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ARE DOLPHINS RECIPROCAL ALTRUISTS?

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There has been little discussion about dolphin behavior in the debates over the social evolution of higher mammals. A major reason has been that until recently few studies were available that allowed comparison. In recent years some quantitative studies of dolphin gross social architecture have been completed. Further, some important anecdotes about the behavior of these animals at sea and in captivity have been repeated often enough that some assessment of them can also be made. One feature, often mentioned, is that dolphins show altruistic behavior toward schoolmates, or even toward cetaceans of other species. This behavior, if true, is important in the present debate about the function and occurrence of reciprocal altruism in nature. We attempt here to assess the proposition that dolphins and other toothed whales might be reciprocal altruists, and thus join the ranks of the highest of mammals in terms of the evolution of social behavioral mechanisms. This assessment has special importance because the odontocete lineage has probably been separate from other placental mammals since the early Cenozoic. Our examples come mostly from the most modern odontocete groups, especially the family Delphinidae, though some examples of epimeletic behavior come from the most primitive family, the Platanistidae.

Here we are concerned only with reciprocity mediated by learning, thus excluding other forms of mutualism (see Axelrod and Hamilton 1981). As defined by Trivers (1971) it is a system of altruistic behavior that can function independently of genetic relatedness. It is believed by many to have been an important mechanism in the development of human society, and perhaps those of higher primates as well. It functions as follows: In the two-party model, an individual, A, performs an altruistic act for another individual, B, in a situation where it has the opportunity to receive a future increase in inclusive fitness via reciprocity from B. The basic requirement of the system is that the eventual increase in A's inclusive fitness must exceed the cost of the initial altruism. Because reciprocal altruism is not based on kinship, a method of discriminating against cheaters (e.g., one who does not reciprocate) is required, since in the absence of such discrimination, nonreciprocating individuals would outcompete reciprocating ones and the system would collapse. The inherent instability of such a system could give rise to a kind

of evolutionary warfare in which the development of detection systems is pitted against better and better methods of cheating (see Trivers 1971 for a discussion of this mechanism).

The mechanism must normally work, however, in multiparty situations where the altruistic tendency becomes societal in scope, and where individuals have the opportunity to learn about the altruistic and cheating tendencies of others through social communication. In this case selection may favor an individual, A, dispensing altruism to another individual, B, even when A knows that B will not recompense him fully, or at all, in the future. The eventual increase in A's inclusive fitness will come from an increased tendency of those individuals who learned of A's altruism to act altruistically toward him. As Trivers points out, such multiparty interactions may create selection pressures for individuals to demonstrate generalized altruistic tendencies, with individuals being regarded as cheaters if they fail to dispense altruism at approximately the same level as others in the system. The operation of reciprocal altruism becomes driven by the benefits of sociality to the aware individual even though in terms of selection it continues to be based on individual fitness. The selection for generalized altruism, is, we believe, important in explaining much human behavior and may have shaped important aspects of dolphin society. The idea has had a long genesis. As Williams (1966) points out, a number of people including Darwin have alluded to the importance of reciprocal altruism in human evolution. Since Trivers' (1971) extensive treatment of the subject, however, little use of the concept has been made in studying animal societies (but see Packer 1977).

Hamilton (1972) notes that reciprocal altruism is probably restricted to perceptive and intelligent animals. He suggests that this points to primates and especially to man. West Eberhard (1975, p. 82) is in agreement with this opinion since reciprocal altruism "requires meticulous contemporaneous controls on cheating." Williams (1966) suggests that reciprocal altruism is confined to a minority of the Mammalia and notes that "a competition for social goodwill cannot fail to have been a factor in human evolution, and I would expect that it would operate in many other primates" (p. 95). He goes on to suggest (pp. 95-96): "Perhaps this evolutionary factor might operate in the evolution of porpoises. This seems to be the most likely explanation for the very solicitous behavior they sometimes show toward each other."

The phylogenetic limits of learning-mediated reciprocal altruism lie, we suspect, with development of awareness of self and others as the basis for social relations. After all, if one animal is consciously altruistic to another it is manipulating the communications relationship between the two animals, and thus engaging in second order behavior. Another way of stating it is that reciprocal altruism is probably restricted to those animals that have "a theory of mind," as defined by Premack and Woodruff (1978). They say: "An individual has a theory of mind if he imputes mental states to himself and others" (p. 515). They include among such inferred mental states: "Purpose or intention, as well as knowledge, belief, thinking, doubt, guessing, pretending, liking and so forth" (p. 515). How far this capacity ramifies in the animal world is uncertain and very difficult to determine as Griffin (1976) has pointed out. However, correlates of awareness, such as guilt,

may be found in the social carnivores. We do not expect reciprocal altruism to have arisen only once, in primates, but instead expect its origins to lie more broadly in higher order sociality itself.

Trivers (1971) argues that reciprocal altruism can only arise in situations where there are many opportunities for reciprocation, either through frequent proximity, or over long periods of time. Thus, an abundance of altruistic acts would be fostered by such features as extended parental care, long life, and low dispersion rates. We point out that in the multiparty model sociality itself increases the chances for altruism to a much greater degree than any of the features listed above. Therefore, selection for the features of sociality, we expect, has a major evolutionary linkage with reciprocal altruism. Reciprocal altruism can be manifested by mutual assistance in combat, in feeding, and in various protective measures members may take either individually or as a group.

DOLPHINS AND ALTRUISM

Symmetry.—Trivers notes that symmetrical social relationships promote altruistic acts, while strong social asymmetry tends to subdue them. Hierarchies are inherently asymmetrical social relationships. Therefore they might be expected to militate against the expression of reciprocity. Most of the information about hierarchical relationships in dolphins comes from studies of captives (Bateson 1974; Tavolga and Essapian 1957). The causes of a hierarchy in captivity will probably produce spatial ordering in nature. Thus a dolphin school might be hierarchical in captivity and be a structured society with geographically arranged parts in nature, ordered by mature animals. It is common in wild schools to note segregated groups of juveniles, young, mothers and young, or older adults. Sexual separation also occurs on a seasonal basis in some groups, such as sperm whales (*Physeter catodon*), where males may gather and occupy a part of the total school range at certain times of the year (Norris and Dohl 1980*b*). In some cases, even though the school as a whole may contain asymmetries, within these segregate groups much greater symmetry is the rule.

