Animal Social Complexity

Intelligence, Culture, and Individualized Societies

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At sea, female and immature sperm whales are typically found in cohesive groups of about 10–40 individuals that move and act together in a co-ordinated manner (Best 1979; Whitehead et al. 1991). These groups are the social entities in which calves are born and raised, individuals forage, and mating takes place. Members are known to exhibit a wide variety of aid-giving behaviors, including allomaternal care (e.g., “babysitting” and perhaps allonursing; Whitehead 1996) and behaviors that result in communal protection of the group, sometimes to the point of self-sacrifice (e.g., issuing alarm calls, forming defensive formations, and aggressive or defense attack; Scammon 1874; Caldwell & Caldwell 1966; Caldwell et al. 1966; Berzin 1972; Pitman et al. 2001). Traditionally, these behaviors were easy to interpret as kin helping kin in stable matrilineal groups (Ohsumi 1971; Best 1979). Results from recent photo-identification and genetic analyses, however, show that these groups are neither particularly stable nor matrilineal (Richard et al. 1996; Christal et al. 1998; Mesnick 2001). If kin selection is not a viable hypothesis, then other explanations are required.

Adult female and immature sperm whales of both sexes appear to live in a fission-fusion society with the observed “group” being comprised of tempo-
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We used both mitochondrial (mtDNA) and nuclear markers (dinucleotide repeat microsatellite loci) to investigate relatedness in "groups" and "units" of female and immature sperm whales sampled during mass strandings (all beached animals sampled) and from live animals at sea (partially sampled units and groups). Results are consistent within and between the two data sets. Here, we focus on the data obtained from one of the mass strandings (from Stanley, Tasmania) and from one "unit" known from long-term photo-identification records (Galápagos Island samples; see also Chapter 17) to illustrate the main findings.

The cluster diagram of pairwise relatedness values for 10 adult females from the Stanley stranding is shown in Figure 6A.1. This analysis indicates that there were some close relatives among the stranded females but that not all individuals were closely related. Females whose pairwise relatedness values fall within the range expected for first-order relatives include a mother-fetus pair (9669 and 9673) and a cluster of four closely related adult females (9664, 9666, 9665, 9667). Individuals whose closest relative falls within the range expected for a second-order relation include an older female (9671) with 61 growth layer groups (GLG; the number of growth layer groups identified in tooth sections) who could potentially be the grandmother or aunt of several other females in the stranding (9663, 9665, 9668, and 9669). There was one female, with 46 GLG, not closely related to any of the others (9670). All individuals in the stranding shared a single mitochondrial haplotype. This latter finding is unusual among the groups we have looked at; all other units and groups from which we have collected five or more samples, except this one, contained two to four mtDNA haplotypes (n = 3 stranded groups and 10 groups and 1 unit sampled at sea; Mesnick 2001).

The cluster diagram of pairwise relatedness values for five of nine adult females in one Galápagos "unit" is shown in Figure 17.2 of Chapter 17. Two mtDNA haplotypes were present in the unit. No pairwise relatedness values fell within the range expected for first-order relations although all the individuals were known from photo-identification records to be long-term associates.

Our analysis of sperm whale samples and four other recent studies, covering three different ocean basins, show no genetic evidence of a strictly or largely matrilineal unit or group of sperm whales, albeit no living unit or group has been completely sampled (Dillon 1996; Richard et al. 1996; Christal 1998; Bond 1999; Mesnick 2001). Although we do not know
Figure 6A.1. Relatedness among the 10 adult females (and one fetus) that stranded at Stanley, Tasmania, in 1998. The strength of genetic relationships was calculated by estimating the probability of a microsatellite allele co-occurring in two different animals; higher values represented greater than average relatedness (Relatedness 5.0; Queller and Goodnight 1989). On this scale, first-order relations (parents and offspring) would theoretically have a relatedness value of 0.5 (full sibs would have a mean value of 0.5); second-order relations (grandparents and grandchildren, aunts or uncles and nieces or nephews or half sibs) would have a mean relatedness value of 0.25, and so on; observed values are distributed around these means. Individuals with high degrees of relatedness appear close to one another on the cluster diagram. Listed at the right are estimates of age based on the number of growth layer groups (GLG) identified in tooth sections. UPGMA clustering was done using MEGA 1.01 (Kumar et al. 1993).

