

BIOLOGY OF MARINE MAMMALS

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Communication and Cognition

What are your associations with the words "marine mammal cognition and communication?" If you immediately think of big brains, high intelligence, and complex communication, then you are not alone. We humans have big brains and like to think of ourselves as an intelligent species. During the course of evolution, our hominid ancestors evolved larger brains for their body size, and this increase in brain size has traditionally been interpreted as an increase in intelligence. What then are we to make of the fact that the largest brain on the planet belongs to the sperm whale (*Physeter macrocephalus*)? The brain of an adult human weighs about 1 to 1.5 kg, but the brain of a sperm whale may weigh near 8 kg. John Lilly argued that an animal with the sperm whale's brain must have philosophical abilities that are "truly godlike" (Lilly 1975:220). However, sperm whales are much larger than humans, and the larger an animal is, the larger its brain tends to be. What about a dolphin with a body size closer to our own than a whale weighing 30 to 40 metric tons? An adult bottlenose dolphin, *Tursiops truncatus*, weighing 230 kg might have a brain weighing 2 kg. How does this compare to humans, where body sizes of 50 to 100 kg may be associated with brains weighing from 1 to 1.5 kg? Jerison (1978, 1986) has analyzed variation in body weight and brain weight among mammals and concludes that the ratio of brain weight to body weight in bottlenose dolphins is similar to that for humans.

Some of the most successful popular books on animal behavior argue that dolphins with bodies similar in size to those of humans and with brains as big as ours must be as intelligent. The books of John Lilly (e.g., 1967, 1975) launched a strong popular conception linking large brains, intelligence, and languagelike communication in dolphins and whales. Less publicity has attended the reaction of biologists to Lilly's claims. For example, Wilson (1975) rated dolphins no more intelligent than dogs. Bottlenose dolphins have performed well in animal language experiments (Herman et al. 1984, Herman 1986), but there is disagreement about whether their performance is any better than that of California sea lions (*Zalophus californianus*) (Schusterman and Krieger 1984, 1986; Schusterman and Gisiner 1986, 1988; Herman 1989), which have brain and body size ratios similar to those of most mammals (Worthy and Hickie 1986, see Pabst, Rommel, and McLellan, Chapter 2, this volume).

I personally do not believe that it is meaningful to attempt to fit different species along a linear scale of intelligence. There are hundreds of tests for intelligence within our own species, but we still have trouble defining human intelligence. How then can we ever hope to rank different levels of non-human intelligence? Many psychologists have moved away from attempts to define some pure "general intelligence" in humans and are instead defining multiple human

intelligences (e.g., Gardner 1983). Non-human animals also have different clusters of sensory, cognitive, and motor abilities. These differences make it difficult to test behaviorally for some pure "general intelligence," if such a thing exists at all (see Wartzok and Ketten, Chapter 4, this volume).

The recognition that it may be more useful to assess different cognitive skills than one general "intelligence" makes it clear that it was naive to relate brain size to intelligence. To the extent that different parts of the brain are designed to process different kinds of information, it may be more productive to relate specific brain areas to specific cognitive or sensory abilities. For example, variations in spatial learning abilities have been correlated with variation in size of the hippocampus in birds (Krebs et al. 1986) and rodents (Schwegler and Crusio 1995). However, we do not yet know enough about information processing in the brain to predict different cognitive abilities from measuring the size of different brain areas.

We humans use a language that appears to be more complex than communication in other animals. Can we use complexity of communication to relate intelligence to large brains? There are serious problems with this approach. For example, the honeybee, which has a brain weighing on the order of milligrams, has a dance language (von Frisch 1967) that, to my mind, represents just as high an achievement of animal communication as anything demonstrated in wild marine mammals, no matter how large their brains. This may say more about the brilliance of honeybee biologists and the difficulties of studying marine mammals than about the full potential of these different species. We often learn more about cognitive skills in mammals when we ask animals to learn artificial communication systems than when we attempt to understand the full complexity of their own natural communication systems.

Why discuss communication and cognition in the same chapter? Most approaches to both communication and cognition emphasize *information*. The cognitive sciences differentiate themselves by their focus on information flow within an organism or between the environment and the organism. Most discussions of communication emphasize the form and manner in which information is transmitted between organisms. How information is received and perceived provides a critical intersection between communication and cognition; this is described by Wartzok and Ketten (Chapter 4, this volume). However, the people who study animal communication usually are trained in different disciplines than those who study animal cognition. Studies of animal communication have typically come from an ethological tradition emphasizing observation of animals in the wild, coupled with limited experimentation (e.g., Tinbergen 1951). Studies of animal cognition have emphasized training

animals under carefully controlled artificial conditions (e.g., Roitblat 1987). This has meant that "animal language" studies, in which people train captive animals to communicate using artificial languages, are viewed as part of animal cognition. It is surprisingly difficult to compare these studies with those of natural communication systems in the same species. I hope that by combining both topics in the same chapter, the reader will more easily see where they may benefit in the future from closer integration.

The marine mammals are a diverse group, but there has been relatively little communication or cognition research on several taxa such as sea otters, polar bears, dugongs, and manatees. A systematic comparison of communication and cognition in all marine mammal species would be difficult, given the paucity of information on so many species. My approach will be to illustrate principles by going into details about a few species, selected because they have been well studied. Most of the relevant research has been conducted with the pinnipeds and cetaceans. My own marine mammal research has focused on the whales and dolphins, and I have a bias toward discussing these species.

This chapter starts with a discussion of different sensory modalities for communication in marine mammals and why the marine environment might favor the acoustic mode for long-range communication. The best understood examples of acoustic communication in marine mammals are then described and related to the problems posed by different forms of social organization in different species. The cognition section begins with a short description of animal "language" experiments. We use our own human language to learn about each other's mental experiences. The underlying assumption behind animal language training is that it may open a similar window on the minds of animals. As you read this section, think about how well these experiments meet this goal. The second part of the cognition section discusses cognitive abilities such as imitation, emphasizing evidence from untrained behaviors in captivity and the wild. The cognition section closes with a review of brain size in marine mammals and of proposed functions for these large brains.

Communication

As Wartzok and Ketten (Chapter 4, this volume) indicate, marine mammals have well-developed senses of touch, sight, and hearing. In most terrestrial environments, a visual display can be seen farther than a sound can be heard. Of all the ways to transmit information through the sea, however, sound is the best for communicating over distance. Whales may hear one another at ranges of tens of kilometers, but they see one another at ranges of no more than tens of meters. The unique suitability of acoustic signals for long-range

communication in the sea does not limit the usefulness of other senses for shorter range communication, however. Chemical, tactile, and visual modes of communication are briefly reviewed in the following sections, and then I focus in more detail on acoustic communication.

Chemical Communication

Chemical communication is common among terrestrial mammals and many marine organisms but appears to be limited among marine mammals. Pinnipeds do use odor cues, for example, for mother-infant recognition, but these are primarily used in air (e.g., Terhune et al. 1979). The olfactory bulbs and nerves are used by terrestrial mammals for sensing airborne odors. These are reduced in mysticetes and absent in odontocetes (Breathnach 1960, Morgane and Jacobs 1972). Little is known about how marine mammals may sense waterborne chemicals (Kuznetsov 1974; Kuznetsov 1979, cited in Bullock and Gurevitch 1979; Nachtigall 1986), but there are some suggestions of use of pheromones (e.g., Norris and Dohl 1980). If marine mammals have only limited use of chemical communication, this may stem in part from the limited ranges of diffusion in water compared to the mobility of these animals.

Tactile Communication

Marine mammals use tactile sensation for a variety of purposes. The whiskers or vibrissae of seals are very sensitive to movement or vibration, and the walrus (*Odobenus rosmarus*) can even discriminate the shapes of objects using its mustachelike vibrissae (Kastelein and van Gaalen 1988, Kastelein et al. 1990). Walruses feed on the ocean bottom in murky water, and presumably they use their vibrissae to detect and select their prey. It is likely that touch is also important for communication at short range, but the details of tactile communication among marine mammals are not well understood. In many species, a mother and her young keep literally "in touch" by maintaining physical contact as they swim, and sea otter (*Enhydra lutris*) mothers carry their young at sea. Social interactions between manatees (*Trichechus* spp.), a relatively solitary species, are characterized by "mouthing, nuzzling, nudging, and embracing" (Hartman 1979). Muzzle-to-muzzle contact is also common among pinnipeds when they greet one another (Evans and Bastian 1969). Dolphins and whales may rub or caress one another with their flippers or other appendages. Among active schools of wild spinner dolphins (*Stenella longirostris*), some 30% of the members may engage in caressing at any one time (Johnson and Norris 1994). Gentle rubbing seems to play an important role in maintaining affiliative relation-

ships in some dolphin species, perhaps analogous to social grooming in primates (Norris 1991, Samuels et al. 1989). Gentle touching by humans can provide positive reinforcement to captive bottlenose dolphins (Defran and Pryor 1980).

For many cetacean species, sexual contact appears to have a variety of social and communicative functions in addition to procreation. Sexual activity is often reported for all-male groups, and copulation is commonly observed between animals that are not sexually mature. Caldwell and Caldwell (1972a) report that all of the infant male bottlenose dolphins they observed in captivity attempted to mate with their mothers within a few weeks of birth. Nursing appears to stimulate the mother, who often initiates sexual activity with the calf. Nursing itself may become a ritualized display reinforcing the mother-calf bond (Brodie 1969). Although pilot and sperm whales start taking solid food by their second year of life, some individuals may suckle for more than a decade (Best 1979, Kasuya and Marsh 1984). If these teenage whales obtain most of their nutrition from their own foraging, suckling may take on a communicative or affiliative role.

Marine mammals engage in a variety of contact behaviors in aggressive interactions, but few studies have isolated a signal role as opposed to the physical displacement, pain, or harm the contact causes. This raises an important distinction for communication researchers. If I tell you to jump in a lake, I am sending a signal to you, but if I push you in, then any communicative signal pales in comparison to the physical effects of my act. Communication is defined as the transfer of information between two organisms. If you jump in the lake after I tell you to, you are responding to the information I sent. If you jump into the lake because I pushed you, you are responding to the physical effects of my action. Signals are likely to be used both to assess potential competitors and in dominance interactions, but more research is needed to clarify the role of communication in aggressive interactions.

Visual Communication

Vision is well developed among most marine mammals, and most species are reported to have some visual signals. Both aggressive and sexual interactions often involve visual signals at close range. Many aggressive visual signals in marine mammals follow patterns that are common among other mammals, including vigorous moving of the head toward another animal, prolonged staring at another animal, jerking the head, opening the mouth, or even making threats that resemble biting actions. Some behaviors appear to increase the apparent size of a male and may function as visual displays. For example, male humpback whales (*Megaptera novaeangliae*) competing for access to females may lunge with their

jaws open, expanding the pleated area under the lower jaw with water. Visual signals that have been identified in submissive interactions among dolphins include flinching, looking away, and orienting the body away from another animal. Thrusting or presenting the genital region toward another animal may function as sexual visual signals. Direction of gaze is an important visual cue among primates, and human observers can often tell immediately when a dolphin or seal is making eye contact (Pryor 1991). Although the behavioral consequences have not been well studied, gaze cues may be important for marine mammals in clear water as well as in air. Many male seals and toothed whales have secondary sexual features that may function as weapons or armor during fights between males. Males of many species have enlarged teeth or tusks compared to conspecific females. For example, although female narwhals (*Monodon monoceros*) seldom have erupted teeth, adult males have one left tooth that is elongated into a tusk up to 3 m long. Other males may have manes of hair or thickened areas of callused skin. Although these traits may initially have evolved as weapons or armor, they may also function as visual signals either for potential male competitors or for potential female mates.

Many pinniped and cetacean species have distinctive pigmentation patterns that may even be individually distinctive in species such as the humpback whale (Katona et al. 1979). Whereas biologists find these pigmentation patterns to be very useful for species and individual identification, little is known about whether marine mammals use them as signals in their own social interactions. Most biologists have emphasized the role of pigment patterns as camouflage or disruptive coloration against visual predators (e.g., Madsen and Herman 1980). Variation in pigmentation and morphology is also correlated with age-sex classes among dolphins of the genus *Stenella* (Perrin et al. 1991). Large adult male *Stenella* often have a large postanal hump, which accentuates a threat posture involving a peculiar downward curve of the tail. Norris (1991) suggests that a dolphin making this threat looks similar to an attacking shark, and he suggests that the postanal hump in male *Stenella* mimics the claspers of an adult male shark. Norris even describes a threatening male *Stenella* swimming with sideways tail motions like those of a shark predator of these dolphins but very unlike the up-and-down tail motion typically used by dolphins for swimming. This intriguing idea that a threat signal mimics a predator is speculative and remains to be tested.

Exhaling to produce underwater bubbles creates a set of visual displays that are unique to aquatic animals. Some dolphins occasionally blow streams of bubbles that are highly synchronized with the production of a whistle vocalization (Caldwell and Caldwell 1972a). These bubble streams are a highly visible marker identifying who vocalized, but it is

not known whether dolphins respond to this visual accompaniment of the acoustic signal. Humpback whales produce bubble streams in aggressive interactions. Large competitive groups of humpback whales are common during the winter breeding season. Most of these groups have a clear structure in which one adult male, called the "principal escort," apparently guards a central or "nuclear animal," usually a female (Tyack and Whitehead 1983). Principal escorts emit streams of bubbles typically in a line as long as 30 m. The bubble streams often are placed between a challenging male and the nuclear animal, perhaps as a visual screen.

With the exception of bubbles, which are unique to aquatic animals, the visual signaling of marine mammals is similar to that of their terrestrial relatives. Terrestrial animals also have visual agonistic displays that appear to be ritualized from fighting behavior; they use gaze cues; and they use pigmentation patterns for camouflage or for species identification or individual identification. However, there are differences in the range of vision in air versus water. As terrestrial animals, we think of vision as the sense of choice for detecting distant objects. In most aquatic environments, however, daytime vision is limited to a few tens of meters.

Acoustic Communication

The communication modality where marine mammals really stand out is the acoustic channel. Over the course of evolution, marine mammals have come to exploit almost the entire spectrum of sounds that humans have learned to use for exploration and communication under the sea. Large whales can produce loud sounds well below our hearing range that can be detected at ranges of hundreds of kilometers (Payne and Webb 1971, Spiesberger and Fristrup 1990). Dolphins and porpoises can hear sounds more than five times above our upper limit of hearing (Au 1993). To illustrate acoustic communication in marine mammals, I first define some basic acoustic terms and then describe what we know about echolocation and acoustic communication in several of the best studied species.

Because underwater sounds are foreign to most people, I explain acoustic terms using more familiar sounds. Musical tones have different pitches, so that middle C, for example, is lower than the C an octave above it. The physical feature of these sounds that causes the different pitches we perceive is called *frequency*. You can lower the frequency of a stringed instrument by increasing the length of a vibrating string that is at a constant tension. The longer the string, the slower the vibration, and the lower the frequency of sound produced. The frequency of a sound is defined by the number of cycles per second. The modern name for the unit of frequency is the *Hertz*, and 1000 Hertz are called a *kiloHertz*, abbreviated

kHz. A musical tone has a corresponding frequency. When an instrument plays a note, it produces a sound that is centered around this frequency. In acoustic terms, it has a narrow frequency *bandwidth*, or is *narrow band*. In the modern orchestra, the A above middle C is 440 Hz. The A an octave above this is double the frequency, or 880 Hz. When an instrument plays a tone, such as 440 Hz, it also often produces sounds at various multiples of this frequency, such as 880 Hz. These higher frequencies are called *harmonics* of the fundamental frequency of 440 Hz. A sound that contains just one frequency or harmonically related frequencies is called a *tonal* sound. A melody consists of a series of different notes or discrete frequencies. A trombone or a siren can also make continuous changes in frequency. These changes in frequency are called *frequency modulation*. Not all sounds are *narrow band*. For example, when a bat hits a baseball, it makes a crack or click that gets loud very quickly, lasts for a very short time, and includes lots of frequencies. This click has a sudden onset or rapid *rise-time*, short *duration*, and broad bandwidth. The range of frequencies in a sound is called the frequency *spectrum* of the signal. Marine mammals make an enormous diversity of sounds ranging from simple clicks to complex series of clicks to frequency-modulated tonal sounds.