Sexual dimorphism, which we consider to be an indicator of asymmetry, varies greatly between various species of dolphins and their allies. At one extreme are the sperm whales (*Physeter catodon*) in which males may be nearly twice the length of females, and killer whales (*Orcinus orca*) with males showing much greater size and dorsal fins more than twice the height of female fins. At the other extreme are oceanic schooling dolphins whose sex is hard to determine by features of pattern or body form, as for example *Delphinus delphis*, and some species of the genera *Lagenorhynchus* and *Stenella*. Nonetheless behavioral traits possibly associated with reciprocal altruism such as epimeletic behavior seem to be distributed widely through the cetacea in both dimorphic and nondimorphic forms. We suspect that intragroup symmetries produced by ordering of school structure could largely nullify the effects of sexual dimorphism upon the employment of reciprocal altruism in dolphins.

Longevity.—Dolphins and other odontocetes are clearly long-lived animals, though the criteria used for aging have been subject to debate (Bryden 1972;

Klevezal, cited in Yablokov et al. 1972). The most comprehensive recent work is that of Kasuya (1976) who developed a method of reading cementum layers in teeth beyond the age at which dentinal layers ceased to be laid down. His method shows sexual maturity in the oceanic dolphin *S. attenuata* between about 9–12 yr, with a maximum age of more than 45 yr. Kasuya et al. (1974) report that some individuals of *S. attenuata* are functioning parts of the reproductive population until 30 yr of age. Ohsumi (1966) reports maximum age in sperm whales at 77 yr. At any rate, in comparison to other mammals the life span of dolphins is sufficiently great for significant opportunity for altruistic exchanges to occur.

Dispersion rates.—We can cite only two examples where the dispersion rate of marine mammal populations can be judged. Recent studies of the dialects and movement patterns of killer whale (*O. orca*) pods in Puget Sound, Washington, and adjacent British Columbia suggest great constancy of pod composition. Very distinct dialects are developed between adjacent pods, and while pods meet and intermix briefly, they completely separate again and few cases of long-term intermixing appear to occur (Ford and Fisher, in press; Bigg 1979). Wells et al. (1980) studying a school of Atlantic bottlenose dolphins in which most members were recognizable by tags or scars, found little intermixing at the boundaries with adjacent schools over 10 yr time.

Parental care.—Parental care periods and associations between parents and young can be quite long in dolphins. Tavalga (1966) reports that in times of stress young captive bottlenose dolphins (*Tursiops truncatus*) returned to the close company of their mothers “for several years.” Nursing, too, is often fairly extended; Tavalga (1966) notes young returning to nurse for up to 18 mo.

Mutual dependence and predation.—It is a common misconception that predation upon dolphins is low and that life in the sea is easy. The reverse, at least for the smaller species, is true. It seems secure that only by virtue of living in cohesive, alert schools can dolphins survive at sea. Sharks are probably major predators of many smaller species (see American Institute of Biological Sciences 1965; Caldwell and Caldwell 1972). In open water, for species such as common dolphins (*D. delphis*), spotted and spinner dolphins (*S. attenuata* and *S. longirostris*), some populations of the bottlenose dolphin (*Tursiops sp.*), and white-sided, striped, or dusky dolphins (genus *Lagenorhynchus*), sharks are evident predators. As much as 6% of some schools may show shark-bite scars (Wells et al. 1980) and there are many records of shark predation on dolphins from other sources, such as stomach contents (Wood et al. 1970). Some spinner dolphins observed by Norris in Hawaii showed obvious shark scars including some in which essentially the whole tail or posterior body had been grasped by a shark, from which the dolphin had somehow freed itself. Arnold (1972) notes that harbor porpoises (*Phocoena phocoena*) attacked by white sharks (*Carcharodon carcharias*) typically had their tails severed from their bodies. For schools of dolphins traveling at sea sharks are probably always a presence. The point was brought home to one of us (Norris) while attempting to fish at night from the stern of a tuna seiner in the midst of the oceanic spinner and spotted dolphin range. Though many shipjack were hooked, none could be retrieved before being severed by sharks. Seines containing tuna and dolphins usually contained sharks, or the sharks could be seen patrolling the periphery of the net. Tropical and temperate oceanic dolphins typically travel in

sizeable schools. Schools tend to be smaller in shore-dwelling species such as the harbor porpoise, *Phocoena phocoena*, and only in bays or rivers does one encounter single dolphins. The point is that these schools are protective systems in which many animals search the environment for predators. Dolphin schools at sea are apt to be noisy, producing cascades of echolocation clicks (Norris and Dohl 1980*b*).

Mutual assistance.—Care-giving, or epimeletic behavior (see Scott 1958) is widespread and common throughout the cetacea, including both the Odontoceti (porpoises, dolphins, and toothed whales) and the Mysticeti (baleen whales). Caldwell and Caldwell (1966) have prepared an extensive review of known examples through 1965. Many examples have entered the literature since then, and some will be cited later. The Caldwells note that such behavior may be directed both at adults and young by other adults, and that it includes many examples of the otherwise rare succorant behavior in which an animal in distress is physically aided by another animal. They divide their examples of care-giving into three classes: standing by, excitement, and supportive behavior. Such epimeletic behavior is only part of mutual assistance and hence we will also point out examples involved in feeding, birth, and other essential functions of the dolphin school.

Standing by occurs when an animal or animals stays with another animal in distress but does not offer evident aid. They note that such behavior often includes remaining in dangerous situations far longer than would be the case had there been no distressed animal.

Excitement includes such behavioral sequences as approaching an injured comrade, showing violent or excited behavior in such circumstances, including interposition of the aiding animal between a captor and its prey, biting or attacking capture vessels, and pushing an injured member away from a would-be captor. Most of the examples come from capture attempts, either in fishery operations or in capture operations for zoos and aquaria. We feel that the term "excitement" is not particularly explanatory and will interchange *assistance* for it.

Supporting behavior occurs when one or more animals support a distressed animal at the surface and is a special but frequently observed case of assistance behavior. Epimeletic behavior was listed by Caldwell and Caldwell (1966) as having been reported for the odontocete families Platanistidae, Ziphiidae, Physeteridae, Monodontidae, and Delphinidae (*sensu latu*). The following are a few examples from the total literature.

