in order to determine the extent to which animals are able to understand others.

Animal welfare implications

In this section, we will focus on the humane treatment of dolphins and whales. The cetacean central nervous system differs from that of other mammals. Cetaceans returned to an oceanic existence approximately 70–90 million years ago, before evolutionary advances in the neocortex of other land-based mammals are postulated to have occurred (Morgane *et al* 1986). As a result of this evolutionary divergence between cetaceans and other mammals, it has been suggested that the cetacean ‘neocortex’ may have functional similarities to the paleocortical structures of other mammals (Jerison 1986). These paleocortical structures play important roles in emotional and motivational behaviour. Thus, it is possible that the higher brain functions of cetaceans are more related to emotion and motivation than is the case for other mammals (Jerison 1986).

The notion that cetacean brains may have evolved to emphasize emotional and motivational behaviour fits well with the anecdotal behavioural evidence we have presented to indicate that cetaceans may be capable of deception and empathy. In turn, this would indicate that cetaceans are aware of others, as well as themselves. Given that these animals may experience a range of emotions and be sensitive to the emotions of conspecifics, it seems clear that the emotional needs of cetaceans must be considered in both natural and captive environments. Free-swimming dolphins and whales are often harassed by boaters attempting to interact more closely with these wild animals. Such behaviour may produce negative emotions in the animals, particularly if young or feeble animals are among those being pursued. In captive environments, existing social bonds should be considered when deciding whether to transfer animals from one location to another. If the social group is important for members of a species, captive animals should be given ample opportunity to form and maintain social relationships. The captive cetacean’s welfare is enhanced when mental stimulation is consistently provided (Kuczaj *et al* 1998), indicating that both cognitive and emotional needs are important considerations for the welfare of dolphins and whales.

References

- Adams E S and Caldwell R L 1990 Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. *Animal Behaviour* 39: 706-716
- Bel’kovich V M, Krushinskaya N L and Gurevich V S 1969 The behavior of dolphins in captivity. *Priroda* 5: 18-28
- Byrne R W and Whiten A 1985 Tactical deception of familiar individuals in baboons (*Papio ursinus*). *Animal Behaviour* 33: 669-673
- Byrne R W and Whiten A 1988 *Machiavellian Intelligence*. Oxford University Press: Oxford, UK
- Byrne R W and Whiten A 1992 Cognition evolution in primates: evidence from tactical deception. *Man* 27: 609-627
- Caldwell R L and Dingle H 1975 Ecology and evolution of agonistic behavior in the stomatopods. *Naturwissenschaften* 62: 214-222
- Cockcroft V G and Ross G J 1990 Observations on the early development of a captive bottlenose dolphin calf. In: Leatherwood S and Reeves R (eds) *The Bottlenose Dolphin* pp 461-478. Lawrence Erlbaum Associates: New Jersey, USA
- Connor R C 2000 Group living in whales and dolphins. In: Mann J, Connor R C, Tyack P L and Whitehead H (eds) *Cetacean Societies* pp 199-218. University of Chicago Press: London, UK
- Connor R C and Norris K S 1982 Are dolphins reciprocal altruists? *The American Naturalist* 119: 358-374
- Connor R C and Peterson D 1994 *The Lives of Whales and Dolphins*. Henry Holt and Co: New York, USA