Underwater Acoustics and Patterns of Acoustic Communication

The structure of the sounds that a marine animal uses to solve a problem is influenced by the physics of sound in the ocean. Seawater is an excellent medium for sound propagation, and this opens up the opportunity for remarkable abilities of echolocation and long-range acoustic communication. In this section, I explore how marine mammals have evolved specializations to solve these problems.

Echolocation

Echolocation is usually defined as the ability to produce high frequency clicks and to detect echoes that bounce off distant objects. Echolocation is a good example of how difficult it is to make ironclad distinctions between communication and cognition. Echolocating animals produce signals that are similar to those of communicating animals, but the echolocation signal is not produced to transfer information to another animal. Rather it is used for the signaling animal to learn about its environment. The flow of information from the animal to the environment is like a communicative process, but the flow of information from the environment to the animal is like a cognitive process.

The only marine mammals known to have evolved a specialized ability of echolocation are the toothed whales. We know the most about echolocation in the smaller toothed

whales that can be kept in captivity. Dolphins can echolocate objects at a greater distance than they can typically see them. An echolocating dolphin can detect a target about the size of a ping-pong ball almost a football field away (Murchison 1980). This target is so small that you could not even see it in air from that range. The increased potential range of echolocation compared to vision may make it particularly useful for detecting obstacles or prey. If a toothed whale were swimming rapidly in murky water or at night, it seldom could see an obstacle rapidly enough to avoid it, but echolocation would detect an obstacle far enough away to give even fast-swimming animals plenty of time to respond. Many marine mammals also feed at great depth or at night when there is little light. Some may visually detect luminescent prey nearby, but there are circumstances where vision has a more limited range than echolocation for detecting prey underwater. Most studies of dolphin echolocation have taken place under carefully controlled conditions with captive animals and artificial targets. We know very little about how wild dolphins use echolocation to solve tasks such as avoiding obstacles or detecting, selecting, and capturing prey.

Echolocation is not used only at great distances. Many echolocation tasks may function primarily at ranges of less than several meters. Free-swimming bottlenose dolphins trained to discriminate fish from inedible targets generally did not turn toward the fish until it was only 3 to 3.5 m away (Airapetyants and Konstantinov 1973). Dolphins often inspect objects with echolocation at ranges as close as a few centimeters away. Dolphins can use echolocation to discriminate the shape of targets—even targets with exactly the same shape, differing only in composition (e.g., Kamminga and van der Ree 1976).

Bats are the other mammals that are highly skilled at echolocation. Extensive neurobiological studies have shown that bats have sophisticated neural mechanisms to process echolocation sounds. The processing by some bats of distance to a target object involves remarkable temporal precision (Simmons 1973), and bats have sophisticated mechanisms to compare an echo to the particular pulse from which it came (Simmons et al. 1975). We know toothed whales use high frequencies for echolocation, but we know little about how they process sounds for echolocation.

The optimal frequency for echolocation depends on the size of the target. Objects or features that are much smaller than the wavelength of the impinging sound do not reflect the sound very efficiently. The wavelength, λ , of a sound equals the speed of sound, c , divided by the frequency, f , therefore: $\lambda = c/f$. The speed of sound in seawater is close to 1500 m/sec (Urlick 1983). This suggests using sound frequencies on the order of 150 kHz or higher to detect targets of a size around 1 cm (i.e., if $\lambda \approx 0.01$ m, then $f = c/\lambda = 1500/0.01$

= $1500 \times 100 = 150,000$). Dolphins and porpoises have evolved specializations for producing and hearing such high frequency sound. Bottlenose dolphins hear best around 50 kHz, but they hear well above 100 kHz. Figure 7-1 shows the specialization for high frequency hearing of several toothed whale species compared with seals and fish.

Dolphins produce echolocation clicks with frequency emphases that match their auditory sensitivity relatively closely, as might be expected for the task of extracting faint echoes from noise. The echolocation clicks of bottlenose dolphins are very short ($<100 \mu\text{sec}$), with a rapid rise-time and a relatively broad bandwidth from several tens of kHz up to near 150 kHz (Fig. 7-2A; Au 1993). Several other toothed whales, such as porpoises of the genus *Phocoena* and delphinids of the genus *Cephalorhynchus*, produce more narrow band pulses in the 110- to 150-kHz range (Fig. 7-2B; Kamminga and Wiersma 1981). Au (1993) suggests that the smaller animals producing clicks illustrated in Figure 2B may simply be incapable of producing clicks as loud, short, and broadband as those shown in Figure 2A. However, *Cephalorhynchus* is more closely related to *Tursiops* than to *Phocoena*, and this suggests that *Cephalorhynchus* and *Pho-*

coena have independently converged on very similar morphology, behavior, and patterns of vocalization. Their echolocation clicks may also be an adaptation to the niche for which they seem to have converged (Watkins et al. 1977). When different species of bats produce clicks as different from one another as the clicks of *Tursiops* and *Phocoena*, this difference is associated with a different mode of sonar processing. Among bats, narrow-band longer duration clicks are associated with an echolocation system that relies on using Doppler shift to detect moving targets in a cluttered environment (Neuweiler et al. 1988). It is possible that *Cephalorhynchus* and *Phocoena* may process echolocation signals very differently from the well-studied bottlenose dolphins (Ketten 1997, Tyack 1997). We know next to nothing about how these species echolocate. Imagine how exciting it will be to study how they use echolocation and how they process the echoes from their clicks.

Dolphins can vary both the loudness and the frequency spectrum of their clicks. There is some evidence that bottlenose dolphins and beluga whales (*Delphinapterus leucas*) shift the frequency of their clicks to avoid noise if it is present in the normal frequency range (Au 1993). This would be

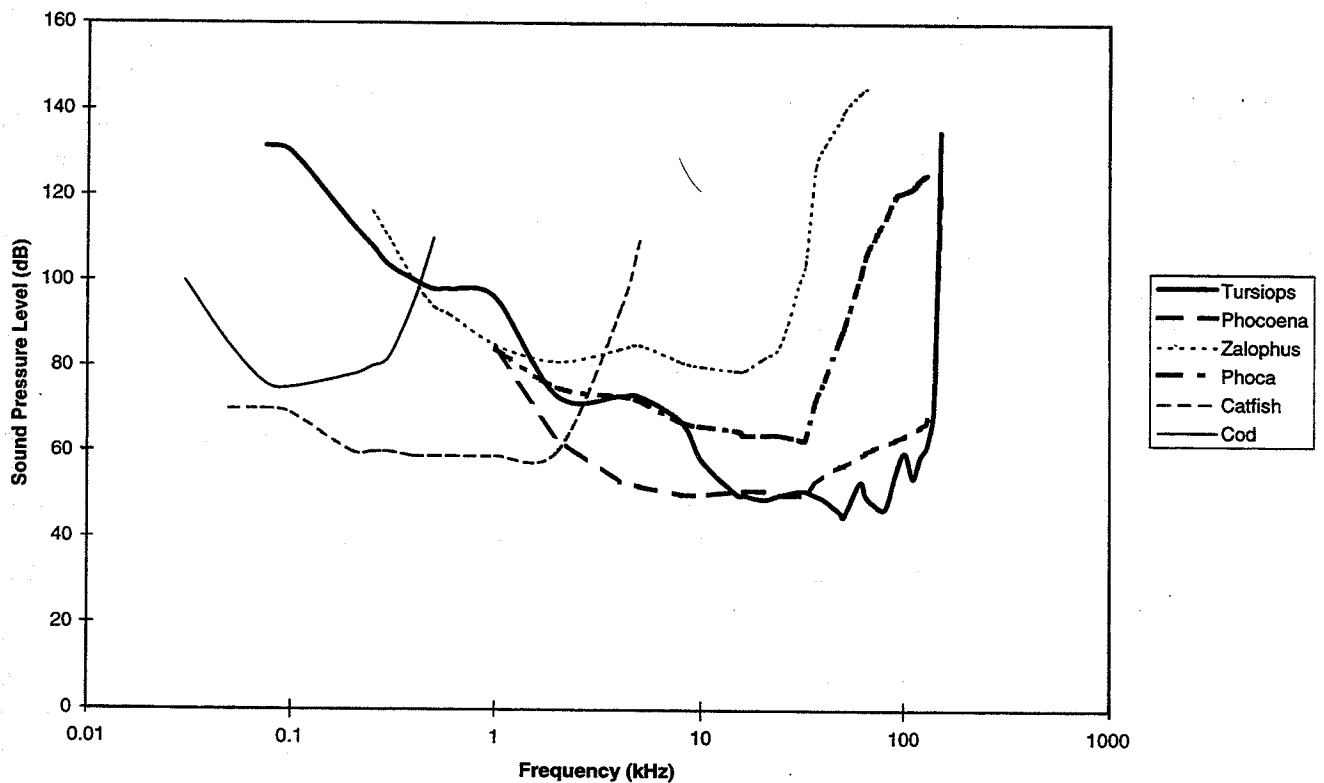


Figure 7-1. Audiograms of odontocete cetaceans specialized for high-frequency echolocation compared with several seal and marine fish species. (Audiograms: bottlenose dolphin [*Tursiops truncatus*], Johnson 1966; harbor porpoise [*Phocoena phocoena*], Andersen 1972; California sea lion [*Zalophus californianus*], Schusterman et al. 1972; harbor seal or common seal [*Phoca vitulina*], Möhl 1968; catfish, Poggendorf 1952; cod, Chapman and Hawkins 1973.)

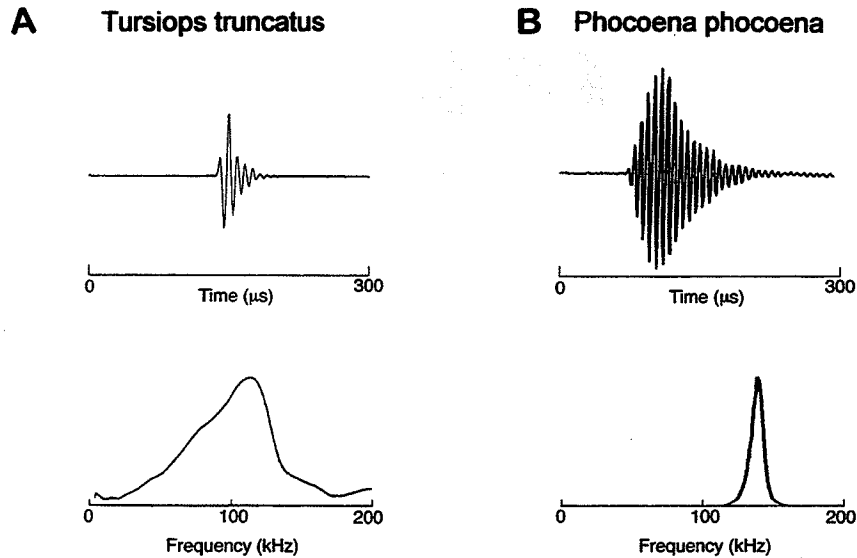


Figure 7-2. (A) Waveform and frequency spectrum of the echolocation click of a bottlenose dolphin (*Tursiops truncatus*). (From Au 1993.) (B) Waveform and frequency spectrum of the echolocation click of a harbor porpoise (*Phocoena phocoena*). (From Kamminga and Wiersma 1981.)

analogous to switching from a channel in a walkie-talkie with a lot of radio interference to one that is less noisy. Not much is known about whether or how dolphins modify their clicks depending on the echolocation problem on which they are working. For example, do dolphins adaptively modify their clicks to improve information in the echo from a particular target?

The clicks of bottlenose dolphins are very directional in the higher frequencies. Dolphins closing in on a target make both lateral and circular scanning motions, similar to shining a flashlight beam over an object. Bottlenose dolphins usually wait to hear the echo from a target before they produce the next click, and as they close in on the target, the interval between pulses usually decreases (Au 1993). This sounds to our ears as individual clicks blending into a buzz sound, but the dolphins are capable of much better temporal resolution in their hearing.

Low-frequency Sounds of Finback and Blue Whales

Not only have marine mammals evolved uses for sound well above our limit of hearing, but the largest of the baleen whales also produce sounds so low in frequency that they are an octave or more below the lowest sounds we can hear. Finback (*Balaenoptera physalus*) and blue (*B. musculus*) whales make sounds about as loud as a medium-sized ship, centered around 10 to 30 Hz (Fig. 7-3). Blue whale sounds last several tens of seconds (Cummings and Thompson 1971, Edds 1982), whereas those from finbacks are comprised of series of 1-sec pulses (Watkins et al. 1987). Identifying which species is producing a sound can be challenging. You can count on one hand the blue whales identified in published reports to have produced these calls. One good day at sea with blue whales could materially improve our data on this topic. This re-

search area is at the early stages of exploration and discovery. Some people do not like problems where so little is known, but the most exciting experiences I have had as a marine mammalogist involved problems like this where a few days' observation made a significant contribution to our understanding.

The sounds of blue and finback whales have a variety of features suggesting that they are adapted for long-range communication (Payne and Webb 1971). These sounds have a simple structure that is often repeated over and over, increasing their detectability. During their breeding season, finback whales may produce a series of 20-Hz calls lasting typically many hours and up to longer than one day (Watkins et al. 1987). The low frequency of these calls also appears to be an adaptation for long-range communication. The higher the frequency of a sound, the more of its energy is dissipated into heat as it passes through water (Urlick 1983, Tyack 1998). The frequency of these whale sounds is low enough that there is very little absorption of the sound energy, even over ranges of hundreds of kilometers. Sound energy is also lost when a signal interacts with the sea floor or surface, but there are a variety of ocean sound channels in which sound energy can be entrained, avoiding surface and bottom loss. In the shallow Arctic sound channel, the best propagation occurs in the 15- to 30-Hz frequency range (Urlick 1983); many finback and blue whale signals concentrate energy in this band.

Calculations for sound propagation in the deep ocean suggest that the 20-Hz finback whale signals could be detected at ranges of hundreds of kilometers (Spiesberger and Fristrup 1990). Figure 7-4 shows many of the paths that such a sound would take over a range of 400 km. The sound rays shown in Figure 7-4 were calculated using the variation in speed of sound with depth shown on the left side of the

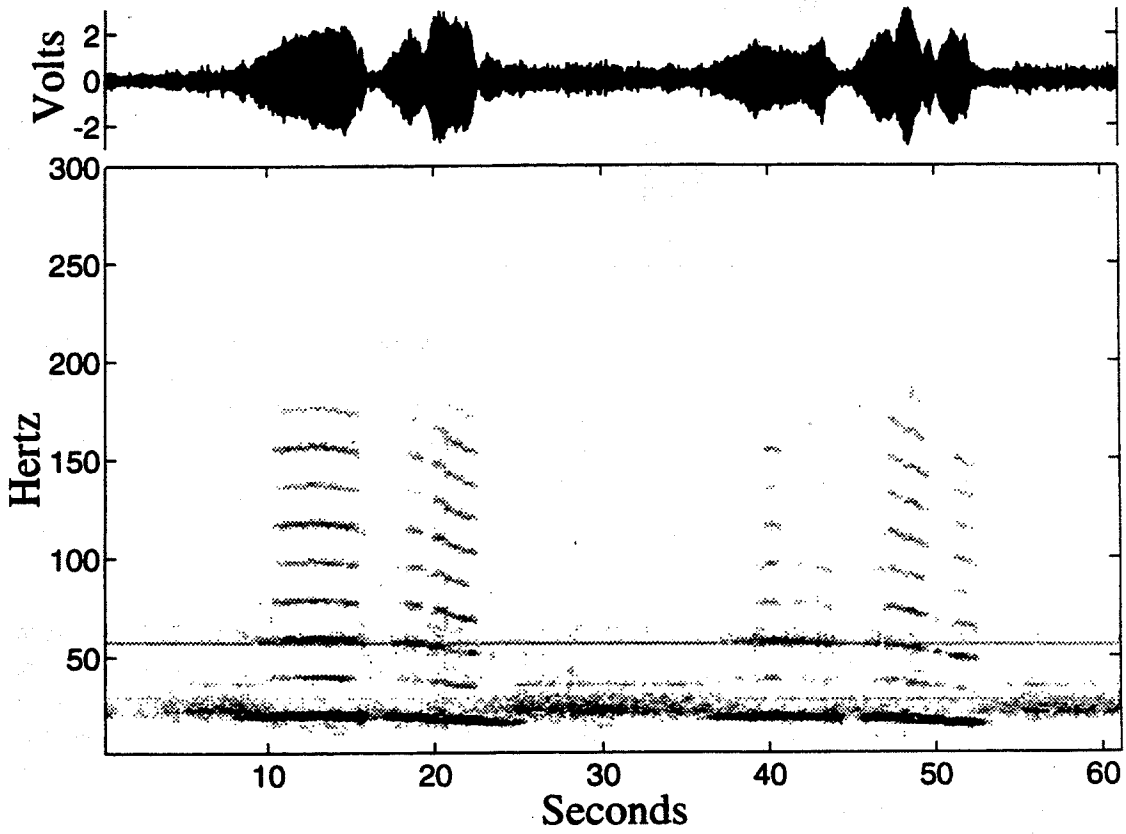


Figure 7-3. Low-frequency vocalization of a blue whale.