During capture, whether or not the captive is being killed in the process, toothed whales, from dolphins to sperm whales (both males and females) will often "stand by" the captive during its struggles. They may circle it and swim very close at times to the capture vessel. This does not always occur, and sometimes a captive will be abandoned. This behavior was used by whalers as a means of taking more than one animal from a school. Especially when a baby could be secured alive, schoolmates gathered around it and could be harpooned, sometimes until most or all of a school had been taken (Nishiwaki 1962). Both sperm whales (Davis 1874) and bottlenose whales, genus *Hyperoodon* (Southwell 1884), were taken in this manner.

Such standing by is not limited to single-species interactions but has been observed at sea between two widely different genera. For instance, Norris

(1958) reports that during the capture of a young adult female Pacific pilot whale (*Globicephala melaena scammoni*) a group of Pacific striped dolphins (*Lagenorhynchus obliquidens*) stood by the struggling whale during capture, and remained even when the whale was being immobilized alongside the capture vessel and brought aboard. The reader is referred to Caldwell and Caldwell (1966) for many additional examples of standing by, described for nine genera.

Assistance behavior takes many forms and is also common in cetacea. It includes such patterns as pressing against and biting restraining lines of ensnared or harpooned animals during capture, propelling injured animals away from captors, and the angry attacks of females when young are caught or disturbed. An example is given by Norris and Prescott (1961) in which an adult pilot whale (*G. m. scammoni*) was shot and killed instantly. It drifted in rigor toward the capture vessel. When it was about 2.5 m from the vessel's rail, two other pilot whales rose on either side of the animal, which was sliding just beneath the surface, and pressed their snouts on top of its head, took it down and away from the vessel, and were not seen again. Note that the animal was not supported in a stereotyped fashion but taken away from would-be captors in a manner opposite of that used in supportive behavior.

Supporting behavior has been described in several species of toothed whales. One distinct class consists of a female, who may be the mother, lifting a dead baby and carrying it on her head or back, or by holding a pectoral fin in her mouth. Sometimes the mother will carry the corpse until it reaches an advanced state of decay. Typically the supporting dolphin carries the body up and down with her as she swims and dives (Hubbs 1953 and Moore 1953, *Tursiops*; Norris and Prescott 1961, *Globicephala*).

A fundamentally different kind of supporting behavior consists of an adult animal of either sex pressing a distressed schoolmate to the surface. The supporting animal usually does not feed, stations itself beneath the sick animal either in inverted or normal orientation, pressing upward, leaving this station only long enough to breathe, but keeping the stricken animal at the surface. The behavior ceases either when a sick animal recovers enough to swim by itself, or dies (Brown and Norris 1956 and Pilleri and Knuckey 1969, *Delphinus*; Siebenaler and Caldwell 1956, *Tursiops*; Caldwell et al. 1963, *Globicephala*). Though most common intraspecifically, the latter kind of supporting has been noted between members of different genera, as will be discussed later.

Many aspects of the life of schooling dolphins have come to involve mutual assistance beyond those just discussed, and these often seem related to reciprocity. In fact, the dolphin school and all its changing geometry becomes a system devoted to ordering reciprocity for its members. It is a mutual protective formation, and for this reason a place where all life functions for a dolphin can occur.

It is possible that dolphins may help mothers during birth by removal of a stillborn calf or the afterbirth. Brown et al. (1966) report that a captive Pacific striped dolphin helped remove the stillborn of a common dolphin. It has been a puzzling fact that stillborn dolphins, either washed ashore or found in oceanarium tanks, are often severely raked with tooth marks, especially over the posterior body and flukes, which may indicate that they have been pulled from the mother (Norris, personal observation). Such pulling of objects from schoolmates took a

peculiar turn when one captive roughtooth dolphin (*Steno bredanensis*) pulled the hypodermic syringe from a tankmate during medical treatment. The assisting animal then became quite aggressive toward the veterinarian (Norris, personal observation). One wonders if such treatment is afforded clinging remoras that often attach to dolphins, or to the small shark *Isistius brasiliensis* that bites 5-cm diameter discs of blubber and muscle from dolphins in warm temperate seas (Jones 1971).

Resource sharing and cooperative feeding.—We know of two examples of resource sharing by odontocetes. On September 14, 1963, off the lee coast of Oahu, Hawaiian Islands, a school of 16 false killer whales (*Pseudorca crassidens*) was seen feeding on a fish (mahimahi [*Coryphaena hippurus*]) by the captain (Georges Gilbert) of the Sea Life Park collecting vessel *Imua*. On five occasions an adult was seen with a large fish (the fish commonly reaches 16 kg and is quite elongate) crossways in its jaws. Two young whales then approached from either side of the adult and began to tear at the extended head and tail of the fish. No aggressive interactions between the whales were seen. Since viable twins are considered almost nonexistent in cetacea, it is likely that the young animals came from two separate parents (Norris, field notes).

A similar example comes from Brower and Curtsinger (1979) who observed a roughtooth dolphin school of 10 animals off the lee coast of the island of Hawaii, feeding on mahimahi. One dolphin carried a captured fish most of the time but gave it up occasionally. Others swam up and pulled pieces of flesh from the fish, or as the original member worried the large fish, picked up pieces that had been broken free and were drifting. The holder of the fish seemed not to object to such sharing, and in fact the fish was passed from dolphin to dolphin. The behavior was seen in two instances, 5 days apart.

Several isolated examples of cooperative feeding patterns have been recorded for cetacea, which have been reviewed by Norris and Dohl (1980*b*). Most citations relate to encirclement of prey. Some examples suggest that fish may become nearly immobilized and hence easy prey during encirclement. The cause is not clear but might relate to induction of a hypoxic state in the fish because of crowding, the induction of lactic acid build up resulting from prolonged pursuit, or debilitation because of intense ensonification by the pursuing dolphins (B. Møhl and K. S. Norris, MS). In one case a human observer was able to reach into such a fish school, surrounded by Pacific striped dolphins and pick up fish at the surface by hand (Norris, personal observation). Killer whales (*Orcinus*) reportedly encircle sea lion or dolphin schools and then a single member races through the school making a kill. It is hard to see how dolphins might make kills of swift swimming fish such as the mahimahi cited earlier, without cooperative behavior, since the fish are much swifter in burst speed than the dolphins (Lang 1966).

