

Creatures of Culture?

Making the Case for Cultural Systems in Whales and Dolphins.

By Scott Norris

On a typical summer day, the waters of Johnstone Strait, in British Columbia, are abuzz with the clicks, whistles, and pulsed calls of killer whales. These animals—the summer residents of the inland waterways off northern Vancouver Island—are perhaps the most intensively studied whale population in the world. Through research based on the ability of observers to visually identify every individual in the population, scientists have put together an extensive and detailed outline of the whales' social relationships over the last three decades. And since the early 1980s, researchers have had hydrophones in the water, recording myriad hours of whale conversation.

The glimpse these studies provide into the life of a creature as far removed from ourselves as the killer whale represents a triumph of field biology. Among the tight associations of family groups known as pods, researchers have found stable and distinct vocal patterns, or dialects, that appear to be maintained and transmitted by social learning. For a growing number of scientists, the implications of such patterns are clear: Killer whales are highly cultural creatures and may stand alongside—and perhaps in some ways ahead of—chimpanzees as the exemplar of a nonhuman animal whose life and evolution is shaped by cultural processes. And killer whales may not be unique: in recent years, intriguing evidence of cultural processes has surfaced in other whale species as well.

But as one might expect, claims of culture in cetaceans (whales and dolphins) have sparked controversy. The idea that nonhuman animals can possess culture has long been a contentious issue among behavioral scientists. Recently, biologists, psychologists, social scientists, and philosophers squared off in a lengthy printed debate over the existence of culture in whales and dolphins. The occasion of this remarkable discussion was the publication, in the journal *Behavioral and Brain Sciences* (Volume 24, April 2001), of a paper by two whale researchers who attempted the first general review of the evidence for culture in cetaceans. Hal Whitehead and Luke Rendell, both of Dalhousie University in Halifax, Nova Scotia, Canada, argued that cetaceans possess cultural faculties unique in the animal kingdom—except for humans. The paper appeared together with 39 written commentaries, some supportive and some strongly critical, and an authors' response.

If nothing else, Rendell and Whitehead's paper and the subsequent debate signify a coming of age in cetacean field studies. The discussion is important not just for the light it sheds on one particular group of organisms but also because it points to larger questions, as well as to what may well be a significant gap in our understanding of animal evolution. Culture is one of only two mechanisms by which information is shared and handed down among members of a population (genetic inheritance is the other). And while research over the past century has done much



Photo: Scott Norris

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The Interpretation of Culture

Culture may be broadly defined as shared variation in behavior that is generated and maintained by social learning, for example, through imitation or teaching. Although many researchers generally agree with this definition, sharp differences exist over its interpretation and application. For Rendell and Whitehead, as for many field biologists, the specific mechanism of information transfer is of less importance than the patterns it generates. Social learning is often very difficult to demonstrate directly. But the presence of culture can be established by observation and deduction: when behavioral differences exist that cannot be accounted for by genetic or environmental factors, cultural transmission must be occurring. The strength of this approach, Whitehead notes, "is that it is firmly rooted in what the animals actually do in the wild."

Critics have several responses. First, it may often be quite difficult to rule out alternative hypotheses suggesting that either genes or learned individual responses to differing environments are responsible for behavioral patterns. Often implicit in this argument is the notion that social learning, thought to be a more complex and cognitively demanding phenomenon than individual learning, should be invoked only as an explanation of last resort. In effect, when it comes to animals, it may be safer to assume that individuals repeatedly reinvent the wheel than to suppose they learn from or imitate the behavior of others, at least until proven otherwise.

A second approach to animal culture is one generally favored by psychologists and behavioral researchers working in experimental settings. According to this view, culture should not be attributed to a species until controlled experimental studies have established a cognitive capacity for social learning—imitation and teaching in particular. “In order to understand cultural phenomena you have to understand the underlying processes, and not focus solely on the results of those,” says Stan Kuczaj, a behavioral psychologist at the University of Southern Mississippi, in Hattiesburg. Although the debate over definitions and evidence remains polarized to some extent, many researchers agree that multiple approaches are needed to understand the behavior of advanced and highly social animals like chimpanzees and whales. And although some scientists still deny culture even to chimps, strict behaviorist approaches may be on



Photo: Scott Norris

Researchers monitor and record whale vocalization using water hydrophone arrays deployed from boats and from shore stations.

the wane. At the same time, observational studies are now gaining some of the scientific rigor they have lacked in the past. For Rendell and Whitehead, the important thing is to approach culture in such a way that all of the evidence may be considered. Given all that has been learned from field studies, they argue, culture should not be denied pending experimental data that may be impossible to collect for many cetacean species.