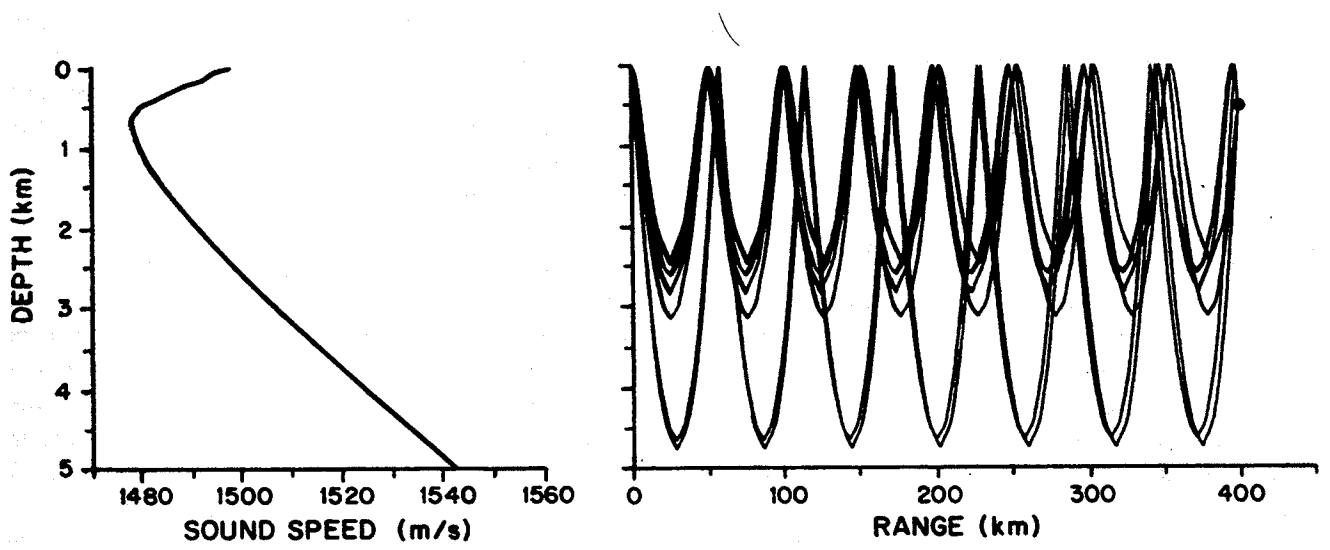


Figure 7-4. (Left) A typical profile of sound speed versus depth for temperate or tropical seas. (Right) Calculated ray paths for a finback 20-Hz pulse produced at a depth of 35 m and detected at a receiver 500 m deep and 400 km away. The ray paths illustrate the general patterns of propagation of this kind of signal in deep temperate or tropical seas. (From Spiesberger and Fristrup 1990.)

figure. The variation in sound speed in the ocean causes sound to refract, just as the variation in the speed of light between the air and the glass in an optical lens causes the light to refract. There is a minimum in sound speed in temperate and tropical waters near 1 km depth. Sound rays that start upward from this depth speed up and refract back downward. Downward-heading rays also speed up after they pass below the depth of the sound speed minimum, and they refract back upward. If you look at the density of rays in Figure 7-4, you can see that most of the sound energy concentrates near the depth of the sound speed minimum, also called the SOFAR channel (Urlick 1983). An underwater microphone placed near this depth would be more likely to detect a distant sound than would one placed at random near the surface. However, the acoustic rays converge near the surface every 52 km, in what is known as a convergence zone. Although baleen whales are not known to dive as deep as the SOFAR channel, a whale swimming near the surface through a convergence zone might experience an increase in sound level of tenfold or more, perhaps even within a few tens of meters (Urlick 1983). While finback calls carry long distances, it is hard to imagine that a whale would often find another whale after detecting it hundreds of kilometers away. Finback whales do swim 10 km/hr or more (Watkins et al. 1984), and their series of 20-Hz pulses may last for up to a day (Watkins et al. 1987). However, look at Figure 7-4 and think of a whale that seldom dives more than a hundred meters or so. Such a whale might hear a distant whale several convergence zones away, but to be able to find that whale, it would have to determine which direction to swim and then keep detecting it as it encountered another convergence zone every 50 km or so. Our ignorance of the diving patterns and of the low-frequency hearing sensitivity of whales makes it impossible to predict with confidence the ranges over which they can hear conspecific signals. Baleen whales are not thought to dive deep enough to enter the SOFAR channel, but we have little data on the dive patterns of whales. We do not know how deep they typically dive at sea, or whether they might dive especially deep to listen for distant signals.

The different rays shown in Figure 7-4 travel different distances and would vary in their time of arrival from 259 to 260 sec (about 4.3 min). Because the sound itself lasts about 1 sec, a whale would hear a complex superposition of arrivals. Acoustic oceanographers can often resolve these different rays or modes of travel, and can use this information to learn about the location of the source or about the ocean in between. We know nothing of whether whales perform similar processing. However, the high repeatability of these simple pulses clearly increases their detectability over long distances.

It is very difficult to record low-frequency signals from a

boat because any motion of the sensor creates flow noise at these frequencies. However, the end of the Cold War opened the door for biologists to use a remarkable new tool (Costa 1993). For decades, the U.S. Navy placed underwater microphones, called hydrophones, deep in the ocean. These were cabled back to shore, and the signals were transmitted to central analysis rooms where sounds picked up from entire ocean basins were integrated. The operators of this sound surveillance system (the acronym is SOSUS) could listen for the sounds of ships over the entire North Atlantic or North Pacific. In the past few years, Christopher Clark of Cornell University has pioneered the use of this system to track whales over distances of hundreds of kilometers. Figure 7-5 shows a track of one whale, called Old Blue, tracked by Clark and Lt. Charles Gagnon of the U.S. Navy. Clark's group has recorded, mapped, and analyzed thousands of calls from baleen whales.

The SOSUS gives us the ability to follow vocalizing whales at ranges of hundreds of kilometers. The only other technique that allows us to track the whales over these great ranges involves tagging whales with a device that can telemeter their location (e.g., Watkins et al. 1984). Figure 7-6 shows how far a finback whale can move in just 1 week during the feeding season. Many whales also have annual migrations of thousands of kilometers, from polar feeding areas to tropical breeding areas. Several biologists have suggested that marine mammals might be able to sense echoes of low-frequency vocalizations from the sea floor to orient or navigate with respect to bathymetric features (Norris 1969, Payne and Webb 1971, Thompson et al. 1979). This would be quite different from the high frequency echolocation of toothed whales but might function, for example, as a depth sounder or to detect a distant island or continental shelf (Tyack 1997). It has also been suggested that bowhead whales (*Balaena mysticetus*) migrating in the Arctic could detect rough ice ahead by listening for echoes from their calls (Ellison et al. 1987). Development of more sophisticated tags that measure the depth of dives or that record sounds received by the whale may help us to determine whether the whales themselves can use sound to perceive information from the surface or bottom of the oceans in which they live and migrate.

Sexual Selection and the Evolution of Advertisement Displays

The introduction of this chapter describes communication as an exchange of information. Yet communication can also reflect an attempt by a signaler to manipulate the behavior of a recipient (Krebs and Dawkins 1984). For a human example, you can buy a newspaper to get information, but you cannot escape advertisements put on the page to get you to buy something else. Animals also produce advertisement dis-

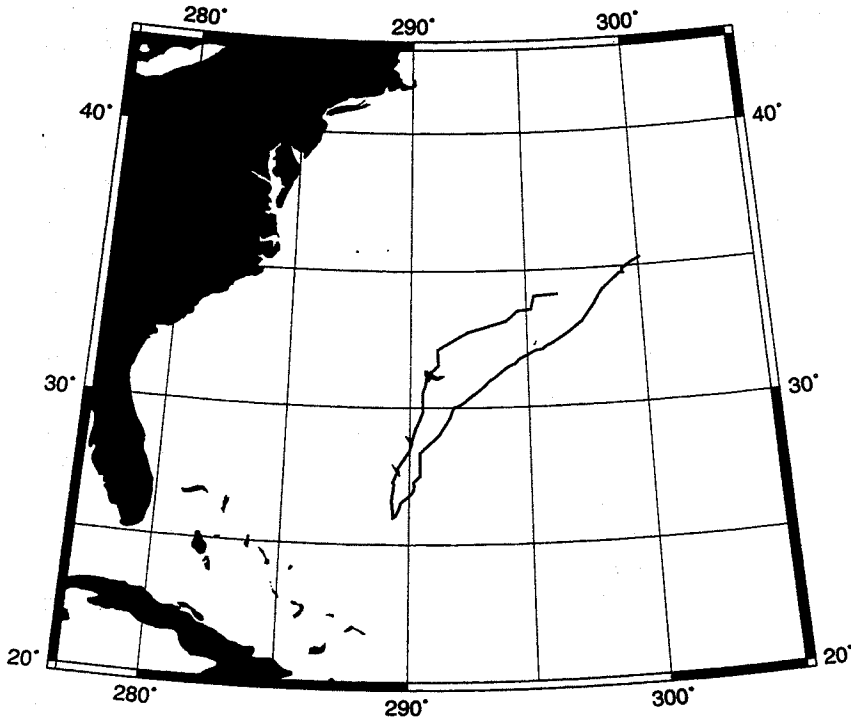


Figure 7-5. Track of vocalizing blue whale made using U.S. Navy's SOSUS arrays.

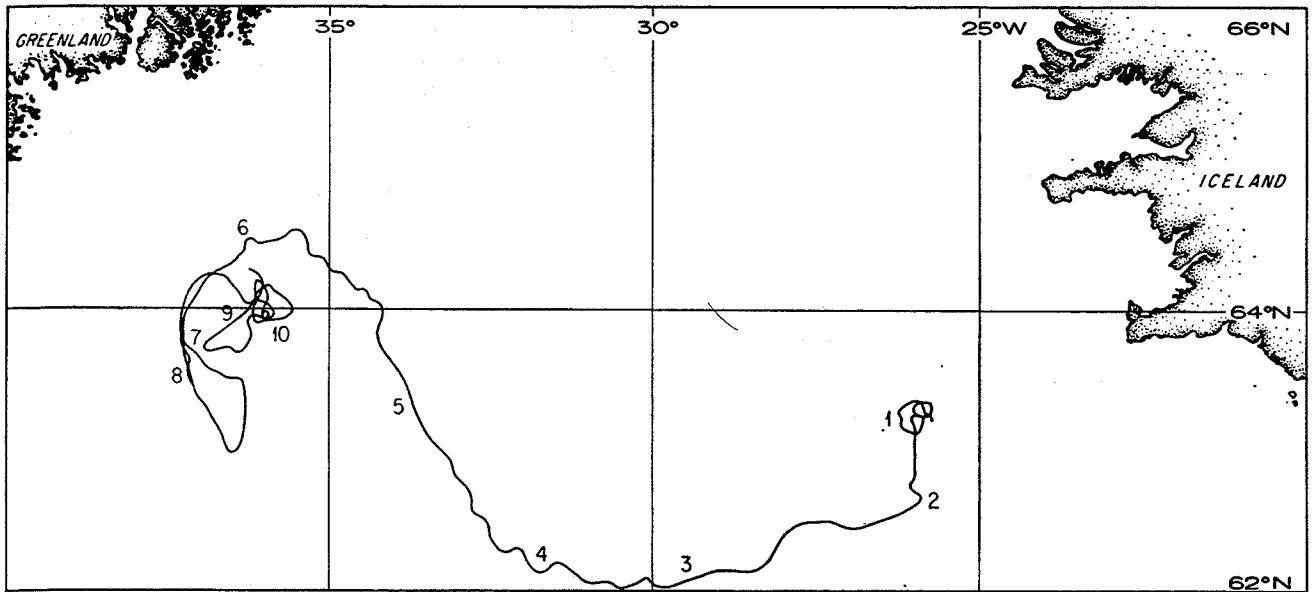


Figure 7-6. Track of a finback whale tagged with a radio and followed from a ship for one week. (From Watkins et al. 1984.)

plays, and their structure cannot be understood unless one considers how the signal is designed to manipulate choices of animals that hear the display. For example, communication is often described as an exchange of individual signals and immediate responses. However, one animal may produce a long series of advertisements to modify the outcome of one choice by a listening animal. The listening animal may only make its choice after hearing hundreds or thousands of advertisements from many different signalers. Advertisements

are also typically very flashy and attention-getting. This makes them better known than many other kinds of animal signals. Examples include the songs of birds and whales. Songs are usually defined as acoustic displays in which a sequence of notes is repeated in a predictable pattern.

Songs of Humpback Whales

STRUCTURE. Perhaps the best known marine mammal vocalizations are the songs of the humpback whale (Payne

and McVay 1971, Winn and Winn 1978). Unlike the low-frequency calls of finback and blue whales, which we can scarcely hear, the songs of humpbacks cover the frequency range of most human music: from about 30 Hz up to about 3 kHz. These songs sound so beautifully musical to our ears that they have been commercial bestsellers. Humpback whales sing continuously for hours, primarily during the breeding season. The song is made up of fewer than ten themes (Fig. 7-7), each of which is made up of phrases or series of sounds lasting about 15 sec. Phrases of one theme repeat a variable number of times before a new theme is heard. Humpbacks tend to sing themes in a particular order, and it often takes about 10 min before a singer comes back to the initial theme.

COMPARISONS WITH BIRDSONG. Many different animals produce long, complex songs. The best known are those of birds. Humpback songs might at first seem much more complex than birdsong, as the song of the whale lasts many minutes whereas the songs of most birds last only a few seconds. There are two reasons why these appearances may be misleading. First, what is called one song may differ between whales and birds. When the wren sings AAABBB, it is said to repeat song A three times and song B three times as it moves through its song repertoire. When the whale sings

AAABBB, it is said to repeat three phrases from theme A and then three phrases from theme B as it completes its song. Thus, what is called a song in the bird may be more appropriately compared to a phrase from the song of the humpback whale. Second, if humpback song is speeded up about 14 times, it sounds to my ears remarkably like a bird such as the Bewick's wren (*Thryomanes bewickii*), which repeats one song type a few times before switching to another song type (Kroodsma 1982). Conversely, much more complexity is audible in each note of a slowed-down bird song than was apparent at the natural speed. The whale stretches its song over what seems a leisurely pace to a human, whereas the bird uses a greater frequency range but compresses its song over a duration so short that human ears miss some of the detail. We cannot be sure what level of nuance whales and birds pick up at the natural paces of their own signals. Signal-processing engineers often compare disparate signals by multiplying the duration and the frequency range to obtain what is called the time-bandwidth product. Changing the playback speeds makes bird and whale song sound similar; this suggests that the songs of some birds and whales may have comparable time-bandwidth products.