*The Three Models: Reciprocity, and Discriminatory,
and Nondiscriminatory Nepotism*

We believe that the behavioral examples cited above represent reliable reporting of events in the lives of dolphins. What do they mean in terms of reciprocal altruism theory? As Trivers (1971) points out, the conditions necessary for the

evolution of reciprocal altruism are also optimal for the operation of kin selection. We must therefore consider the possibility that the entire range of dolphin altruism is a product of kin selection and that reciprocity might not exist in dolphin societies. Kin-directed altruism (nepotism) can be either discriminatory or non-discriminatory, so the potential of both types for explaining dolphin altruism must be explored. Which of these forms of nepotism is likely to predominate in a population depends upon the cost of typical altruistic acts to the donor, the benefits of those acts to the receiver and the pattern of relatedness within the population. Such relatedness patterns will, in turn, be determined by the number of in and out migrants (see Discussion in Hamilton 1975). The difficulty in determining these factors precludes the possibility of using them to deduce the nature of dolphin altruism. However, by applying kinship and reciprocity models to what is known of dolphin behavior and social organization, we have been able to assess whether or not dolphins are likely to employ reciprocity.

Discriminatory nepotism.—This model requires that dolphins dispense altruism according to Hamilton's (1964, p. 19) generalization: "The social behavior of a species evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbor's fitness against his own according to the coefficients of relationship appropriate to that situation."

A method of discerning degrees of relatedness by the animals involved is required here. This can be accomplished by learning where stable social relationships parallel genetic ones (Alexander and Borgia 1978), or phenotypic recognition may be involved, as suggested by Hamilton (1964). Although Alexander and Borgia (1978) argue that phenotypic recognition mechanisms are unlikely, the recent discovery of kin preference in infant pigtail macaques (*Macaca nemistrina*) by Wu et al. (1980), in which an infant chose to associate with siblings never before seen, lends credence to Hamilton's suggestion.

With regard to dolphins we discern a range of possibilities, with some species potentially operating according to the rules of discriminatory nepotism and others seemingly not doing so. As described earlier, the killer whale, *Orcinus orca*, forms extremely stable polygynous pods of modest size with distinct dialects, in which recognition and closeness of kin would fit the discriminatory nepotism model. Because individuals and sexes are recognizable, it is known that even though such pods occasionally contact one another they separate again into their original groups (Chandler et al. 1977).

Permanent intermixture seems to be infrequent. It is interesting to note that some other large odontocetes are also polygynous, and like the killer whale, highly dimorphic, and travel in medium- to small-sized schools. Examples are pilot whales and false killer whales. These species form highly cohesive schools that are frequently involved in live mass stranding incidents, which we regard as partly a result of such polygyny (Geraci and St. Aubin 1979; Porter 1977).

On the other hand, when one looks at the social structure of the smaller dolphins, the discriminatory kinship model immediately encounters serious problems. Recent studies have shown that some dolphin genera (*Tursiops*, *Sousa*, *Stenella*, *Lagenorhynchus*) generally have extremely fluid social structures. Typically a herd has been found to be composed of subgroups which may vary continually in size and composition. Würsig (1978) found that a South Atlantic

bottlenose dolphin (*T. truncatus*) herd numbering more than 50 animals contained both some subgroups that remained stable for months before changing, and many other animals whose relationships seemed more immediately fluid. Norris and Dohl (1980a), working with a spinner dolphin (*Stenella longirostris*) population of approximately 250 animals, could discern no long-term stable groups except for the entire herd occupying approximately 115 km of coastline. They did not, however, discount the possibility that small, possibly stable associations based on kinship could be undiscovered because of the small number of marked animals upon which their findings were based (50 animals of an approximately 250 animal school). Saayman and Taylor (1979), working with a small population (ca. 25 animals) of humpback dolphins (*Sousa* sp.), found essentially complete fluidity. Wells et al. (1980), working with a population of 102 bottlenose dolphins living along a 40-km stretch of Florida coast, found no intermixing with adjacent herds. Within the population, intragroup association varied in a fluid manner on a daily basis, though some association patterns were repeatedly seen.

In sum, these recent studies of dolphins suggest high fluidity, even within rather large groups of animals. If the structure of dolphin societies were regulated by discriminatory nepotism only, little fluidity of relationships would be expected. By considering the forms of dolphin altruism discussed above, one can see that this holds true even if all the members of a population are related enough to make assistance worthwhile to a potential donor. Assume that all the members of a given population suffer the same chances of needing assistance. A donor would benefit more by aiding a close relative than a distant one so that merely swimming with a group of distantly related individuals rather than closely related ones would represent a cost in inclusive fitness. Thus one might expect dolphin subgroups to be stable and composed of close relatives where the degrees of relatedness are highest. At this early stage of our understanding of dolphin schools, only the polygynous societies of larger odontocetes can be explained as being structured largely by kin selection.

It should be noted that fluidity should be a secondary adaptation based upon the recognition of a large number of other animals by a given individual. Once the potential for such recognition exists the fluidity can maximize the possible number of altruistic relationships. A quantitative relationship can be expected in which fluidity becomes important as individuals come to know more individuals than exist within a given level of kin association.

Of even more serious consequence to the discriminatory nepotism model as the sole shaping force of dolphin society are reports of interspecific and even intergeneric assistance behavior in dolphins. These cases have involved both polygynous and nonpolygynous odontocete species (e.g., *Globicephala* and *Lagenorhynchus*) with both partners being donors of altruism (see, e.g., Caldwell et al. 1963 for an example of a pilot whale carrying a dead striped dolphin).

Nondiscriminatory nepotism.—This is the most frequently suggested model for explaining dolphin altruism (Dawkins 1976; Matthews 1978; Wilson 1975). Referring to observations of epimeletic behavior in dolphins, Wilson (1975, p. 475) writes: "By itself the behavior is not as complicated as, say, nest building by weaver birds or the waggle dance of honey bees. It could well represent an innate,

stereotyped response to the distress of companions. Drowning that results from an incapacitating injury must be one of the chief causes of mortality among cetaceans. The automatic rescue of offspring and other relatives contributes greatly to inclusive fitness and is likely to have been fixed in the innate behavioral repertoire of the species."

First, it is important to note that dolphin behavior seems typified much more by learning than by innate patterns. In captivity they are extremely flexible animals and every part of their repertoire is subject to conditioning, including, remarkably, erections (Lilly 1966). Beyond this they are capable of second order learning, or deuterolearning (Pryor et al. 1969). That is, they are capable of understanding the domain of communication within which they operate. The case is instructive in understanding what sort of mammals dolphins are. Roughtooth dolphins (*Steno bredanensis*) were required by standard conditioning techniques to perform novel behavior before they came to the trainer's platform for a reward. They soon made the intuitive leap that "new" behavior was required and began to pour out large numbers of invented patterns never before seen in captivity or at sea (corkscrew swimming, gliding upside down with the tail out of the water, etc.). Herman (1980) provides two additional examples of second order learning from his studies of dolphin cognition in which his subjects generalized learned sample matching rules to new sample sounds or tasks not previously encountered.