Matrilineal Whales—Structure and Tradition

The strongest case for cetacean culture may come from killer whales. The social universe of these animals consists of a highly stable, hierarchical set of relationships based on the matriline, that is, the family group consisting of a mother and her offspring. In British Columbia, male whales remain with their mothers until the mothers die. Females eventually mate and form their own matriline. Small numbers of related matrilineal groups band together in highly cohesive units known as pods. Pod members travel and forage together; in over 20 years of study, no individual has switched from one pod to another. At an even higher level, different pods preferentially associate and share vocal elements with one another. Some even engage in what has been described as a ritualized greeting ceremony.

Do the vocal dialects of resident killer whale pods constitute culture? Because the pods all share the same waters and interact extensively, the different dialects cannot be explained in terms of

responses to different environments. Indeed, the fact that separate dialects are maintained despite extensive social interaction among the groups is precisely what sets killer whales apart from other animals in which dialects have been described. In a number of songbird species, for example, stable regional dialects are maintained, but only for separate populations. But could the patterns of variation in killer whale calls be due to genetic inheritance? This would be possible if mating usually occurred between members of the same pod. Such an explanation, however, now appears unlikely. A recent genetic analysis of the resident population by Lance Barrett-Lennard, of the University of British Columbia, found that killer whales tend to mate with individuals from other pods, who sound very different from themselves.

In perhaps the most sophisticated study to date, researchers John Ford and Volker Deecke, of the Vancouver Aquarium Marine Science Center, combined data from Barrett-Lennard’s genetic study with a powerful computer analysis of vocal variation in two killer whale matrilineal groups through time. Closely related groups of whales typically have many vocal elements in common. The researchers used a highly sensitive index of acoustic similarity to compare specific call types shared by the two groups, recorded over a period of 13 years. The analysis revealed that while call types did undergo gradual modification through time, they did not diverge from one another. As with human languages, cetacean vocal elements typically become modified in a gradual and largely random manner over time, a process known as cultural drift. The fact that similar changes occurred in separate groups strongly suggests that an additional process—social learning—was taking place.

“The only way the calls could have changed in parallel is if modifications were not only transmitted within each group, but from one group to the next,” Deecke says. “There was no genetic exchange between the two groups, which rules out the possibility of genetic coding for the calls.”

Sperm whales also have a matrilineal social structure, although group membership is more variable than in killer whale pods. Different sperm whale groups use distinctive and stable patterns of clicks—known as codas—that cannot be explained by genetic or environmental factors. Whitehead’s group has found that vocal repertoires correlate with patterns of predator-inflicted markings, raising the possibility that different communal defense strategies are culturally inherited. Sperm whales have been observed defending themselves from killer whale attacks in both tail-out and head-out formations, but there are no data as to whether groups consistently use one strategy or the other.

Matrilineal species, including sperm, killer, and pilot whales, all have about 10 times less genetic diversity in their mitochondrial DNA than other whales and dolphins. In sperm whales, Whitehead has found a strong correlation between groups in similarity of coda dialects and mitochondrial DNA patterns. He has also shown that the lower diversity cannot easily be explained by such factors as reduced mutation rates or past population bottlenecks. The alternative Whitehead proposes is that the genetic patterns are the result of selection acting on mater-

nally inherited cultural traits (*Science* 282: 1708-4711). Cultural differences that give certain groups an edge in survival or reproduction could, over time, result in greatly reduced diversity in the maternally inherited mitochondrial genome. The hypothesis implies that culture may exist at a deeper level than mere vocal dialects, which are probably not in themselves selectively advantageous. "I think probably it doesn't come down to dialects, but more likely to group knowledge," Whitehead says. "For example, knowing where to go to get food to survive an El Nino event."

Conformity and Change

Humpback whales are best known for their elaborate songs, highly structured vocalizations that may last 20 minutes or longer. Culture in humpbacks is manifest not in small group affiliations and dialects but in population-wide conformity to ever-changing musical fashions. In striking contrast to the stable dialects of killer and sperm whales, humpback songs are faithfully duplicated by all the males in a breeding population, which may be spread out over an entire ocean basin. In any given year, for example, virtually identical songs are sung by whales wintering in Hawaii and Mexico, 4500 kilometers apart. Over time, however, the song of any humpback population gradually changes, piece by piece, through the modification of individual song elements.