Kroodsma (1982) developed several different measures of the complexity of the song repertoires of Bewick's wrens, and these measures can be used to compare humpback song

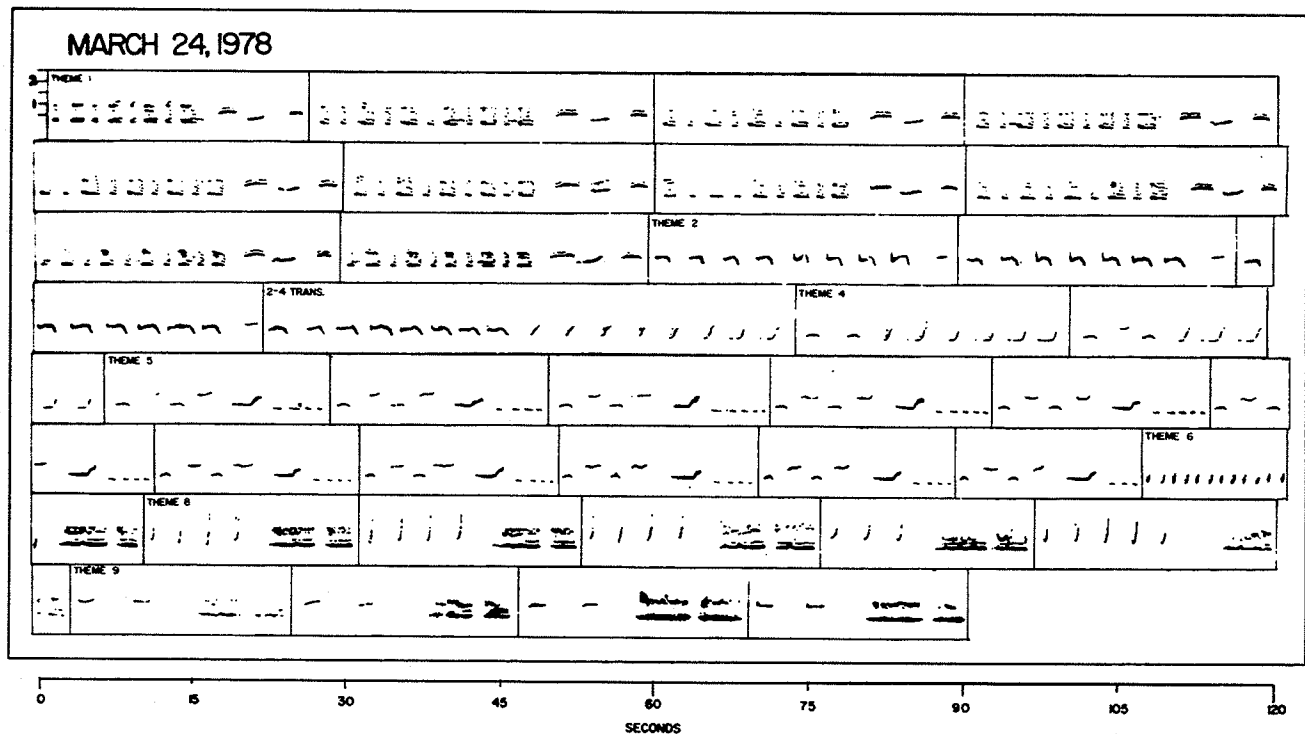


Figure 7-7. Spectrogram of the song of a lone humpback whale from the Hawaiian Islands. Each line represents 2 min, and this song took 14 min before repeating the initial theme. Each theme is made up of repeated phrases, and the boundary between phrases is marked by vertical lines. The first phrase of each theme indicates the number of the theme. (From Payne et al. 1983.)

to that of this avian songster (Table 7-1). Both the bird and whale songs are made up of sounds that may be repeated many times. The complexity of highly repetitive songs might be inflated compared to songs that contain sequences of different sounds. To correct for this, Table 7-1 includes a correction for durations and time-bandwidth products that counts just one example of each repeated sound.

Table 7-1 shows that the songs of humpback whales and Bewick's wren are roughly comparable by several indicators of song complexity. While the total song duration for the whale greatly exceeds that of the wren, the corrected song duration of the humpback (15–20 sec) is only slightly greater than that of the wren (9–15 sec). The corrected time-bandwidth products of whale and wren overlap.

Now let us compare the whale to a real champion avian songster: the long-billed marsh wren (*Telmatodytes palustris*). As mentioned above, transitions between themes in the songs of humpbacks should be compared to transitions between songs in the song repertoires of a songbird. Figure 7-8 illustrates these transitions for humpback whales and for the long-billed marsh wren. The large numbers in this figure represent themes for humpback whales and songs for the marsh wren. For the humpback themes, I have tallied almost 1200 transitions from one theme to another, using data from many different whales recorded during one singing season in the Hawaiian Islands (Tyack 1982). For the marsh wren, I reproduce a figure from Verner (1975), which tallies transitions between songs sung by one male during one long song bout. The marsh wren has more variable song transitions, but in

general it does have preferred paths to switch between its 100 or so songs. Although the data from humpback song stems from many whales over an entire singing season, the transitions between themes of humpback song seems much simpler than transitions between songs of the wren, with more systematic transitions between fewer than ten themes.

The real key to the complexity of humpback song is the way it changes over time. Until now we have compared the songs of humpbacks at any one time to song repertoires of birds. Some songbirds add songs to their repertoire over several years. Humpbacks do not show a similar slow increase in complexity of their repertoire with age; instead all individuals within a population sing songs that are very similar at any one time, and they all slowly change their entire songs more or less in synchrony over weeks and months. The song of each individual is much more like the songs of other individuals recorded at the same time than it is to itself recorded, say, a year later (Guinee et al. 1983). Within a population, song gradually evolves over time so that few elements of the song are preserved over many years. Sounds may change in duration, frequency, and timbre; they may disappear from the song entirely, and new sounds may appear in some other part of the song. Analysis of songs recorded off Bermuda over a period of more than two decades showed that once a particular song phrase disappeared, it never recurred (Payne and Payne 1985). Humpbacks live for decades, so the lifetime production of song is much more complex than suggested by the complexity of the song recorded at any one time.

In this section, I have emphasized comparisons of humpback song to birdsong, but some popular descriptions attempt to compare whale song to human language. For example, Sagan (1980) uses the length of the song to argue that a humpback song may contain the same amount of information as *The Iliad* or *The Odyssey* of Homer. This analogy is misleading for several reasons. The information content of the human text is calculated by the number of letters multiplied by the number of bits required to specify a letter. This requires much less information than would be required to record and reproduce the actual stream of speech. The information content of humpback song is calculated by how much data would be required to reproduce the sounds. This requires much more information than could be achieved by an efficient coding scheme, such as the alphabets used to represent speech or musical notation used to represent a symphony. No one knows how humpbacks represent or encode song. Humans use rhythmic structure and frequent repetition of similar sounds as an aid to remembering vocally transmitted material. Guinee and Payne (1988) suggest that the rhythmic structure and repetition in humpback song also function as mnemonic aids for the whales. Rhythm and rep-

Table 7-1. Comparison of Acoustic Complexity of Songs of Bewick's Wren and the Humpback Whale

Bewick's Wren ^a	Humpback Whale
Number of songs: 10–20	Number of themes: 5–8
Total phrases: 36–88	Total units: 15–20 ^b
Song repertoire duration (sec): 27–40	Song duration (sec): 264–2100 ^c
Corrected song repertoire duration (sec): 9–15	Corrected song duration (sec): 15–20 (average 1 sec unit duration × 15–20 sec)
Time-bandwidth product (kHz-sec): 87–147	Time-bandwidth product (kHz-sec): 528–4200 (assume 2 kHz bandwidth)
Corrected time-bandwidth product (kHz-sec): 31–72	Corrected time-bandwidth product (kHz-sec): 30–40

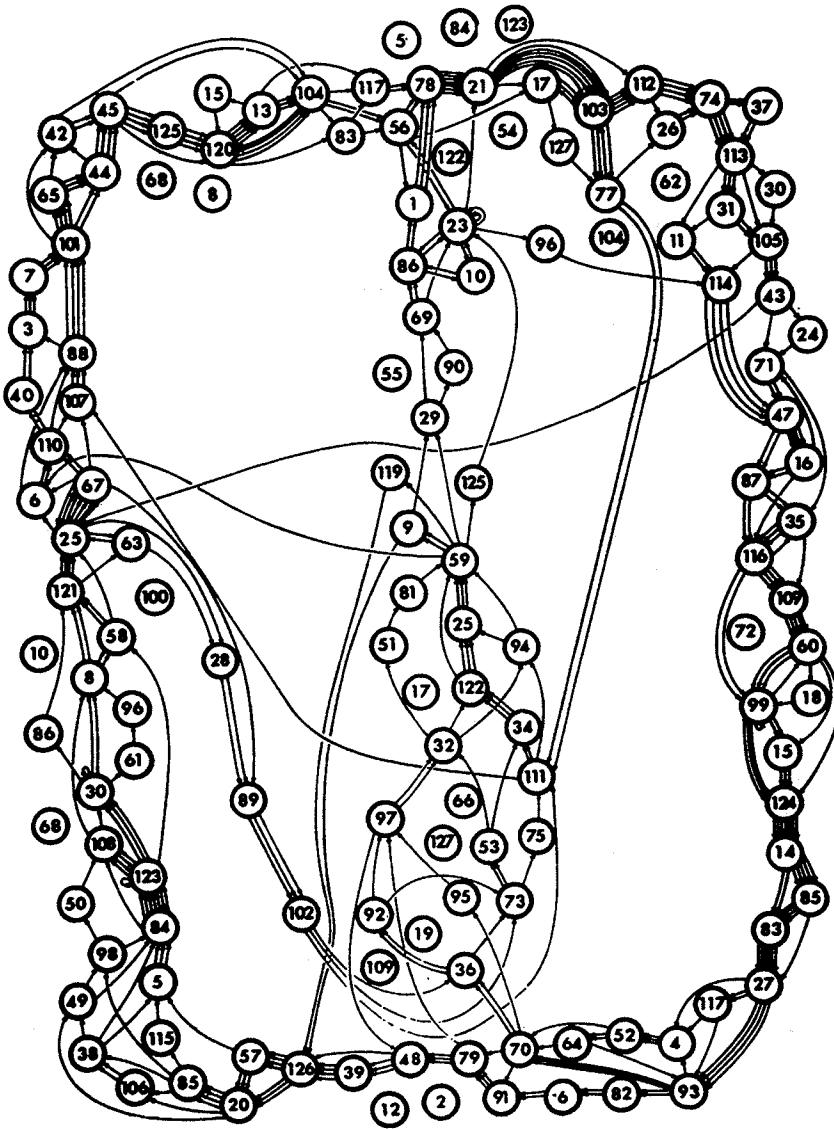
The songs of birds and whales may contain repeated sounds. The corrections for song duration and the time-bandwidth product only count repeated sounds once.

^aFrom Kroodsma 1982.

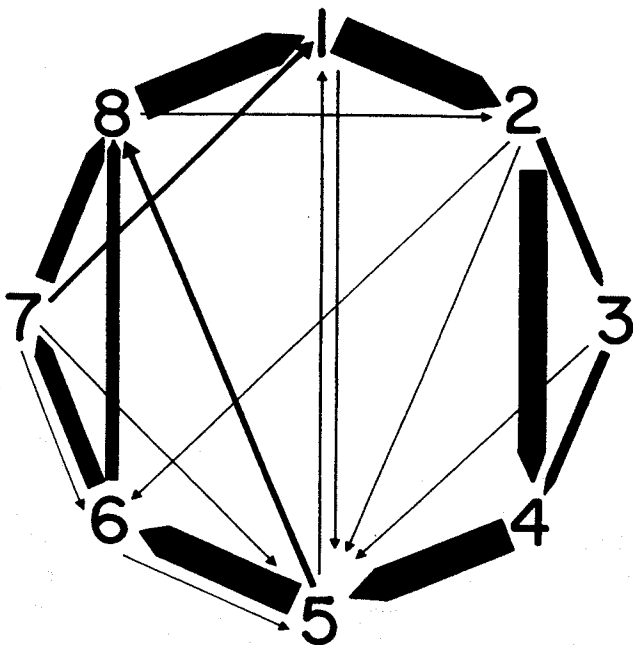
^bFrom Winn and Winn 1978; total number of different units and corrected durations depend strongly on subjective judgments of what constitutes the same unit. Here I have used Winn and Winn's (1978:113) definition and count of syllables that tends to lump rather than split. Splitters might double the number.

^cFrom Payne and Payne 1985.

Figure 7-8. Transitions between songs in the repertoire of a long-billed marsh wren (A) and between themes in the song of a humpback whale (B). Both songs in the wren and themes in the whale tend to cycle in a particular order, but the wren cycles among many more songs than the whale cycles through themes. (Long-billed marsh wren, Verner 1975; humpback whale, Payne et al. 1983.)



A



B

etition of sounds appear both in music and in nonsense rhymes, not to mention many non-human signals; therefore these features need not be associated with linguistic processing. The Sagan (1980) analogy to human oral verse seems to imply that humpbacks use their songs to pass down an oral tradition with semantic content. There is no evidence that specific sounds within the song carry any such information. The process of song change is so rapid and so complete that it seems unlikely that each variation in the song reflects variation in what the song communicates to other whales.

FUNCTIONS OF HUMPBACK SONG. So much for the acoustic structure of humpback song. Can we say anything about why humpbacks sing? Humpbacks sing primarily during the winter breeding season, and nearly all of the singing humpbacks whose sex has been determined have been males (Baker et al. 1990, Glockner 1983, Palsbøll et al. 1992). Most singing humpbacks are alone, but they are highly motivated to join other whales (Tyack 1981, 1982). Aggressive behavior is often observed after a singer joins other males. Singers are less likely to join a female, but behavior associated with sexual activity is observed when a singer joins a female (Tyack 1981, 1982).

Charles Darwin (1871) coined the term sexual selection for traits such as reproductive advertisement displays that are concerned with increasing mating success. There are two ways sexual selection can work. It can increase the ability of an animal to compete with a conspecific of the same sex for an opportunity to mate with a member of the opposite sex (intrasexual selection) or it can increase the likelihood that an animal will be chosen by a potential mate (intersexual selection). A variety of results have encouraged biologists to suggest that humpback song plays a role in male-male competition: (1) song appears to maintain distance between singers (Tyack 1981, Helweg et al. 1992); (2) no known females were attracted to playbacks of song (Tyack 1983, Mobley et al. 1988); and (3) aggressive interactions (particularly between singers and known males) are much more commonly observed than sexual interactions (particularly between singers and known females) (Tyack 1981, 1982).

These behavioral observations are clearly consistent with the idea that song plays a role in mediating male-male interactions. Some acoustic features of humpback song are also consistent with intrasexual selection. Baker and Cunningham (1985) suggest that intrasexual selection tends to select for rapid song change and convergence in the songs of different male songbirds. Both rapid change and convergence between individuals are striking features of humpback song. Catchpole (1982) suggests that a small repertoire of syllables and repetition of bird song types (or repetition of phrases for humpbacks) are also typical of a male repulsion role for song.

However, just because humpback song appears to be used in male-male interactions does not mean that it is not also used by females to select a mate. Both intra- and intersexual selection often operate at the same time on the same display (for a discussion regarding bird song, see Catchpole 1982). The use of songs to mediate spacing between singers says nothing about whether females are also an important audience. Females are often more discriminating than males in responding to an advertisement display such as song. None of the song playbacks conducted with humpback whales duplicated all of the potentially relevant features of song, and this may account for some of the lack of response of females to playbacks. Furthermore, as Catchpole (1982) points out for songbirds, aggressive male-male interactions are much more obvious in many species than male-female interactions. Just because the responses of male humpbacks to song are seen more frequently than those of females does not mean that the subtler responses of females to singers are not biologically significant. The critical question here is whether females choose a male for mating based on the song. Because copulation has never been observed in humpback whales, the answer must wait observation of mating or genetic analysis of paternity.

In the absence of direct data on the use of song in female choice, there may be some indirect evidence from the acoustic structure of the song. Intersexual selection selects for increased complexity, beauty, or costliness of the display. Humans, at least, judge humpback song to be complex and beautiful. Catchpole (1982) also suggests that continuous singing, lack of matched countersinging between males, and lack of a singing response to song playback are also diagnostic of a female attraction role for song. Humpback whales often sing continuously for hours; they do not respond to the song of another male by matching the song; neither do they respond to song playbacks by singing themselves. Humpback song clearly has attributes of both intra- and intersexual selection and is more complex than would be expected for a signal used only for male-male interactions (Helweg et al. 1992).

Two different approaches predominate for modeling how intersexual selection may lead to the evolution of elaborate displays. The basic question is why do females choose particular features of males who contribute nothing but their genes to the offspring? The two approaches are called (1) "Fisher's hypothesis," or "the runaway process" versus (2) "good genes," or "the handicap hypothesis." The runaway process emphasizes positive feedback between the female preference and elaboration of the male display (Fisher 1958, Lande and Arnold 1981). Let us start by assuming that females have developed a preference for a longer tail or more complex acoustic display. This could arise because (1) the dis-

play was correlated with some valuable inherited trait; (2) the display could make the male more easy to find; or (3) females could simply have some bias to respond preferentially to a particular stimulus. Whatever the origin of the preference, the tendency for females with stronger preferences to mate with males with exaggerated displays means that genes for the preference will covary with genes for the exaggerated display. If females on average select males with exaggerated displays, then the next generation will have more sons with exaggerated displays and more daughters with the preference. This creates a positive feedback loop, potentially producing a runaway process leading to extreme and exaggerated development of secondary sexual characters in males and preferences in females.