Further, epimeletic behavior is not performed in a rigid and stereotyped way. It occurs, instead, in response to new situations, including those never before encountered by the animals. Witness the case of the pilot whale that had been shot (cited earlier) in which the animal slid at the surface toward the collecting vessel. The aiding animals, instead of supporting the dead whale, pressed it down from above and took it away from the vessel. Dolphins pressing against a restrained animal during capture surely are not behaving in a stereotyped fashion since the inexorable drawing in of a struggling animal by a shipboard winch on a taut line is something their ancestors never knew.

One piece of cetacean behavior that is more difficult to deal with is the phenomenon of mass stranding, which particularly afflicts the small- to medium-sized schools of large polygynous odontocetes. Most school members die from these strandings. The animals resolutely swim onto beaches, and die from exposure, drowning, or sand inhalation. The case described by Porter (1977) of a stranding of false killer whales (*Pseudorca*) on Dry Tortugas Island is instructive. The author notes: "... only one, the large male which eventually died, showed evidence of serious wounds. He lay on his side with his blowhole occasionally submerged, bleeding slowly from his right ear. His blood clouded the otherwise clear tropical water around him. He was flanked on either side by fourteen or fifteen whales which kept moving in toward the center of the aggregation, noses pointing toward the beach. This wedge-shaped configuration was maintained for three days until he died, with only the whales on the outside of the pod leaving the tightly bunched group sporadically, and then just for a few minutes" (p. 88). A curious and important fact about this stranding in contrast to those on more turbulent beaches, was that the gathered whales were mostly floated sufficiently so that they could swim away, but did not. The most likely explanation, it seems to us, is that the

social bonds within these polygynous schools are so strong that if leaders strand, so do the others. Much the same high degree of interdependence upon the flock or herd can be seen in some ungulates, such as sheep.

Other workers, however, have argued differently. Evans and Bastian (1969) cite the case of a female Atlantic bottlenose dolphin carrying a dead leopard shark on its snout for 8 days, as described by Norris and Prescott (1961). Evans and Bastian felt the behavior was "strongly counterdictive" to the hypothesis that dolphins act "intentionally" in cases of epimeletic behavior. We believe otherwise. The dolphin, a very old female, was indeed obsessive about her burden and resisted both feeding and having the shark removed during the time she carried it up and down just as dolphins bearing dead babies do. It was not as if she thought the breath of life remained in the shark. Support behavior, on the other hand, involves careful attention to keeping the struggling animal at the surface and clearly involves the prevention of water inhalation. It was clear that the old dolphin behaved toward the shark as if it were a dead baby, and not a struggling comrade. It is, we suppose, in the eye of the beholder, but to us, knowing the characteristics of dolphins, the behavior seemed neurotic rather than a stereotyped response given by an animal in response to a sign stimulus.

For a number of reasons, we consider nondiscriminatory nepotism to be an extremely unlikely mechanism for the explanation of cetacean epimeletic behavior. First, according to Hamilton (1964), discriminatory nepotism is a superior mechanism and would therefore replace nondiscriminatory nepotism where possible. A basic requirement of discrimination is the ability to recognize individuals. Dolphins clearly recognize each other, as is shown by the existence of hierarchies in captivity, sometimes including two genera (Bateson 1974). This ability is evident to every dolphin trainer, since the animals recognize their trainers and sometimes have strong favorites among them (Norris 1974). Dolphin whistles have been shown to contain individual markers, or signatures, and trained dolphins have been shown to discriminate unerringly between the whistles of several individual dolphins, even of other species (Caldwell et al. 1971).

If dolphin epimeletic behavior is performed in a nondiscriminatory manner, one would expect regularities about how and to whom it is offered. Many times female dolphins are supported when in distress, but Bel'kovich et al. (1969) observed a female bottlenose dolphin being abandoned by a male even though "she constantly emitted distress signals." Often adult males are simply abandoned during capture, but once again this is not always the case. Only young seem to be uniformly assisted. The model of a conscious society with individual relationships based on a variable set of emotional drives seems to fit these and other observations much better than the innate model.

Finally, the interspecific, and sometimes intergeneric assistance behavior require explanation if one is to believe in nondiscriminatory nepotism as the basis for epimeletic behavior. The numerous reports of intergeneric and interspecific altruism seen in captivity might be explained as being a result of unnatural associations. This possibility is rendered highly unlikely as reports of interspecific associations in the ocean are frequent (see Brown and Norris 1956; Norris and Prescott 1961; Fiscus and Niggol 1965; Perrin 1972; Leatherwood and Walker

1979; Saayman and Tayler 1979; and Norris and Dohl 1980*b*). The context of these associations is highly variable; in some cases the associations seem to be temporary, such as at feeding aggregations (Norris and Dohl 1980*b*), while in other cases the species involved seem to travel together regularly (e.g., spinner and spotter dolphins, Perrin 1972; Pacific bottlenose dolphins and North Pacific pilotwhale, Norris and Prescott 1961). Usually when traveling together different species remain in distinct groups but this is apparently not always the case. We will give a few examples here. Brown and Norris (1956) report that when *Delphinus* and *Lagenorhynchus* travel together their groups are sometimes intimately mixed. Leatherwood and Walker (1979) observed right whale dolphins, *Lissodelphis borealis*, in associations with eight other marine mammal species but only with Pacific striped dolphins, *Lagenorhynchus obliquidens*, did intimate mixing of groups appear to occur. Saayman and Tayler (1979) observed associations between bottlenose dolphins (*Tursiops aduncus*) and humpback dolphins (*Sousa* sp.) in which, on three occasions, single humpback dolphins swam with groups of bottlenose dolphins and appeared to be "fully integrated members" (p. 208), while on two other occasions bottlenose dolphins appeared to act aggressively towards lone humpback dolphins. They even report a "playlike" encounter involving approximately 13 juvenile and two adult bottlenose dolphins and a group of seven adult humpback dolphins. They note: "The behavior displayed, with much underwater action and many long-jumps and side-flops, was characteristic of bottlenose rather than humpback dolphins. The latter, in this case, were behaviorally indistinguishable from the bottlenose dolphins" (p. 209).