whether these groups are representative of historical (pre-whaling) sperm whale social structure, contemporary groups of female and immature sperm whales generally contain more than one matriline, as indicated by the presence of multiple mtDNA haplotypes. Both units and groups contain clusters of closely related animals, but some individuals have no close relations. The view of sperm whale social structure that is emerging is one of kith (close, but not genetically related companions) and kin.

These results present us with an intriguing question, rare among non-humans: why do individuals, who may be unrelated, come to the aid of others, and sometimes even risk their lives to do so? Aid-giving behavior can arise along three major pathways: kin selection, reciprocity, and mutualism.
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maintained as a by-product of selfish acts (Dugatkin 1997). Individuals may derive inclusive fitness benefits by helping relatives (kin selection; Hamilton 1964). They may have an opportunity for repeated interactions and reciprocation (reciprocal altruism; Trivers 1971). Finally, it may be mutually beneficial, either incidentally or when the well-being of one’s companions has an important effect on one’s own fitness (Trivers 1971; Connor 1986; Lima 1989). Although we do not know whether some of the most spectacular “altruistic” behavior, such as risking one’s life for another and allonursing, happens outside of matrilines, our data raise this possibility.

Hamilton (1964) and Trivers (1971) predicted that aid-giving behavior will be selected for in species that are long-lived, reside in relatively stable, small social groups, have the ability to recognize individuals, and have long periods of parental care; all characteristics attributable to groups of female sperm whales (Connor & Norris 1982). Aid-giving behavior is also favored when individuals cooperate in defense against a common enemy. Hamilton (1971), explaining the evolution of gregariousness in animals, suggested that the selfish avoidance of a predator can lead to aggregation and that this tendency is intensified when the individuals become mutually dependent on the presence of one another for a successful defense. He coined the term “selfish herd” to emphasize that there is nothing in the least altruistic about the behavior of individuals in these aggregations. Rather, it becomes worth keeping others alive to protect yourself (Connor 1986; Lima 1989). In short, “selflessness is a form of selfishness” (Robert Pitman, personal communication).

This behavior is particularly evident in open habitats. Among terrestrial mammals, the most gregarious are those that inhabit open grassy plains rather than forests. Among fish, schooling is particularly evident in open water (Hamilton 1971). In cetaceans, group size is significantly larger farther from shore; the most gregarious species are those that live in the pelagic realm, the open ocean far away from any cover (Norris & Dohl 1980). Protection from predation by sharks and killer whales is hypothesized to be the causal factor for the evolution of cetacean schools, which function as protective systems for their members (Connor & Norris 1982).

For sperm whales, Whitehead & Weilgart (1991) suggested that calf protection is likely to be the most important function of sociality among females. Whitehead and colleagues (1991) and Whitehead (1996) argue that this may well be adaptive in a species in which adults make long feeding dives to depths where their calves cannot follow. At the surface, the calves are
vulnerable to killer whales and other potential predators. Sociality is further enforced by evidence of allomaternal care, the individuals becoming mutually dependent on one another for communal care of the young as well as defense. It is interesting to note that in primates, young, nulliparous females most frequently display allomaternal or "aunting" behavior (Nicolson 1987) whereas our data suggest that for cetaceans older females may exhibit such care. Conceivably, female sperm whales and their dependent young reside in a social, ecological, and physical environment in which all three major pathways for the evolution of aid-giving behavior (kin selection, reciprocity, and mutualism maintained as a by-product of selfish acts) may operate, reinforced by defense against common enemies.

We suggest that for the sperm whale and other cetacean species that live, raise young, and contend with predators in the pelagic realm, it is the bonds developed through association, cooperation, and lactation that hold these sometimes unrelated females together. Indeed, in the case of sperm whales, it may take a group to raise a calf.