The good genes approach emphasizes that male displays signal the male's genetic quality in some trait that is beneficial independent of the female's mating preference itself. Zahavi (1975) pointed out that you can think of extravagant displays like the peacock's tail as costly and stressful handicaps. The stress of the handicap may reveal the male's condition, which might otherwise be concealed, or the extent of the handicap may express the male's condition. For a humpback example, Chu and Harcourt (1986) suggest that humpback females may select singing males based on how long they can stay underwater and hold their breath. There are clear acoustic cues when a singer surfaces, and most singers surface once per song cycle. Chu and Harcourt (1986) argue that breath-holding ability may be a good indicator of a male's stamina and physical condition. The problem with this argument is that song duration changes as humpbacks slowly evolve every feature of their song. In the beginning of one year, the song may average 7 min, whereas 4 months later it will have doubled in length (Payne et al. 1983). The next season, it may start long and decrease in length. Each individual whale is more likely to sing songs of the current length than what they were singing a few months earlier or later. If humpbacks were using song to advertise their breath-holding ability, then each individual would be expected either always to sing as long as he was able, or to sing longest at that part of the breeding season when his chances of mating were highest. This does not seem consistent with the observations that whales at any one time sing songs of similar duration and that the songs change over time with no repeated seasonal pattern.

Female humpbacks may, however, be able to use song to monitor the outcome of competitive interactions of many males scattered over many tens of square kilometers. Singing males are frequently interrupted by other males. The singer usually stops singing when joined, providing a clear acoustic indicator of the joining. Shorter song bouts and higher joining rates for singers were observed by Tyack

(1981) during the peak of ovulation as suggested by whaling data from other areas (Chittleborough 1958). During this period (in February) around 60% of the singers followed off Maui sang for less than 1 hr, whereas humpbacks often sang for many hours during other periods of the winter breeding season. Many of the interactions looked like one male displacing another, where either the singer or joiner would start singing relatively near where the two animals split, and the other whale would swim away. If most of the interactions that cause singers to stop involve this sort of male-male competition, and if successful males are interrupted less or for briefer periods of time, then a receptive female might be able to monitor many such interactions at a comfortable distance with minimal effort before she chooses a mate.

Even if female humpback whales use song to monitor interactions, this does not mean that they do not also have preferences for particular kinds of song. When I think admiringly of the incredible aesthetic design features of the peacock's tail or the humpback's song, I cannot help but believe that something more than handicaps are involved in the evolution of these traits. Many human artists are deeply moved by the artistic values of the ornaments and songs of non-human animals. As Darwin (1871) himself pointed out for other species, we clearly may have to thank the evolving aesthetic sensibilities of generations of female humpbacks for the musical features of the males' songs that have sold millions of recordings.

Reproductive Advertisement Displays in Other Marine Mammals

I have described humpback song in some detail because it is the best known of all advertisement displays in marine mammals. Yet songs are known from a variety of other marine mammals. Bowhead whales spend their winter breeding season in icy Arctic waters, where humans seldom venture. Their songs have been recorded in the spring as they migrate past Point Barrow, Alaska (Ljungblad et al. 1982). Bowhead songs are more simple than those of humpbacks, consisting of a few sounds that repeat in the same order for many song repetitions. As with humpback song, bowhead songs appear to change year after year. However, little is known about behavior concurrent with singing, and there are few reports of bowhead whales observed during their winter breeding season when they concentrate in the Bering Sea.

The long series of 20-Hz pulses produced by finback whales may also function as a reproductive advertisement display. The seasonal distribution of these 20-Hz series has been measured near Bermuda, and it matches the breeding season quite closely (Watkins et al. 1987). However, finback whales also appear to be more common in waters near the latitude of Bermuda during the winter breeding season.

Similar recordings in more polar waters will be required to test how frequently these whales produce 20-Hz series outside of the breeding season.

Some pinnipeds also repeat acoustically complex songs during the breeding season. Even casual listening in polar waters often reveals the strange songs of ice seals. Stirling (1973) sampled sounds of ringed seals (*Phoca hispida*) from winter to spring and found an increase in vocalizations correlated with increased agonistic behavior during the breeding season. The bearded seal (*Erignathus barbatus*) produces a downward-trending warbling song that sounds like an alien spaceship in some Grade B sci-fi movie (Cleator et al. 1989). The Alaskan Inuit call this seal the "singer" because part of the song can often be heard in air. The songs of bearded seals are heard frequently during the peak of the breeding season in May, but by July song is seldom heard around bearded seals. All 15 of the bearded seals collected after being identified as singers by Ray et al. (1969) were sexually mature adult males. Male walrus (*Odobenus rosmarus*) also perform ritualized visual and acoustic displays near herds of females during their breeding season (Fay et al. 1981, Sjare and Stirling 1993). Males inflate modified pharyngeal pouches to produce a metallic bell-like sound (Schevill et al. 1966). When walrus surface during these displays, they may make loud sounds in air, including knocks, whistles, and loud breaths. They then dive, producing distinctive sounds underwater, generally a series of sharp knocks followed by gong- or bell-like sounds. Usually several males attend each female herd, and it is not known whether females or other males are the most important audience for this display (Sjare and Stirling 1993).

Antarctic Weddell seals (*Leptonychotes weddellii*) also have extensive vocal repertoires, and males repeat underwater trills (rapid alternations of notes) during the breeding season. Males defend territories on traditional breeding colonies. These trills have been interpreted as territorial advertisement and defense calls (Thomas et al. 1983). Whether females may also use them in selecting a mate is unknown.

Correlations between Social Structure and Patterns of Acoustic Communication

Most communication signals evolve to solve specific problems in social behavior. In fact, communication and social behavior are just two different ways of expressing the same thing. This section traces correlations between the problems posed by the social lives of different species and the species' communication signals. Understanding the social functions of communication signals requires more detailed behavioral observations than are available for most marine mammal species. Some of the best-studied species include killer

whales (*Orcinus orca*), bottlenose dolphins, and sperm whales (*Physeter macrocephalus*).

CALLS THAT IDENTIFY STABLE GROUPS IN KILLER WHALES. The most stable groups known in any mammal are those found in fish-eating killer whales in the coastal waters of the Pacific Northwest. Associations between individual killer whales have been tracked since before 1970, giving more than 25 years of longitudinal data. The only way a killer whale group, called a pod, changes is by birth, death, or rare fissions of very large groups (Bigg et al. 1987). Fish-eating killer whales are most unusual among mammals in that neither sex disperses from its natal group. Killer whales produce a variety of sounds, including clicks used in echolocation, tonal whistles, and pulsed calls, some of which form repeated discrete calls and others that are highly variable (Ford 1989). The discrete calls predominate when killer whales are traveling or foraging. Whistles and more variable pulsed calls are more common in groups engaged in social interaction. The whistles and variable-pulsed calls are difficult to subdivide, but the discrete calls form easy-to-categorize call types.

Each pod of killer whales has a group-specific repertoire of discrete call types. This pod-specific repertoire is stable for many years (Ford 1991). Each individual whale within a pod is thought to produce the entire call repertoire of that pod. Analysis of variation in call use within a pod suggests that some calls may be more common in resting groups, others more common in active groups. However, each discrete call in the pod's repertoire can be heard regardless of what the pod is doing. Different pods may share some discrete calls, but none share the same entire call repertoire. The entire repertoire of a pod's discrete calls can thus be thought of as a group-specific vocal repertoire. Different pods may have ranges that overlap and pods may even associate together for hours or days before diverging. Individual pods have clearly defined subpods and matrilineal groups that seldom split up, but these subpods may separate and converge. These group-specific call repertoires in killer whales are thought to indicate pod affiliation, maintain pod cohesion, and to coordinate activities of pod members.

MOTHER-OFFSPRING RECOGNITION IN MARINE MAMMALS. Killer whales have unusually stable groups. Other marine mammals have more fluid groupings, but there may be strong bonds between individuals within these groups. The mother-young bond is one of the most fundamental in mammals.

All mammalian young are born dependent on the mother. Newborn mammals need to suckle frequently and, in many species, depend on the mother for thermoregu-

lation and protection from parasites and predators. Most mammals have a vocal system for regaining contact when mother and offspring are separated. These "isolation" or "distress" calls are produced by infants within days of birth and are particularly elicited by isolation. Most mammalian isolation calls are frequency-modulated tonal calls, are longer and louder than other infant calls, and become fixed in a stereotyped structure as the animal ages. Examples come from a variety of terrestrial taxa including primates (Newman 1985), felids (Buchwald and Shipley 1985), bats (Balcombe 1990), and ungulates (Nowak 1991). Once a mother and offspring have become separated, there is a risk that the mother might miss her own offspring and accept some other young animal as her own. Parents often devote considerable resources to their young, and this creates a risk that other animals might attempt to parasitize their parental care. These problems create a selective pressure for the evolution of mother-infant recognition mechanisms. In many of the species tested, mothers can recognize the calls of their young; in some, the young recognize similar calls from the mother. These infant isolation cries appear to represent a widespread and basic mammalian adaptation.

Colonially breeding seals often face difficult mother-young location and recognition problems. In many otariids, a mother leaves her young pup on land in a colony of hundreds to thousands of animals, feeds at sea for a day or more, and then must return to find and feed her pup. Among Galapagos fur seals (*Arctocephalus galapagoensis*) pups spend more time calling during their first day of life than later, and mothers learn to recognize the calls of their young within the first day of life (Trillmich 1981). Mothers give pup-contact calls as early as during birth. Later, mothers can signal with a pup-attraction call to a pup that is moving away. When a mother returns from feeding at sea, she comes up on the beach giving pup-attraction calls. Her own pup usually seems to recognize her call and approaches. If a pup approaches to suckle, the mother sniffs the pup for a final olfactory check. If it is not her offspring, she almost always rejects the pup, a rejection that can cause injury or occasionally death to the pup (Trillmich 1981). There is thus a strong incentive for both mother and pup to recognize each other correctly. Playback experiments of pup-attraction calls indicate that 10- to 12-day-old pups prefer their mother's call, and this recognition persists until they become independent at more than 2 years of age (Trillmich 1981). Other otariids, such as sea lions, show similar patterns of calling and recognition (Trillmich 1981, Schusterman et al. 1992).

Many phocid seals only suckle their young for a few weeks or less. They typically do not leave for long foraging trips but remain near the pup for the duration of suckling (see Costa and Williams, Chapter 5; Boyd, Lockyer, and

Marsh, Chapter 6; and Wells, Boness, and Rathbun, Chapter 8, this volume). However, the female does frequently enter the water in between nursing bouts. Although nursing females are less gregarious than otariids, the phocid mothers still need to find their own pups and prevent suckling from others. Land-breeding phocid seals use a combination of geographic, acoustic, and olfactory cues for mother-infant recognition. Location cues are important among gray seals (*Halichoerus grypus*). Fogden (1971) reports that the pup remains where it was last suckled. In between suckling bouts, a mother usually returns to the water. When she next hauls out, the mother returns to where she last suckled. This means that a female can often use location cues to help narrow down the number of pups that might be hers. Among phocid seals that breed colonially on land, mothers do recognize calls of their pups (elephant seals [*Mirounga* spp.], Petrinovich 1974; gray seals, Fogden 1971).

Mother-pup recognition is more difficult for ice-breeding seals because the topography of the ice frequently changes. Terhune et al. (1979) suggest that female harp seals (*Phoca groenlandica*) have so few landmarks on the ice that they approach pups in a random manner, and therefore, must remain close to their pup for the duration of suckling. In spite of the less predictable location cues on the ice, Terhune et al. (1979) suggest that harp seal mothers may not identify the calls of their pups, but rely on a combination of visual and olfactory cues at close range. During most mother-pup approaches, neither the mother nor the pup vocalized, but the mother usually sniffed a pup upon approach.

Comparisons of recognition mechanisms in related species allow testing of the hypothesis that the cost and reliability of recognition mechanisms scale to the risk of misallocation of parental care. As in the study of animal songs, some of the strongest data come from birds. For example, barn swallows (*Hirundo rustica*) raise their young apart from other broods; therefore, location is a good predictor of kinship throughout the period of parental care. Although barn swallow chicks make a begging call, parents do not distinguish between the calls of their own and unrelated chicks (Medvin and Beecher 1986). Young cliff swallows (*Petrochelidon pyrrhonota*), on the other hand, intermingle within a colony while still being fed by their parents. Cliff swallow parents can discriminate the begging calls of their own offspring from those of other young (Stoddard and Beecher 1983). Cliff swallows have evolved both a more distinctive begging call in the young and more rapid discrimination of begging calls by adults (Loesche et al. 1991). Similar results suggest that colonial birds switch from location cues to identifying their own offspring at the time when the young from different broods intermix (Beer 1970, Miller and Emlen 1975). The differences in recognition systems of phocid and otariid seals seem to fol-

low the predictions of this model. Mother–infant recognition systems in phocids do not seem to be as reliable as those of otariids (Reiter et al. 1978). Trillmich (1981) suggests that this difference may derive from the lower gregariousness, shorter duration of suckling, and increased predictability of location cues for phocid versus otariid seals.

The young of many dolphin and other odontocete species are born into groups comprised of many adult females with their young, and they rely on a mother–young bond that is even more prolonged than that of otariids. Many of these species have unusually extended parental care. For example, both sperm whales and pilot whales (*Globicephala macro-rhynchus*) suckle their young for up to 13 to 15 years (Best 1979, Kasuya and Marsh 1984). Bottlenose dolphin calves typically remain with their mothers for 3 to 6 years (Wells et al. 1987). These dolphin calves are precocious in locomotor skills and swim out of sight of the mother within the first few weeks of life (Smolker et al. 1993). Calves this young often associate with animals other than the mother during these separations. This combination of early calf mobility with prolonged dependence would appear to select for a mother–offspring recognition system in bottlenose dolphins. Unless otherwise noted, the unmodified terms “dolphin,” “mother,” and “calf” refer in the following section to the bottlenose dolphin.

Dolphin mothers and young use frequency-modulated tonal whistles as signals for individual recognition. Observations of captive dolphins suggest that whistles function to maintain contact between mothers and young (McBride and Kritzler 1951). When a dolphin mother and her young calf are forcibly separated in the wild, they whistle at high rates (Sayigh et al. 1990); during voluntary separations, it is usually the calf that whistles to signal a reunion (Smolker et al. 1993). Caldwell and Caldwell (1965) demonstrated that each dolphin within a captive group produced an individually distinctive whistle or signature whistle. The Caldwells postulated that signature whistles function to broadcast individual identity. Experimental playbacks have demonstrated that mothers and offspring respond preferentially to each others’ signature whistles even after calves become independent from their mothers (Sayigh et al. 1999).

In spite of the apparent premium on early development of mother–young recognition, there is great variability in the timing of signature whistle development in bottlenose dolphins. Caldwell and Caldwell (1979) studied whistle development in 14 calves born in captivity. They reported that calves whistle within days of birth, but that these early whistles are unstereotyped. Most of the calves in their study developed a stereotyped signature whistle by 1 to 3 months of age, but one calf had not yet developed a signature whistle when it was last recorded at 17 months of age. Preliminary longitu-

dinal studies of whistle development in four free-ranging dolphin calves have also been conducted in waters near Sarasota, Florida, by Sayigh (1992). These results also indicate considerable individual variability in the timing of signature whistle development. Two calves developed signature whistles by 1 to 2 months of age; the third calf developed a signature whistle between 2 and 3.5 months of age, and the last calf did not develop a signature whistle until almost 2 years of age.

To understand mother–offspring recognition, it is more important to investigate when a mother (or calf) is first capable of discriminating her own offspring (or mother) from others, than to document changes in the signals. Adult dolphins have excellent auditory perception, and if a mother spends all her time near her calf, she may learn to discriminate a calf’s unstereotyped whistles well before the calf develops a signature whistle. On the other hand, it may take an animal some time to learn to discriminate a signature signal that is already stereotyped. This illustrates a general point in communication research. Although the signal is the most obvious part of the communication process, how the recipient perceives and responds to the signal is just as important.