Interspecific and intergeneric epimeletic behavior has been reported between species that associate regularly (e.g., pilot whales and striped dolphins) as well as between those that do not (for instance, Brown and Norris [1956] report that an Atlantic bottlenose dolphin attempted to raise a stricken North Pacific striped dolphin). Further, some of the partners in these exchanges are extremely different morphologically. A pilot whale interacting with a striped dolphin is a good contrast of this sort, since epimeletic behavior has been shown toward the other by members of both species. Striped dolphins are chunky, strikingly marked, black, white, and gray animals reaching about 2.2 m in length and weighing 80–90 kg. Pilot whales on the other hand are elongate, almost entirely black animals with bulbous heads, very large fins, and extremely long tails, and they exceed 6 m and may weigh 810 kg. The most parsimonious explanation of these events, it seems to us, is that a generalized perception of distress is possessed by dolphins and that in normal schools the resulting altruism must extend to most members, and in situations where other species are present, often to them as well.

Thus we feel that nondiscriminatory nepotism and discriminatory nepotism both fail as complete explanatory models of dolphin altruism.

Reciprocity.—The two-party model of reciprocal altruism seems insufficient to explain completely altruistic behavior in dolphins. There is ample opportunity for dolphins to learn of the altruistic and cheating tendencies of others in their schools. Further, it is difficult to account for all cases of interspecific and intergeneric altruism under the two-party model, which requires that aid be given in anticipation of reciprocity from the assisted individual only.

The multiparty model, in which individuals show generalized altruistic tendencies, we believe, does provide a means of explanation for dolphin altruism. In this case altruistic acts are dispensed freely and not necessarily to animals that can or will reciprocate. They need not necessarily even be confined to the species of the altruistic individual. In human terms, a person can rescue a helpless fledgling that has fallen from its nest, and this does not imply any conscious intent toward the rest of society. The person is, instead, motivated first by a broad concept of distress and then by a complex of emotional responses, learning, and social standards. To us, the evidence from dolphins clearly fits this model. The interspecific and intergeneric occurrence is explained. The somewhat unpredictable occurrence of altruism (some females abandoned, some males assisted) in dolphins also fits this model.

The fluidity of some dolphin societies is also allowed by this model. Trivers (1971) has pointed out that reciprocal relationships can be manifested as friendships. Dolphins swimming with unrelated "friends" are reasonably assured of assistance if the need arises. The changing composition of dolphin subgroups then represents the maintenance of a large number of viable reciprocal relationships. Generalized altruistic tendencies allow for even greater fluidity of associations, with assistance being provided by "strangers" according to the social standards of the population.

Evolutionary parallels.—If dolphins do employ reciprocal altruism in a manner similar to humans (and possibly other high order mammals such as elephants and chimpanzees), we are faced with a rather remarkable convergence. Dolphin ancestors arose early in the Cenozoic radiation of mammals (Gaskin 1976), probably in Paleocene time. We suggest that the evolutionary climate for reciprocal altruism in both humans and dolphins was formed of similar parts: strong predatory pressures resulting from sea entry in the case of dolphins and invasion of the savannah in the case of prehumans (Alexander [1974] suggests that a major predator on early hominid groups was other groups of hominids), resulting in highly mutually dependent societies. We believe this marked increase in mutual dependence contributed significantly to the evolution of the higher order intelligences seen in humans and dolphins by producing strong selection pressures for individuals to practice reciprocal altruism with greater sophistication. This can be explained in terms of an increase in the costs and benefits of reciprocal interactions. In environments where mutual dependence is low (e.g., low predation pressures) individuals are by definition more self-reliant and thus the costs an individual suffers for not participating or being cheated in altruistic exchanges are low because it can effectively provide for itself. The same reasoning applies to the benefits of receiving altruism in an equivalent exchange or successfully cheating. As mutual dependence increases, however, individuals are no longer able to provide for themselves as effectively so the costs and benefits of their interactions with others increase; i.e., interactions have a greater effect on their fitness. This produces strong selection pressures for more sophisticated mechanisms for gaining the advantage in reciprocal interactions which are manifested as more complicated emotional systems, better memory and foresight, greater learning capacity, and the ability to make second order abstractions, etc. (i.e., many of the components we associate with intelligence). The situation is further compounded when

social communication is brought into the picture. Now, how one individual acts toward another may affect how the society acts toward it. The costs and benefits of a given interaction in this case will be enormously greater, as will the selection pressures for increased intelligence in animals that have been shunted into this evolutionary pathway.

It is interesting to note that the idea that intrasocietal competition resulting from a system of reciprocal altruism contributed significantly to the evolution of higher order intelligence was expressed in rudimentary form by Bateson in 1966 (pp. 571–572).

We need not complain that, as elephants do not talk and whales invent no mousetraps, these creatures are not overtly intelligent. All that is needed is to suppose that large brained creatures were, at some evolutionary stage, unwise enough to get into the game of relationship and that, once the species was caught in this game of interpreting its members' behavior toward one another as relevant to this complex and vital subject, there was survival value for those individuals who could play the game with greater ingenuity or greater wisdom.

Ethics emerges as a set of learned societal understandings about how to behave, undergirded and strengthened by more ancient emotional patterns. Such ethics may involve relationships not necessarily based on true kinship. They may also be subject to cultural evolution and thus their representation may vary from population to population. If, indeed, the unsubstantiated stories of dolphins pushing humans ashore are true, they must be viewed in the same context as humans pushing stranded dolphins back to sea.

One may puzzle about seals and sea lions, the pinnipeds, who are oceanic carnivores but are clearly less behaviorally flexible than dolphins. We feel the key to this difference probably lies in the birth and early nurture of dolphins at sea, while pinnipeds use land and are thus sheltered from predation at this crucial time. Dolphins have clearly evolved schoolwide strategies for sheltering young at sea. McBride and Hebb (1948, p. 6) describe one school response of captive bottlenose dolphins during birth: "During the period of labor, the other porpoises in the tank showed evidence of excitation and frequently would examine the mother closely. At the moment of birth all the porpoises formed a tight school below and on either side of the mother and infant. The behavior was similar to what occurs when something strange is introduced into the tank. In this case the behavior served a purpose, for several of the sand-bar sharks in the tank, attracted by the blood, were milling about the dolphins. The latter however herded the sharks out of their way, as they do whenever the sharks get too close." This observation has parallels in the behavior of schools of mixed spinner and spotter dolphins (*Stenella longirostris* and *Stenella attenuata* resp.) trapped inside yellowfin tuna seines which formed a "tea cup" of aggressive adults around and below mothers, young, and juveniles in a central rafting group of more or less quiescent animals, and which moved as a unit in response to peripheral disturbance (see Norris et al. 1978).