How such conformity is maintained among thousands of singing males across vast distances is not entirely understood. Songs may be spread during the summer months, when different groups come into contact with one another, but singing during the summer is thought to be rare. Alternatively, some researchers suggest, songs may actually be heard over very long distances in the deep ocean. Whatever the mechanism, conformity in humpback songs appears to be inexplicable by any process other than social learning. "There appears to be a strong pressure for everyone to sing the 'current' song," Rendell notes. What is most remarkable, he adds, "is the sheer geographic scale over which the songs are shared."

The puzzle of humpback whale singing took a new and unexpected twist last year (in 2001). In an article in *Nature* (408: 537), a group headed by Mike Noad, of the University of Sydney, described an abrupt "cultural revolution" in the song of humpback whales in the Pacific Ocean off the eastern coast of Australia. In 1996, the researchers recorded two individuals singing a song completely different from the one sung by the rest of the population. Two years later, every male in the east coast population was singing the new tune—not an original, it turned out, but an import from the Indian Ocean, on the other side of the continent. The researchers speculated that the song must have been introduced by the movement of a small number of whales from the Indian to Pacific Ocean populations. Such movements are thought to be rare, and since its introduction the song has evolved independently at the normal slow rate in the



Killer whales from several related pods foraging together. University of British Columbia's John Ford has determined that the 16 summer resident pods of Johnstone Strait can be split into four distinct clans based on shared vocal elements.

Photo: Scott Morris

two groups. But why the East Coast males picked up the new song and dumped the old one so quickly remains a mystery. A preference for novelty might be part of the explanation, but this has to be reconciled with the normally strict conformity of humpback vocal culture.

Mind in the Waters

Observational studies in the wild have yielded strong evidence of vocal culture in killer, sperm, and humpback whales. Notably absent from this list is the species whose cognitive abilities are both best known and subject to the wildest speculation—the bottlenosed dolphin. The notion of advanced dolphin intelligence was planted in the public imagination in the 1960s by maverick scientist John Lilly, who speculated about the existence of a dolphin language that might someday be understood by humans.

Although most biologists have remained highly skeptical of such claims, the large and complex dolphin brain—and the feasibility of conducting experimental studies in captivity—have stimulated a great deal of research over the past quarter century. "Tremendous progress has been made in the study, description, and analysis of dolphin cognition since the days of John Lilly," says Louis Herman, a behavioral researcher at the University of Hawaii. Experimental work on dolphins provides the strongest evidence of the kind of individual cognitive capacity and learning ability that may underlie the group patterns of cultural transmission observed in other species. Work by

Herman and his team has shown that bottle-nosed dolphins are capable of acquiring an artificial language. More significantly, through a series of sophisticated experiments, Herman has shown that dolphins appear to possess many of the core properties of grammar and syntax considered fundamental to human linguistic competence.

Researchers and trainers who work with dolphins have long noted their ability not simply to learn behaviors but to modify and invent new ones. "One of the things we've been struck by in dolphins and killer whales is that they make their play more complex and difficult over time," says Kuczaj. Herman notes that such flexibility of behavior—the ability to respond in novel ways to new situations and events—may be considered the very hallmark of intelligence. "The issue of culture in cetaceans relates to the issue of the extraordinary development of the brain in some cetacean species," he says.

Perhaps most relevant to the question of culture is an extensive body of work on dolphin mimicry. The ability of individuals to learn and copy the behaviors of others is a prerequisite for the cultural transmission of information in any animal society. "Imitation can be an efficient mechanism for social learning," Herman says. "Our studies have shown that dolphins are capable of extensive vocal and behavioral mimicry, a seemingly unique combination of abilities among nonhuman animals." Dolphins

appear to understand imitation as a concept, as illustrated by their ability to copy sounds and behaviors almost immediately, without extensive repetition or training. In captivity, mimicry occurs without any training at all. Dolphins may learn each other's trained repertoires through observation only, and caretakers have noted the spread of behavioral fads among tank mates.

A recent study by Vincent Janik, of the University of St. Andrews, demonstrated for the first time the use of mimicry in a dolphin community in the wild (*Science* 289: 1355-1357). Bottle-nosed dolphins develop individually distinctive signature whistles through a combination of learning and subsequent modification in the first few months of life. Janik found that in the wild, individuals out of visual contact communicate with one another by copying and repeating each other's signature vocalizations. This whistle matching suggests that dolphins address each other individually, using learned vocalizations—a phenomenon that may be unique outside of humans.