INDIVIDUAL RECOGNITION IN BOTTLENOSE DOLPHINS. Dolphins do not just use whistles for mother–infant recognition. Calves show no reduction in whistling as they wean and separate from their mother. Whereas adult males are not thought to provide any parental care, they are not known to whistle less than adult females. Bottlenose dolphins may take up to 2 years to develop an individually distinctive signature whistle, but once a signature whistle is developed, it remains stable for the rest of the animal’s lifetime (Fig. 7-9; Caldwell et al. 1990; Sayigh et al. 1990, 1995). These results suggest that signature whistles may also function for individual recognition in contexts other than mother–offspring recognition.

Dolphins also rely on individual-specific social relationships throughout their lifespan. Bottlenose dolphins do not have stable groups as in resident killer whales, but rather live in a fission–fusion society in which group composition changes from hour-to-hour or even minute-by-minute (see Wells, Boness, and Rathbun, Chapter 8, this volume). Although dolphin groups are remarkably fluid, bonds between particular individuals within the groups may be very strong. Some wild individual bottlenose dolphins show stable patterns of association, even within the otherwise fluid patterns of grouping (Wells et al. 1987). As discussed, young dolphins in the wild often remain with their mothers for 3 to 6 years. After they leave their mothers, dolphins may both maintain close ties with members of their natal band as well as join with new individuals for periods of years. For example, some

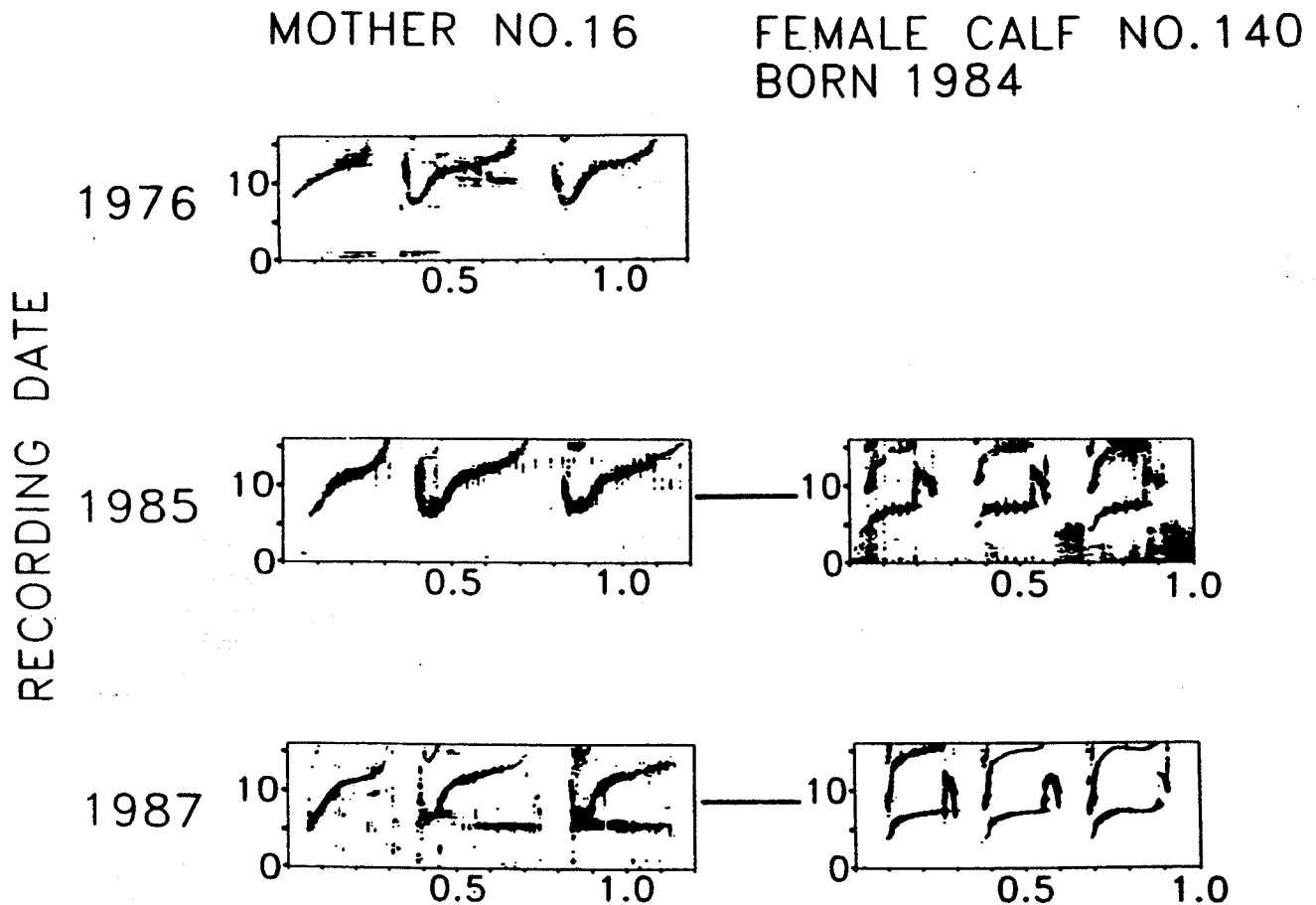


Figure 7-9. Spectrograms of signature whistles from one wild adult female bottlenose dolphin recorded over a period of 11 years and of her daughter at 1 and 3 years of age. Note the stability of both signature whistles. The x-axis indicates time in seconds and the y-axis indicates frequency in kHz. (From Fig. 7-2, Sayigh et al. 1990.)

pairs of adult males are almost always sighted together, even in different groups, for many years (Wells et al. 1987, Connor et al. 1992). Primiparous females may associate with their own mothers during the first few months of life of their own calves (Caldwell and Caldwell 1966). Figure 7-10 shows month-by-month changes in associations between individual wild dolphins sighted off a beach in Patagonia over a year and a half by Würsig (1978). Each row in this figure reflects sightings of one individual. Notice how some individuals always appeared together or left together, whereas other individuals started associating during the observation period. This combination of highly structured patterns of association between individuals, coupled with occasionally fluid patterns of social grouping, argues that individual-specific social relationships are an important element of bottlenose dolphin societies (Tyack 1986a).

Five of the dolphins shown in Figure 7-10 were resighted together 300 km away. Dolphins may range tens of kilometers a day. While swimming in turbid coastal waters, they often disperse out of sight of one another. It is difficult to

imagine how dolphins that share a strong bond could remain together without an individually distinctive acoustic signal such as the signature whistle. Initial studies of signature whistles in adult dolphins, primarily isolated animals, suggested that more than 90% of an individual's whistle repertoire was made up of its signature whistle (for review, see Caldwell et al. 1990). However, the signature whistle hypothesis is not limited to the suggestion that dolphins just monotonously repeat the identical call to maintain contact, like a radio call sign with no other message. The acoustic features of the signature whistle vary as a function of behavioral context (Caldwell et al. 1990, Janik et al. 1994). Even after dolphins have developed the signature whistle, they also steadily increase their production of a repertoire of whistles that differ from the signature whistle (Caldwell et al. 1990).

When dolphins interact, they not only produce their own signature whistles but may also imitate the signature whistles of other individuals with whom they share strong bonds. In one study of two captive adult dolphins, Tyack (1986b) found that each imitated the signature whistle of the other at

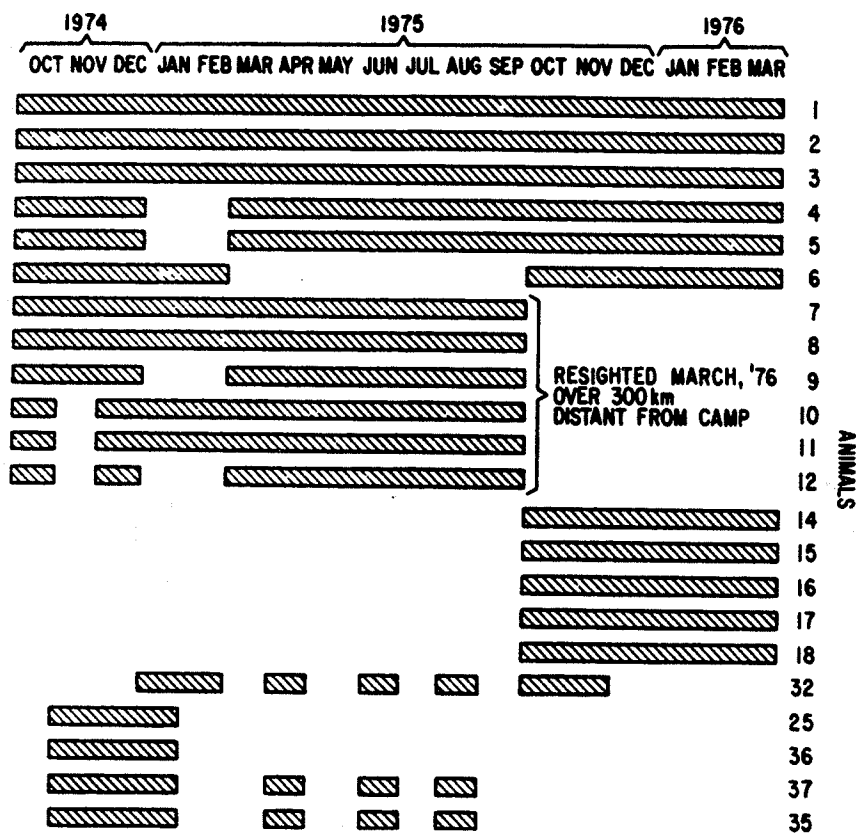


Figure 7-10. Monthly sighting patterns of individual bottlenose dolphins sighted off a beach in Patagonia. Each row represents an individual dolphin identified by natural markings on the dorsal fin. When a month is marked with a cross-hatched bar, it indicates that the individual was sighted from the beach during that month. (From Würsig 1978.)

rates of about 25% (i.e., 25% of all occurrences of each signature whistle were imitations). Rates of signature whistle imitation were near 1% between captive dolphins that were in separate pools but that could hear one another (Burdin et al. 1975, Gish 1979).

Imitation of signature whistles has also been observed between wild dolphins that share strong social bonds. For example, Figure 7-11 illustrates signature whistles of each member of a pair of males sighted together 75% of the time in Sarasota, Florida, along with imitations of the partner's whistle. Imitation of signature whistles has also been observed between wild dolphins that share strong social bonds. For example, Figure 11 illustrates signature whistles of each member of a pair of males sighted together 75% of the time in Sarasota, Florida, along with imitations of the partner's whistle. In a population of wild bottlenose dolphins in the Moray Firth, Scotland, Janik (1997) found whistle matching in 17% of all whistle interactions. An individual-specific response to imitation of signature whistles is illustrated in a case from the Sarasota population, where one adult female, Nicklo, imitated the signature whistle of an older female, Granny (Tyack 1993). Figure 7-12 shows the signature whistles of both dolphins, along with an imitation of Granny's whistle by Nicklo. The whistle imitation was recorded during a 28-min interval when Nicklo was held in a raft. Five other dolphins remained in the net corral: Granny,

Nicklo's 3-year-old calf, another adult female with a 3-year-old, and an 11-year-old male. Nicklo started imitating Granny's whistle about halfway through her time in the raft. Figure 7-13 shows an example where a whistle by Granny (top) was synchronized within 3 sec of an imitation of Granny's whistle by Nicklo (bottom). Statistical analyses of the correlation of synchronous whistles showed that the only time whistles were synchronized occurred when Nicklo started to imitate Granny's whistle, and the only correlation was between Granny and Nicklo's imitation of Granny. Even Nicklo's own calf did not produce whistles synchronized to those of Nicklo. This suggests that one dolphin may imitate the signature whistle of another one to initiate an interaction with that particular individual. However, these animals were not able to interact directly, and more detailed study is required to determine whether dolphins imitate each other's signature whistles to call another individual.

MULTIPLE FUNCTIONS FOR THE CLICKS OF SPERM WHALES. Sperm whales have not been demonstrated to produce any vocalizations other than clicks. Although these clicks sound very simple to our ears compared to humpback song, sperm whales live in societies that would seem to require diverse kinds of communication. Sperm whales are born in relatively stable units of related females, but most individuals have varying degrees of association

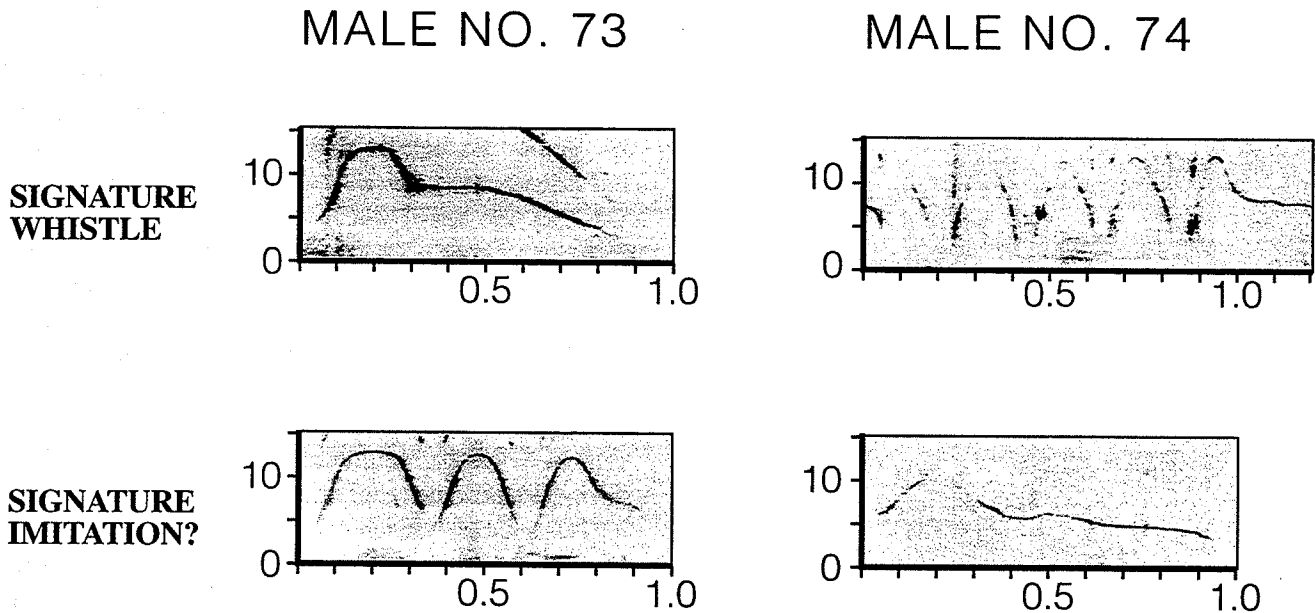


Figure 7-11. Spectrograms of signature whistles produced by two adult male dolphins from the wild population near Sarasota, Florida. These two animals were usually sighted together. Each male also repeated whistles that were similar to the signature of the partner, and these are interpreted as imitations of the partner's signature whistle. The x-axis indicates time in seconds and the y-axis indicates frequency in kHz. (From Fig. 4.16, Sayigh 1992.)

throughout their lifespan, and many rely on bonds with particular animals within their groups (Best 1979). For example, sperm whales appear to have social defenses against predators. Humans are among the most dangerous predators of sperm whales, and there are many reports from whalers of sperm whales coming to the aid of a harpooned comrade (e.g., Nishiwaki 1962, Caldwell and Caldwell 1966). Sperm whales also use a social defense from a killer whale attack (Arnbom et al. 1987). Unlike fish-eating killer whales, male sperm whales leave their natal group and may join mixed-sex juvenile groups or all-male groups as they mature. As subadult male sperm whales grow, they tend to be found in smaller groups of larger whales, until they finally become mostly solitary when they are sexually mature at about 20 to 25 years of age. During the breeding season these sexually mature males swim among the groups of adult females with which they mate. Stable units of related females tend to number about 10 whales, but two different female units often associate for about 10 days at a time (Whitehead and Kahn 1992). Sperm whales may rely on the stable units for protection of calves, whereas these stable units may join together in more fluid groups for benefits from socially coordinated feeding (Whitehead 1996).