SUMMARY

We believe that when taken in its totality, the very scattered and often anecdotal literature on dolphins suggests the existence of a system based to a consider-

able degree on reciprocal altruism. The evidence of epimeletic behavior, though based wholly on anecdotes, is so common as to be overwhelming in its broad detail. The data on school structure, based on reliable marking studies at sea, clearly shows much fluidity of relationship, except in the larger dimorphic, polygynous species; but in both, intergeneric and interspecific cooperative behavior is clear.

Reciprocal altruism carries with it the opportunity for the development of complicated social relationships involving, in addition to altruism, deceit, punishment of those who violate social rules, and complicated communication systems between school members. While we could cite isolated anecdotes supporting this or that development of these sorts, we prefer not to at this point, but instead to conclude that in dolphins we are surely dealing with complicated social systems whose outlines we are now just beginning to understand.

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LITERATURE CITED

- Alexander, R. D. 1974. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5:325–383.
- Alexander, R. D., and G. Borgia. 1978. Group selection, altruism and the levels of organization of life. *Annu. Rev. Ecol. Syst.* 9:449–474.
- American Institute of Biological Sciences. 1965. Conference on shark-porpoise relations. Washington, D. C.
- Arnold, P. W. 1972. Predation on harbor porpoise, *Phocoena phocoena*, by a white shark, *Carcharodon carcharias*. *J. Fish. Res. Board Canada* 29:1213–1214.
- Axelrod, R., and W. D. Hamilton. 1981. The evolution of cooperation. *Science* 211:1390–1396.
- Bateson, G. 1966. Problems in cetacean and other mammalian communication. Pages 569–579 in K. S. Norris, ed. *Whales, dolphins and porpoises*. University of California Press, Berkeley.
- . 1974. Observations of a cetacean community. Pages 146–168 in J. McIntyre, ed. *Mind in the waters*. Sierra Club Books, San Francisco.
- Bel'kovich, V. M., N. L. Krushinskaya, and V. S. Gurevich. 1969. The behavior of dolphins in captivity. *Priroda* 5:18–28.
- Bigg, M. A. 1979. Interaction between pods of killer whales off British Columbia and Washington. Third Biennial Conference of Biol. of Marine Mammals, Seattle, Washington (Abstr.).
- Brower, K., and W. R. Curtsinger. 1979. Wake of the whale. *Friends of the Earth*, New York.
- Brown, D. H., D. K. Caldwell, and M. C. Caldwell. 1966. Observations on the behavior of wild and captive false killer whales, with notes on associated behavior of other genera of captive delphinids. *Los Ang. Cty. Mus. Contrib. Sci.* 95:1–32.
- Brown, D. H., and K. S. Norris. 1956. Observations of captive and wild cetaceans. *J. Mammal.* 37:311–326.
- Bryden, M. M. 1972. Growth and development of marine mammals. Pages 1–79 in R. J. Harrison, ed. *Functional anatomy of marine mammals*. Vol. 1. Academic Press, New York.
- Caldwell, D. K., and M. C. Caldwell. 1972. The world of the bottlenose dolphin. Lippincott, Philadelphia.
- Caldwell M. C., D. H. Brown, and D. K. Caldwell. 1963. Intergeneric behavior by a captive Pacific pilot whale. *Los Ang. Cty. Mus. Contrib. Sci.* 70:1–12.

- Caldwell, M. C., and D. K. Caldwell. 1966. Epimeletic (care giving) behavior in cetacea. Pages 755–789 in K. S. Norris, ed. *Whales, dolphins and porpoises*. University of California Press, Berkeley.
- Caldwell, M. C., N. R. Hall, and D. K. Caldwell. 1971. Ability of an Atlantic bottlenosed dolphin to discriminate between and potentially identify to individual, the whistles of another species, the spotted dolphin. *Cetology* 6:1–6.
- Chandler, R., C. Goebel, and K. Balcomb. 1977. Who is that killer whale: a new key to whale watching. *Pacific Search*, May 1977: 25–35.
- Davis, W. M. 1874. *Nimrod of the sea; or the American whaleman*. Harper, New York.
- Dawkins, R. 1976. *The selfish gene*. Oxford University Press, New York.
- Evans, W. E., and J. Bastian. 1969. Marine mammal communication: social and ecological factors. Pages 425–475 in H. T. Anderson, ed. *The biology of marine mammals*. Academic Press, New York.
- Ford, J. K. B., and H. D. Fisher. 1982. Killer whale (*Orcinus orca*) dialects as an indicator of stocks in British Columbia. *Rep. Int. Whal. Comm.* 32 (in press).
- Fiscus, C. V., and K. Niggol. 1965. Observations of cetaceans of California, Oregon and Washington. U. S. Dep. Inter. Fish and Wildl. Serv. Spec. Rep. 498:12–17.
- Gaskin, D. E. 1976. The evolution, zoogeography and ecology of cetacea. *Oceanogr. Mar. Biol. Annu. Rev.* 14:247–346.
- Geraci, J. B., and D. J. St. Aubin. 1979. Biology of marine mammals: insights through strandings. *Marine Mammal. Comm. Rep. MMC* 77/13.
- Griffin, D. R. 1976. *The question of animal awareness*. Rockefeller University Press, New York.
- Hamilton, W. D. 1964. The genetical evolution of social behavior. II. *J. Theor. Biol.* 7:17–52.
- . 1972. Altruism and related phenomena, mainly in social insects. *Annu. Rev. Ecol. Syst.* 3:193–232.
- . 1975. Innate social aptitudes of man: an approach from evolutionary genetics. Pages 133–155 in R. Fox, ed. *Biosocial anthropology*. Wiley, New York.
- Herman, L. 1980. The cognitive characteristics of dolphins. Pages 363–429 in L. Herman, ed. *Cetacean behavior: mechanisms and functions*. Wiley Interscience, New York.
- Hubbs, C. L. 1953. Dolphin protecting dead young. *J. Mammal.* 34:498.
- Jones, E. C. 1971. *Isistius brasiliensis*, a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. U. S. Natl. Mar. Fish. Serv. Fish. Bull. 69:791–798.
- Kasuya, T. 1976. Reconsideration of life history parameters of the spotted and striped dolphins based on cemental layers. *Sci. Rep. Whales Res. Inst. Tokyo* 28:73–106.
- Kasuya, T., N. Miyazaki, and W. H. Dawbin. 1974. Growth and reproduction of *Stenella attenuata* in the Pacific Coast of Japan. *Sci. Rep. Whales Res. Inst. Tokyo* 26:157–226.
- Klevezal, G. A. 1972. Cited in A. V. Yablokov, V. M. Bel'kovich, and V. I. Borizov. *Whales and dolphins*. Pt. II, chap. 16. Age and growth. Izd-vo, Nauka, Moscow.
- Lang, T. G. 1966. Hydrodynamic analysis of cetacean performance. Pages 410–432 in K. S. Norris, ed. *Whales, dolphins and porpoises*. University of California Press, Berkeley.
- Leatherwood, S., and W. A. Walker. 1979. The northern right whale dolphin, *Lissodelphis borealis*, in the eastern North Pacific. Pages 85–141 in H. E. Winn and B. L. Olla, eds. *Behavior of marine mammals: current perspectives in research*. Plenum, New York.
- Lilly, J. C. 1966. Sexual behavior of the bottlenose dolphin. Pages 503–509 in R. E. Whalen and R. A. Gorski, eds. *Brain and behavior*. Vol. III. The brain and gonadal function. UCLA Forum on Medical Science, no. 3. University of California Press, Los Angeles.
- McBride, A. F., and D. O. Hebb. 1948. Behavior of the captive bottlenose dolphin, *Tursiops truncatus*. *J. Comp. Physiol. Psychol.* 41:111–123.
- Matthews, L. H. 1978. *The natural history of the whale*. Columbia University Press, New York.
- Moore, J. C. 1953. Distribution of marine mammals to Florida waters. *Am. Midl. Nat.* 49:117–158.
- Nishiwaki, M. 1962. Aerial photographs show sperm whales' interesting habits. *Nor. Hvalfangstid.* 51:395–398.
- Norris, K. S. 1958. The big one got away. *Pac. Discovery* 11:3–9.
- . 1958. Facts and tales about killer whales. *Pac. Discovery* 11:24–27.
- . 1974. *The porpoise watcher*. Norton, New York.