- Connor R C, Smolker R and Richards A** 1992 Dolphins' alliances and coalitions. In: Harcourt A and de Waal F (eds) *Coalitions and Competition in Animals and Humans* pp 415-442. Oxford University Press: New York, USA
- de Waal F** 1998 *Chimpanzee Politics*. John Hopkins University Press: Maryland, USA
- Essapian F** 1953 The birth and growth of a porpoise. *Natural History*. November 392-399
- Gory J and Kuczaj S A** 1999 Can bottlenose dolphins (*Tursiops truncatus*) plan their behavior? Paper presented at the biennial Conference on the Biology of Marine Mammals, Wailea, Maui, Hawaii: November 28-December 3
- Gubbins C, McCowan B, Lynn S, Hooper S and Reiss D** 1999 Mother-infant spatial relations in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science* 15: 751-765
- Guggisberg C A** 1972 *Crocodyles*. Stackpole Books: UK
- Hauser M D** 1997 Minding the behaviour of deception. In: Whiten A and Byrne R (eds) *Machiavellian Intelligence II* pp 112-143. Cambridge University Press: New York, USA
- Jerison H J** 1973 *Evolution of the Brain and Intelligence*. Academic Press: New York, USA
- Jerison H J** 1986 The perceptual worlds of dolphins. In: Schusterman R J, Thomas J A and Wood FG (eds) *Dolphin Cognition and Behavior: a Comparative Approach* pp 149-166. Lawrence Erlbaum Associates: New Jersey, USA
- Kuczaj S A, Lacinak C T and Turner T N** 1998 Environmental enrichment for marine mammals at Sea World. In: Shepherdson D J, Mellen J D and Hutchins M (eds) *Second Nature* pp 314-328. Smithsonian University Press: London, UK
- Kuczaj S A, Hill H M, Tranel K, Trone M and Solangi M** 1999 The roles of mothers, peers and other adults in the behavioral development of bottlenose dolphins. Paper presented at the biennial Conference on the Biology of Marine Mammals, Wailea, Maui, Hawaii: November 28-December 3
- Lea S E G** 2001 Anticipation and memory as criteria for special welfare consideration. *Animal Welfare* 10: S195-208
- Leland S** 1997 *Peaceful Kingdom. Random Acts of Kindness by Animals*. Conari Press: California, USA
- Mann J and Smuts B** 1999 Behavioral development in wild bottlenose dolphin newborns (*Tursiops truncatus*). *Behaviour* 136: 529-566
- Marino L** 1998 A comparison of encephalization between odontocete cetaceans and anthropoid primates. *Brain, Behavior and Evolution* 51: 230-238
- Markowitz H** 1982 *Behavioral Enrichment in the Zoo*. Van Nostrand Reinhold Co: New York, USA
- Mercado E, Murray S, Uyeyama R, Pack A and Herman L** 1998 Memory for recent actions in the bottlenosed dolphin (*Tursiops truncatus*): repetition of arbitrary behaviors using an abstract rule. *Animal Learning and Behavior* 26: 210-218
- Merriam-Webster Inc** 1997 *Merriam Webster's Collegiate Dictionary, 10th edition*. Merriam-Webster Inc: Philippines
- Morgane P J, Jacobs M S and Galaburda A** 1986 Evolutionary morphology of the dolphin brain. In: Schusterman R J, Thomas J A, and Wood F G (eds) *Dolphin Cognition and Behavior: a Comparative Approach* pp 5-29. Lawrence Erlbaum Associates: New Jersey, USA
- Norris K and Prescott J** 1961 Observations on Pacific cetaceans of California and Mexican waters. *University of California Publication of Zoology* 63: 291-402
- Parker S T, Mitchell R W and Boccia M L (eds)** 1994 *Self-awareness in Animals and Humans*. Cambridge University Press: New York, USA
- Porter J W** 1977 *Pseudorca* stranding. *Oceans* 10: 8-15
- Pough H F, Andrews R M, Cadle J E, Crump M L, Savitzky A H and Wells K D** 1998 *Herpetology*. Prentice-Hall: New Jersey, USA
- Pryor K, Haag R and O'Reilly J** 1969 The creative porpoise: training for novel behavior. *Journal of Experimental Analysis of Behavior* 12: 653-661

- Ridgway S H** 1986 Dolphin brain size. In: Bryden M M and Harrison R (eds) *Research on Dolphins* pp 59-70. Oxford Science Publications: Oxford, UK
- Ridgway S H** 1990 The central nervous system of the bottlenose dolphin. In: Leatherwood S and Reeves R (eds) *The Bottlenose Dolphin* pp 69-97. Academic Press: New York, USA
- Ridgway S H, Kamolnick T, Curry C and Tarpley R J** 1995 Orphan-induced lactation in *Tursiops* and analysis of collected milk. *Marine Mammal Science* 11: 172-182
- Smolders S J** 1988 Adoption behavior in the bottlenose dolphin. *Aquatic Mammals* 14: 78-81
- Smolker R, Richards A, Connor R and Pepper J** 1992 Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* 123: 38-69
- Sudd J H and Franks N R** 1987 *The Behavioural Ecology of Ants*. Chapman and Hall: New York, USA
- Tavolga M and Essapian F** 1957 The behaviour of the bottle-nosed dolphin (*Tursiops truncatus*): mating, pregnancy, parturition and mother-infant behaviour. *Zoologica* 42: 11-31
- Wells R, Scott M and Irvine A** 1987 The social structure of free-ranging bottlenose dolphins. In: Genoways H (ed) *Current Mammalogy, Volume 1* pp 247-305. Plenum: New York, USA
- Whiten A and Byrne R W (eds)** 1997 *Machiavellian Intelligence II*. Cambridge University Press: New York, USA
- Wilkinson G S** 1984 Reciprocal food sharing in the vampire bat. *Nature* 308: 181-184