Sperm whales feed on squid at depths of 400 to 600 m during dives that typically last 40 to 50 min (Papastavrou et al. 1989). Feeding and diving sperm whales typically produce long series of clicks at regular intervals of roughly 1 to 2/sec

(Worthington and Schevill 1957). Echolocation has not been tested experimentally because sperm whales have never been maintained for long in captivity. Most researchers suggest that these regular clicks are used for echolocation, and also perhaps within a group to keep contact with one another while foraging. During the breeding season, large male sperm whales make especially loud and resonant clicks that sound to my ear like a firecracker exploding inside a metal can. Weilgart and Whitehead (1988) suggest that these resonant clicks may function as a threat display when males compete to accompany a breeding group of females. For example, a male may produce loud clicks when approaching a female group. If a male is already accompanying the group, he might click back. If some feature of these clicks, such as loudness or low frequencies, correlates with a male's competitive ability, then this information may help females to assess the male at a distance and may help a male to assess whether to challenge the other male or not. (Low frequency may correlate with size of the sound-producing organ, as in the musical example of the stringed instrument mentioned in the introductory section.) This dynamic would select for each male making as extreme a version of the display as possible. Figure 7-14 illustrates one of these loud clicks, showing how much longer the duration is than the regular clicks. A bottom echo from the click is also visible on the far right of the figure. If the bottom echo is so obvious to a hydrophone at the sea surface, then it is likely that a sperm whale diving

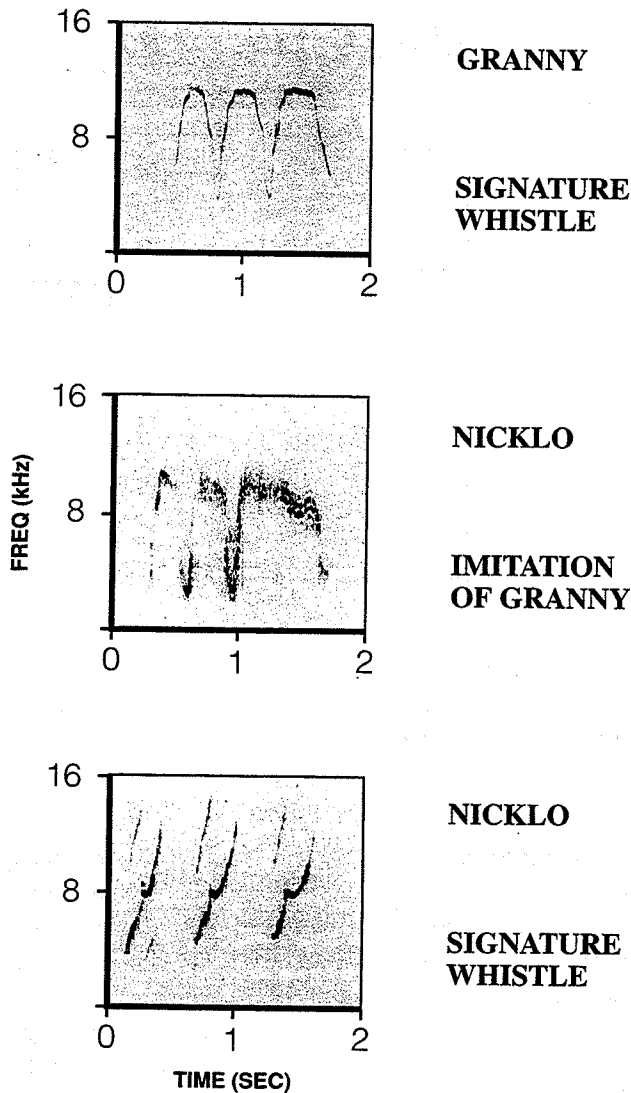


Figure 7-12. Spectrograms of signature whistles produced by two adult female dolphins from the wild population near Sarasota, Florida. The top spectrogram shows the signature whistle of Granny. The bottom spectrogram shows the signature whistle of Nicklo. The middle spectrogram shows an imitation of Granny's whistle produced by Nicklo.

near the bottom may be able to hear similar echoes from fainter regular clicks. Sperm whales dive at rates of 1 to 4 m/sec (Watkins et al. 1993). They have enormous momentum because they weigh up to 30 to 40 metric tons. It would take a diving whale some time to slow its descent. A depth-sounding sonar would be of obvious utility for early warning of the approaching sea floor for an animal that takes some time to slow its dive.

Sperm whales spend most of their time diving, but often in the late afternoon they spend a few hours at the surface, resting and socializing (Whitehead and Weilgart 1991). Especially when they are socializing, sperm whales also pro-

duce distinctive rhythmic patterns of clicks, called codas, often as exchanges between individual whales (Watkins and Schevill 1977). The limited data currently available on codas suggest a variety of potential functions, including individual, group, and regional identification. Although Watkins and Schevill (1977) described codas as individually distinctive, they also described an exchange in which each whale matched the coda of the other whale, an exchange surprisingly reminiscent of imitation of individually distinctive signature whistles in dolphins. Moore et al. (1993) described two shared coda patterns that comprised more than 50% of the codas from many individual whales within many different groups recorded over a large part of the southeast Caribbean. Weilgart and Whitehead (1993) described different shared coda patterns for sperm whales off the Galapagos, and Weilgart and Whitehead (1997) described geographical variation in the proportional usage of different codas. More work is needed to track coda usage of individual sperm whales, within stable units, and over large areas, but the current evidence suggests possible variety in usage for individual and regional identification that is consistent with the variety of problems posed by sperm whale societies.

In summary, there is a clear correlation between the communication patterns of marine mammals and their social organizations. Baleen whales and pinnipeds with large, somewhat anonymous breeding aggregations use reproductive advertisement displays to mediate male-male and male-female interactions on the breeding grounds. Killer whales with highly stable groups produce group-specific repertoires of stereotyped calls. Seals and dolphins with strong individual-specific bonds use a variety of different vocalizations for individual recognition. Sperm whales appear to use deceptively simple clicks to produce a diverse set of signals consistent with their diverse social groupings.

Cognition

As mentioned in the introductory section, cognition is usually defined as information processing within an animal. This is often contrasted with communication, which involves information transfer from one animal to another. The study of animal communication can start with measuring the signals exchanged between animals, but how can one study the internal signals associated with information processing within an animal? The direct neurophysiological approach involves invasive measurement of neural activity, but there has been very little neurobiological research conducted with marine mammals, in part because marine mammals are legally protected from invasive research. Three indirect approaches to studying animal cognition are discussed in this section. The first is "animal language" studies,

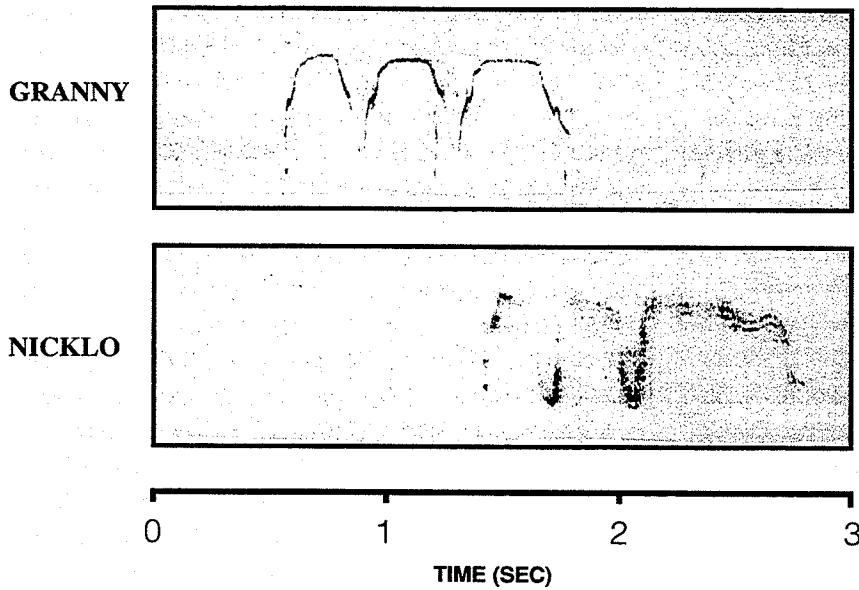


Figure 7-13. Spectrograms of Granny's signature whistle and Nicklo's imitation of Granny's signature whistle produced in the same 3-sec time window.

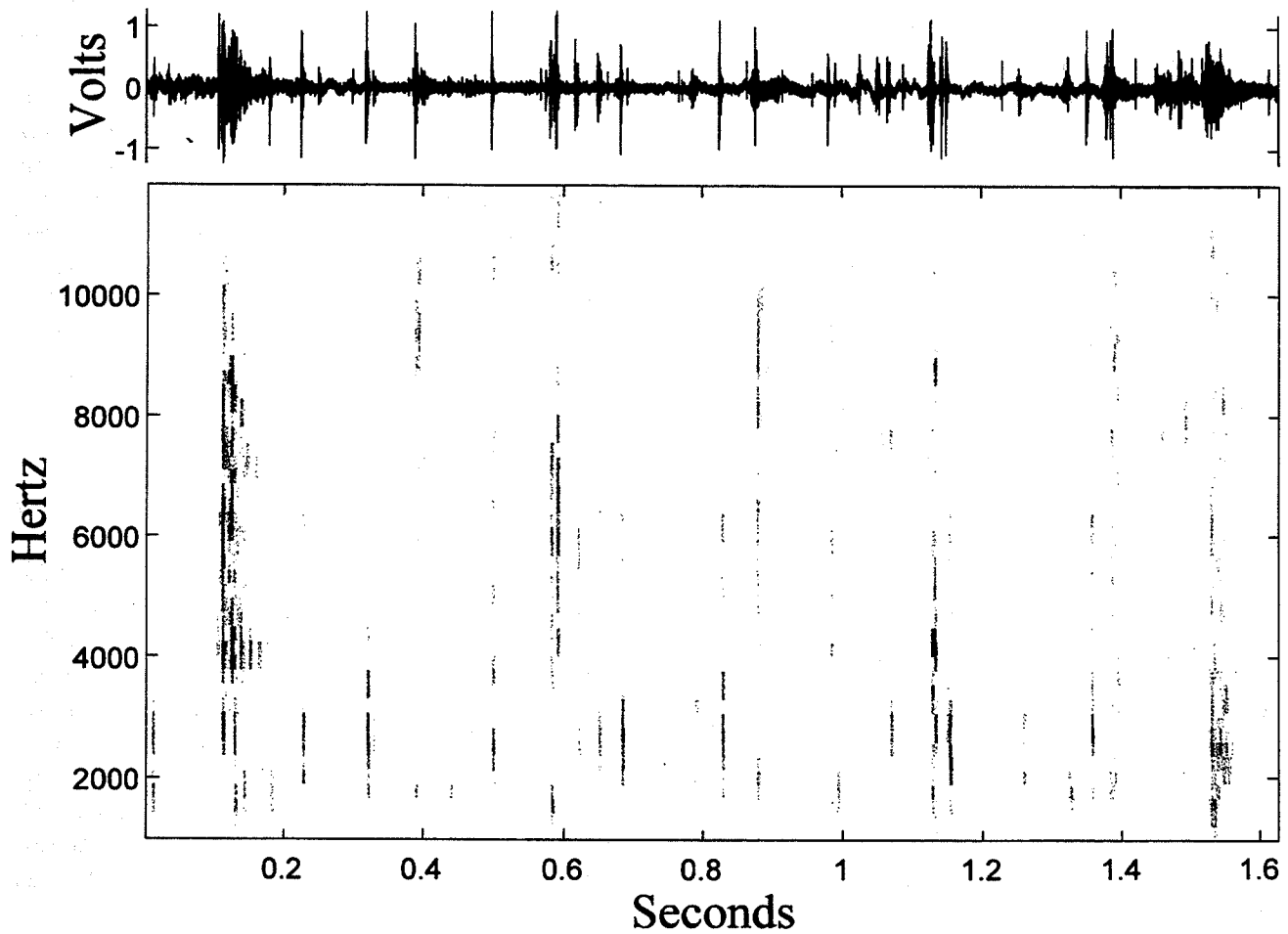


Figure 7-14. Spectrogram and waveform of a loud resonant click on the left of the spectrogram at 0.1–0.2 sec from a male sperm whale. Regular clicks typically last 2–30 msec, and many regular clicks show on the spectrogram as thin vertical lines from 0.3 to 1.4 sec. An echo of the loud click reflected from the sea floor is visible on the right side of the figure at 1.5–1.6 sec.

in which researchers train animals to use an artificial system of communication with some features of human language. The second reviews the importance of learning and imitation in the natural communication systems of marine mammals. The third reviews the question of why some marine mammals have such large brains.

Animal "Language" Studies

Language and Thought

How do humans keep one another informed of what they are thinking? We can use our own form of communication, language, to "share thoughts." Even when we are thinking of something nonlinguistic, say a mental image, we can report on the image using language. Language is not only used for communication. There are modes of thought that seem to be intimately related to language. When we are thinking about something, we often seem to be forming words and sentences within our heads, although we are completely silent. This suggests that the process of language development may influence how we think. Both the use of language to report thoughts and the potential for language to shape thinking have led people to search for an animal "language" to study animal cognition.

For almost a century, humans have attempted to train non-human animals to communicate with people using artificial human-made systems of communication in what are called animal language experiments. These experiments have attempted to find ways to allow animals to report on their thinking, to test the language competencies of animals, and to test whether language training might influence the abilities of animals to solve problems. The early animal language studies adopted the following approach: "We know the conditions under which human infants learn language. If we can just put a smart large-brained animal in a similar setting, perhaps it can also learn to speak." This approach assumes that language acquisition requires only very general intelligence and learning skills. Several psychologists have set out to test these ideas by raising baby chimpanzees in their own homes. A baby chimp named Gua was raised along with the infant son of a couple named Kellogg (Kellogg and Kellogg 1933). Although the boy acquired language at the usual rate, the chimp never did. Another chimp named Viki, raised by the Hayes family, learned to produce crude versions of the words "mama," "papa," "cup," and "up," but never progressed beyond this rudimentary stage (Hayes 1951).

Chimpanzees seem to have problems producing the sounds characteristic of human speech. Chimps are one of our closest evolutionary relatives, but not even they have the

same vocal tract as we do, and they appear to be physically unable to produce some speech sounds (Lieberman 1984). There is also a large body of evidence suggesting that modification of vocalizations is very difficult for non-human terrestrial mammals, including our closest primate relatives (Newman and Symmes 1982, Janik and Slater 1997). If chimps cannot make speech sounds, then training them to speak may be no more promising than training them to flap their arms to fly. Do chimps have a basic cognitive problem with learning language or is it restricted to the vocal channel? These were the questions that Beatrice and Allen Gardner considered as they thought about raising a chimp. The Gardners knew that chimps were reputed to be skilled at imitating gestures so they decided to teach a gestural language used by humans with hearing impairment (Gardner and Gardner 1969). This was much more successful than the earlier attempts with speech, and there have been many similar studies training great apes with gestural languages. Chimpanzees, gorillas, and orangutans have all been trained with gestural languages.

Marine mammals have also been trained in animal language experiments. In the late 1950s, researcher John Lilly noticed that captive dolphins often emit sounds in air with the blowhole open. Under natural conditions, dolphins usually vocalize underwater with the blowhole closed, and the sounds are only faintly audible in air. Lilly became convinced that dolphins could mimic the speech sounds of talking humans (Lilly 1962). When he played the tapes of these purported imitations, few listeners were convinced. Lilly spent years attempting to shape the vocal responses of dolphins to human speech using both food and social rewards, but the imitations did not become more convincing to a human audience. In his own words, "Obviously the pronunciation of *Tursiops* is not very good" (Lilly 1975:346). The best he could do was document that dolphins match the number and duration of staccato bursts of speechlike sounds (Lilly 1965).

Frustrated at the lack of progress, Lilly went to considerable expense to design and build a facility in which humans and dolphins could live together for extended periods. A volunteer lived for 2.5 months with a subadult male dolphin in the specially built facility (Lilly 1967). In his popular writing, Lilly put as positive a spin on this project as he could, but it is difficult to identify positive results of this effort. At least the Hayes' were able to convince their audience that Viki did produce crude versions of four words.

In many ways Lilly's enterprise was even more naive than the similar attempts to raise infant chimps in the home. Among humans, it is much easier for young children to learn language than for adolescents. Even then, it takes years rather than weeks of exposure. For these reasons, the chimp experiments involved psychologists taking infant chimps in

their homes and raising them for periods of years. In contrast, Lilly's volunteer spent a much shorter time living with a subadult dolphin. This shorter duration of 2.5 months with an older animal probably made it less likely that the exposure to humans would influence vocal development in the dolphin, but even this shorter duration was difficult for the volunteer. I am sure that the humans had their own difficulties living with a chimp, but imagine what it must be like for a volunteer to live in pools flooded with two feet of water all the time. For example, one "lesson" learned during this experiment was "Being able to sleep in a dry, comfortable bed each night would eliminate much of the discomfort in the program" (Lilly 1975:198). It obviously was not possible to create an environment where dolphins and humans lived together and both were equally at home.