- Norris, K. S., and T. P. Dohl. 1980a. The behavior of the Hawaiian spinner porpoise, *Stenella longirostris*. U. S. Natl. Mar. Fish. Serv. Fish. Bull. 77:821–849.
- . 1980b. The structure and functions of cetacean schools. Pages 211–261 in L. Herman, ed. Cetacean behavior: mechanisms and functions. Wiley Interscience, New York.
- Norris, K. S., and J. H. Prescott. 1961. Observations on Pacific cetaceans of California and Mexican waters. Univ. Calif. Publ. Zool. 63:291–402.
- Norris, K. S., W. E. Stuntz, and W. Rogers. 1978. The behavior of porpoises and tuna in the eastern tropical Pacific yellowfin fishery: preliminary studies. Final Rep. Mar. Mammal. Comm. Contrib. MM6ACO22.
- Ohsumi, S. 1966. Sexual segregation of the sperm whale in the North Pacific. Sci. Rep. Whales Res. Inst. Tokyo 20:1–16.
- Packer, C. 1977. Reciprocal altruism in *Papio anubis*. Nature 265:441–443.
- Perrin, W. F. 1972. Color patterns of spinner porpoises (*Stenella cf. S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. U. S. Natl. Mar. Fish. Serv. Fish. Bull. 70:983–1003.
- Pilleri, G., and J. Knuckey. 1969. Behavior patterns of some delphinidae observed in the western Mediterranean. Z. Tierpsychol. 26:48–72.
- Porter, J. W. 1977. *Pseudorca* stranding. Oceans 10:8–15.
- Premack, D., and G. Woodruff. 1978. Does the chimpanzee have a theory of mind? II, Special issue on cognition and consciousness. Behav. Brain Sci. 1(4):1–26.
- Pryor, K. W., R. Haag, and J. O'Reilly. 1969. The creative porpoise: training for novel behavior. J. Exp. Anal. Behav. 12:653–661.
- Saayman, G. S., and C. K. Tayler. 1979. The socioecology of humpback dolphins (*Sousa* sp.). Pages 165–226 in H. F. Winn and B. L. Olla, eds. Behavior of marine mammals: current perspectives in research. Vol. 3. Cetaceans. Plenum, New York.
- Scott, J. P. 1958. Animal behavior. University of Chicago Press, Chicago.
- Siebenaler, J. B., and D. K. Caldwell. 1956. Cooperation among adult dolphins. J. Mammal. 37:126–128.
- Southwell, T. 1884. The bottlenose whale fishery in the north Atlantic Ocean. U. S. Comm. Fish Fisheries Rep. 10:221–227.
- Tavolga, M. C. 1966. Behavior of the bottlenose dolphin (*Tursiops truncatus*): social interactions in a captive colony. Pages 718–730 in K. S. Norris, ed. Whales, dolphins and porpoises. University of California Press, Berkeley.
- Tavolga, M. C., and F. S. Essapian. 1957. The behavior of the bottlenose dolphin (*Tursiops truncatus*): mating, pregnancy, parturition, and mother-infant behavior. Zoologica 42:11–31.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 56:35–57.
- Wells, R. S., A. B. Irvine and M. B. Scott. 1980. The social ecology of small inshore odontocetes. Pages 263–317 in L. Herman, ed. Cetacean behavior: mechanisms and functions. Wiley Interscience, New York.
- West Eberhard, M. J. 1975. The evolution of social behavior by kin selection. Q. Rev. Biol. 50:1–33.
- Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, N.J.
- Wilson, E. O. 1975. Sociobiology: the new synthesis. Harvard University Press, Cambridge, Mass.
- Wood, F. G., D. K. Caldwell, and M. C. Caldwell. 1970. Behavioral interactions between porpoises and sharks. Pages 264–277 in G. Pilleri, ed. Investigations on cetacea. Vol. II. Institute of Brain Anatomy, University of Berne.
- Wu, H. M. H., W. G. Holmes, S. R. Medina, and G. P. Sackett. 1980. Kin preference in infant *Macaca nemestrina*. Nature 285:225–227.
- Würsig, B. 1978. Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine Bay. Biol. Bull. 154:348–359.