Bottle-nosed dolphins live in larger, looser communities than other toothed whales, and little work has been done comparing group differences or tracking individual histories through time. But some intriguing evidence of cultural transmission does exist in the realm of foraging behavior. Bottle-nosed dolphins exhibit a variety of individual foraging specializations, some of which may be socially learned. In Shark Bay, Australia, some females have long been observed wearing cone-shaped sponges—benthic organisms apparently harvested by the dolphins—over their beaklike snout, or rostrum. Scientists think the sponges may be used as protection from abrasion while foraging on the ocean bottom. Only a minority of females in the population engage in sponging, but the behavior has been observed in some individuals for over a decade and may be passed down from mother to daughter. And elsewhere in Australia, researchers have described two distinct dolphin communities occupying the same bay but pursuing different foraging strategies. Such evidence may represent only the tip of the iceberg. Cultural transmission may well be common in bottle-nosed dolphins, Whitehead notes, “and it may well be a major influence on behavior. But it's harder to remove the confounding ecological variables for dolphins than for killer and sperm whales.”

The Culture Wars

The attitude of a number of skeptics is expressed in the title of one of the written commentaries to Rendell and Whitehead's paper, “Calling it culture doesn't help.” Many are willing to grant that whales and dolphins are capable of some form of social learning, and they agree that this is an important phenomenon deserving further study. But the concept of culture is, in the words of yet another commentary title, “Slippery when wet.” From a purely behavioral perspective, it may not matter whether social learning in whales amounts to culture or not. “I don't think [the debate over cetacean culture] is productive,” says Patrick Miller, of the Woods Hole Oceanographic Institution. “It simply leads to fights between people who define culture differently.”

But from an evolutionary perspective, culture does matter. It is significant because of the potential for cultural evolution acting alongside natural selection, and for gene-culture coevolution, as has been suggested for the matrilineal toothed whales. Perhaps the key question then is, How cultural are they? One critic writes dismissively that socially learned behaviors in whales “appear to be of the trivial variety: carrying sponges on the head and so on.” But the vocal cultures of killer and humpback whales seem, at least to many researchers, far from trivial. And Rendell believes there is probably much more to discover. “I

am almost certain there is more going on than we have been able to observe,” he says. “What is striking is how strong the evidence is for cetaceans, given the limitations we face in studying them.”

Culture is also important because it has long been viewed as a dividing line between humans and other animals. With evidence of culture accumulating in chimps and whales, this distinction is becoming blurred. It is probably true that in no other species has culture ratcheted upward, or accumulated increasing layers of complexity, as it has in humans. But cetacean cultures do change—and hence evolve. “An exciting aspect of this is that we might be better able to understand how we came to have the kinds of culture that we do, by understanding the evolution of culture in environments radically different from our own,” says Rendell. As in humans, the appearance of culture in whales and dolphins probably is the result of a complex set of interacting factors: brain size and cognitive ability; life history traits, such as duration of parental care and postmenopausal life span; complex social systems; and ecological conditions.

Proponents of cetacean culture believe several features of the marine environment may favor the evolution of social learning and cultural traditions, particularly in long-lived, socially oriented species. Marine ecosystems undergo large changes on time scales of months to years, and at any given moment prey such as krill and fish tend to be highly concentrated in some locations but not in others. Cetaceans are highly mobile animals, and movement appears to be an efficient strategy for coping with both a changing environment and a patchy distribution of resources. This efficiency can be increased if groups follow a coordinated movement strategy using shared information, including knowledge of past conditions that may be passed down intergenerationally. The stable social groups of many whale species provide ample opportunity for such cultural transmission to occur, and selection may favor membership in groups capable of coordinated behavior and information sharing. And as has been proposed for humans, a stable and complex social environment may further the evolution of larger brains capable of more sophisticated forms of social learning. Understanding the full extent of cultural behavior in whales and dolphins remains an enormous task, one that may take generations. But nearly everyone who took part in the recent debate agrees that an important start has been made. “Observational work both in the wild and in captivity is incredibly important,” says Kuczaj. “And so are attempts to demonstrate processes and abilities experimentally. If the groups that do those things continue to talk to one another, we'll make a lot of progress.”

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