Although Lilly's own research never yielded results anywhere near as promising as those of the gestural languages with apes, he published very popular books claiming that dolphins could talk. He made a series of unsubstantiated claims that strayed far from his own research. For example, "The sperm whale probably has 'religious' ambitions and successes quite beyond anything we know" (Lilly 1975:219). At the same time as these books stimulated popular interest, their unsubstantiated claims scared several generations of behavioral scientists away from a potentially fascinating group of mammals for comparative study.

There has also been controversy regarding the question: How languagelike is the performance of apes trained to use gestures? Some investigators report in glowing linguistic terms the production of sentences, the invention of novel compound words or even poetry in their charges (e.g., Patterson and Linden 1981). Other investigators maintain a more skeptical stance and question the data or interpretations of the claims for languagelike performance.

There have been difficulties interpreting studies in which animals are exposed to language as informally as human infants are. The flexibility and lack of control over the training have led critics to question whether the animals spontaneously generate meaningful sequences to which they had not been exposed (e.g., Terrace et al. 1979). Other investigators have responded to these criticisms by using more formal training with experimental controls to teach animals artificial languages. While these controversies were underway, Louis Herman of the University of Hawaii initiated animal language comprehension studies with bottlenose dolphins. Unlike the ape studies, the dolphins were trained to respond to commands but not to use these "commands" as communicative acts of their own. In these studies, Herman (1980, 1986) and Herman et al. (1984) trained dolphins to associate either objects or actions with human-made sounds or gestures using standard conditioning. Figure 7-15 shows some of the acoustic and gestural signals associated with the ob-

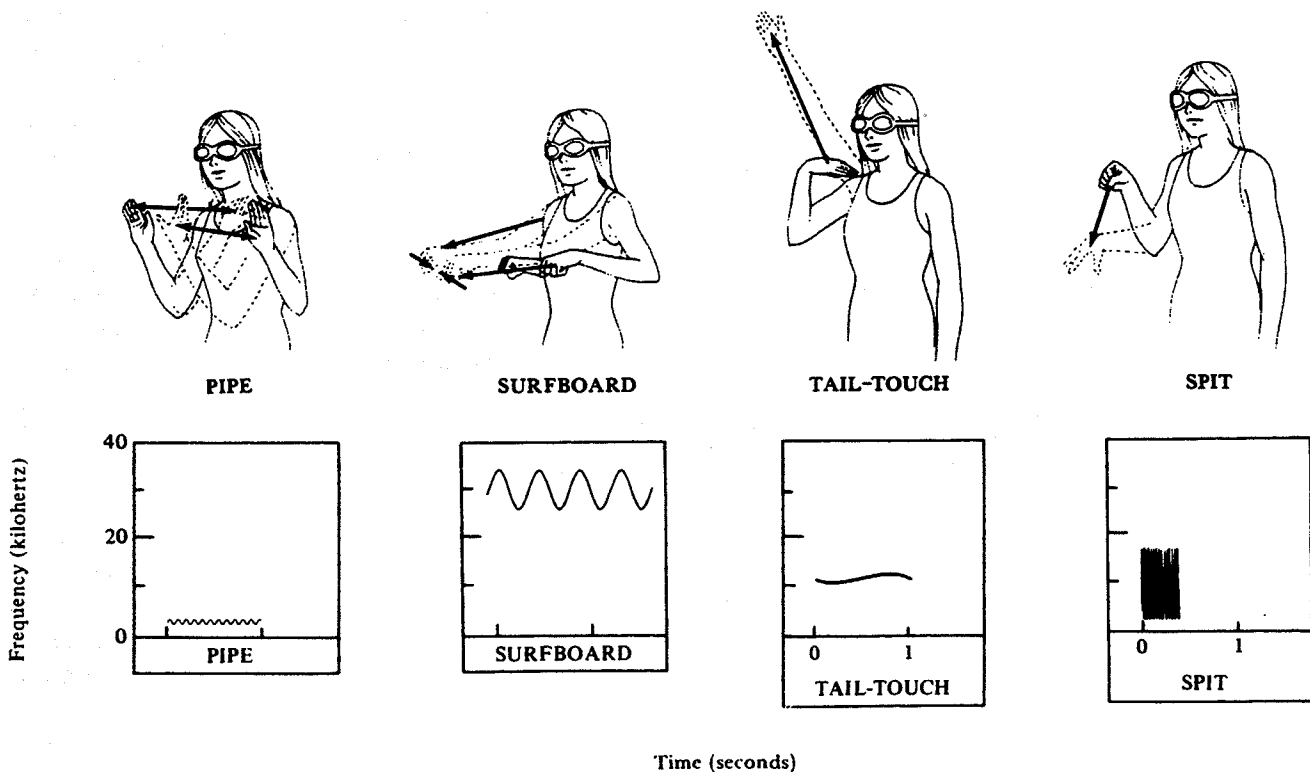


Figure 7-15. Line drawings of acoustic and gestural cues used by Herman's laboratory to train dolphins. (From Herman et al. 1984.)

jects *surfboard* and *pipe* and the actions *touch-with-tail* and *spit*. Herman started this training by presenting a cue when only one object was present. The dolphin would get a fish for touching the object with the tip of her jaw. Then two objects would be introduced, and the dolphin was only rewarded for touching the cued object. New actions were trained using a technique called "shaping." For example, dolphins were trained to put an object in the mouth by presenting the object along with a fish when the *mouth* cue was presented. The dolphin would open her mouth for the fish, and the trainer would put both the fish and the object in the mouth. In later sessions, the trainer would offer the object first and delay giving fish longer and longer. Ultimately, when the dolphin was shown the *mouth* cue, she would hold the requested object in her mouth in expectation of later reinforcement with the fish. Herman et al. (1989) report that dolphins perform with equal success to visual or auditory commands.

Although these experiments are called animal "language" experiments, it is difficult to compare the performance of the animals to the human use of language. One approach to making these comparisons more meaningful is to discuss specific features of language. Two of the most important features of human language are syntax and reference. Human languages are made up of words that can refer to objects, actions, almost anything. These words are structured into meaningful sentences using grammar or syntax. What do animal language studies tell us about syntactic or referential abilities of animals?

Syntax

Most commercial animal training involves training an animal to perform a complex series of behaviors in response to one simple command, but Herman trained the reverse, having animals make a relatively simple response to a complex series of action or object commands. This allowed Herman to study how well dolphins could generalize rules about command sequences designed with an artificial syntax. He trained one dolphin to interpret the string of commands OBJECT1-TAKE-OBJECT2 as if it meant "take object 1 to object 2." The other of his two dolphins was trained to interpret the string of commands OBJECT2-OBJECT1-TAKE as if it meant "take object 1 to object 2," reversing the order of cues compared with the requested actions. The first dolphin could have simply learned to go to objects and perform actions in the same sequence as the commands, but this was not possible for the second dolphin. After extensively training the dolphins with about half the objects that had been associated with cues, Herman et al. (1984) tested how the dolphins would interpret the same sequence involving new objects. For example, the dolphin might be trained on "take

the Frisbee to the basket" and might then be asked for the first time "take the pipe to the surfboard." Only once in these tests did one of the dolphins reverse the requested order, taking object 2 to object 1. Because they had never been exposed to the particular three-command sequences used in the tests, the dolphins must have learned rules for interpreting the order of commands. This performance appears similar to the way English speakers might use word order to understand a sentence.

Dolphins are not the only marine mammal to have been trained in an artificial language. Schusterman and Krieger (1984) replicated many aspects of Herman's results using California sea lions (*Zalophus californianus*) instead of dolphins. Two sea lions learned 16 to 20 cues and also learned to interpret sequences of commands. The sequences of commands used with the sea lions took forms like modifier-object-action. For example, when given the sequence white pipe-flipper-touch, the sea lion was rewarded if it touched the white pipe with its flipper.

Although they used similar training paradigms, Herman and Schusterman have differing interpretations of their experiments. Herman tends to have a more linguistic interpretation, whereas Schusterman doubts that this is appropriate. Herman et al. (1984) and Herman (1986, 1989) describe their three-command sequences as sentences, and they describe the positions within these sentences as grammatical categories. OBJECT1 is defined as a direct object, OBJECT2 as an indirect object, and TAKE as a verb. Schusterman and Gisiner (1986, 1988, 1989), on the other hand, argue that it is inappropriate to describe these experiments in linguistic terms. They argue that although one can train an animal to associate an action with a command, this is not enough to justify calling the action command a verb.

What exactly does it mean to argue that the animals understand commands as grammatical categories? Many modern linguists emphasize that human infants do not seem to be exhaustively trained to use language. Given the enormous diversity of speech environments to which different children are exposed, it is amazing that children exposed to a language come up with such similar rules to generate and understand sentences. Furthermore, a child mastering the past tense, may say "runned" instead of "ran," applying a rule to generate a word the child never heard. Pinker (1989, 1994) argues that this ability of children to create more structure than is present in what they hear provides evidence that language acquisition in humans involves specific innate learning mechanisms preprogrammed to interpret grammar correctly. Animals that do not have the same innate predispositions may only be able to acquire languagelike performance through extensive training. Many linguists would agree

with Schusterman that grammatical categories only make sense as part of a much richer syntactic structure, developed with much less formal training.

Reference

When humans name something with a word, they understand the word to act as a symbol for the thing that has just been named. But what about animals trained to associate a cue with an object? Does the animal understand that the cue refers to the object, or has it simply learned that it will be rewarded if it performs a response when shown a stimulus?

Animals do not need language training to learn associations between a cue and a response. For example, pigeons can be trained to press a red button if shown one object, say a square, and a green button if shown a circle (Carter and Eckerman 1975). This has been called symbolic matching, but does the pigeon think of the red button as a symbol for square, or has it just been trained to do a clever trick for food? Does Herman's dolphin think of a sideways hand-motion as a name for pipe? How can we discriminate the simple conditioning from real understanding of reference?

If an animal can use a signal as a symbol for an object, then it must be able to use the symbol more flexibly than the specific context in which it was trained. All the pigeon trained in symbolic matching has to do to perform correctly is to learn one simple and specific rule. When the pigeon is in a training box and is shown a square, it has to peck the red button to get food. Language-trained dolphins and sea lions were asked to be much more flexible in their responses to symbols. For example, when given a symbol for an object that was not present, the animal clearly acted as if it had a search image for the requested object. If asked to fetch a pipe, when none was present, the animal would search the pool for much longer than if a pipe had been in the pool. The sea lions would often balk at performing a requested action if the requested object was not there, and the dolphins were trained to press a special paddle if a requested object was not in the pool. These animals also had a relatively abstract understanding of requested actions. One of the sea lions was only trained in the water to touch objects with its tail. When for the first time it was asked to tail touch on land, it did so, although the motor pattern for the action was very different for walking than swimming.

To use a signal as a symbol for an object, an animal must also be able to associate properties of the object with the symbol. For example, if you are asked what color a banana is, the word banana allows you to remember that the object is yellow, although there is nothing yellow about the word banana. Some critics of ape language research have questioned whether chimps use signs as symbols or just pro-

duce a sign to get food when they see an object. Savage-Rumbaugh (1986) has pursued these questions about referential communication in her work with chimpanzees. She points out that referential communication depends critically on how chimps are trained. Three chimps in her laboratory were trained to use buttons on a keyboard to request or to label foods and objects such as tools. However, two of the chimps, Sherman and Austin, were trained specifically in skills related to symbolic usage of the buttons, whereas the other one, Lana, had been trained for other purposes such as interpreting strings of button pushes. Savage-Rumbaugh et al. (1980) designed an experiment to test whether these different training histories influenced the ability of each chimp to associate the properties of an object with its symbol. All three of the chimps were able to sort foods and tools into two bins. Therefore, they had clearly formed concepts of the categories of food and tool. Savage-Rumbaugh then introduced two new signs, one for food and another for tools, and they trained the chimps to label cake, orange, and bread with the food sign and key, money, and stick with the tool sign. The chimps were then asked to label new items such as banana as a food or magnet as a tool. Sherman and Austin did this readily, but Lana could not. Although she had learned to make individual associations between each object and the reinforced sign, she had not learned to associate the tool or food signs with the general properties of the objects they represented. Because all three chimps were trained in exactly the same way for this task, it seems that the earlier training influenced their tendency to treat signs as symbols. The abilities of Sherman and Austin to use these signs as symbols were amply demonstrated by the ease with which they could also label signs for objects that had not been used in the training as tools or food. There was nothing foodlike or toollike about the signs. This labeling required the chimps when seeing a symbol to be able to refer to properties of the referent.

Problems Comparing Animal Communication to Human Language

The basic paradigm of animal language studies involves training animals to use a set of signs created by humans in ways that appear similar to some features of human language. However, there are clear differences between how the animals learn to perform these experiments and how human infants learn language. What the animals have actually learned in animal language experiments depends on how they were trained. This is very different from how humans develop language. Human infants are not formally trained as they develop language in the first few years of life. Many parents would have a difficult time teaching grammar even if

asked to do so. It is remarkable that different speakers develop such similar understandings of grammar and word meaning, given the unstructured and variable exposure to speech that they receive as infants. These problems reflect a dilemma in animal language studies. The more the study matches naturalistic language acquisition, as with the chimps raised at home, the more difficult it is to quantify results. On the other hand, the more the study uses formal training and testing sessions, the less the experiment looks like language. This dilemma is particularly problematic for artificial language experiments in which animals undergo extensive training to respond to commands but have no chance for real two-way communication (Locke 1993).

Debates about whether an animal has "true" language have generated more heat than light. We simply do not understand enough about how humans learn and process linguistic information, and not enough about how trained animals process artificial signs, to be able to determine where animal and human performances differ or overlap. It is more useful to isolate specific issues such as whether animals use signs as symbols or can learn syntactic rules. Some of these questions do not require training but can also be studied in the natural communication systems of animals. One of the most important cognitive issues here is how animals learn the signals and the rules for using these signals in natural communication.

Imitation and Social Learning

This section concentrates on the role of learning in the natural behavior of marine mammals. Animal communication does not need to involve complex cognitive processes. The classic ethological view emphasizes how evolution can shape both signaler and receiver (Tinbergen 1951). Natural selection may shape genetically fixed signals (*key* or *sign stimuli*). When a receiver detects the signal, the appropriate response may be released by an *innate-releasing mechanism*. Many such responses are *fixed action patterns* that are also shaped by natural selection. It can be difficult to distinguish between such highly adapted responses and those resulting from intelligence and learning. In Darwin's (1871:39) terms:

... we may easily underrate the mental powers of the higher animals, and especially of man, when we compare their actions founded on the memory of past events, on foresight, reason, and imagination, with exactly similar actions instinctively performed by the lower animals; in this latter case the capacity of performing such actions having been gained, step by step, through the variability of the mental organs and natural selection, without any conscious intelligence on the part of the animal during each successive generation.

How are we to discriminate between communication involving relatively hard-wired connections between species-specific signals and responses from more open systems susceptible to learning by experience?

Vocal Imitation

One place to start is with the signals themselves. The vocalizations of nonhuman terrestrial mammals, including our primate relatives, appear to be only slightly modified by experience and look like classic, genetically fixed species-specific signals (Janik and Slater 1997). Even such drastic treatments as deafening at birth produce only minor modifications of vocal development in some terrestrial mammals, such as slightly longer mews in deafened kittens (Buchwald and Shipley 1985). The importance of genetic factors compared to auditory experience is suggested by studies of primate hybrids, whose calls blend features from both parents but match those of neither (Newman and Symmes 1982, Brockelmann and Schilling 1984). Primates raised in isolation or with foster mothers of a different species still produce species-typical vocalizations (Winter et al. 1973, Owren et al. 1993). The hybrid and cross-fostering results are particularly striking as these animals are constantly exposed to, and must learn to respond to, vocalizations that differ from the ones they themselves produce.

Much more striking effects of auditory input are reported for vocalizations from a variety of marine mammal species. A captive harbor seal (*Phoca vitulina*) was reported to imitate human speech with a New England accent (Ralls et al. 1985). Captive beluga whales are also reported to imitate human speech well enough for caretakers to "perceive these sounds as emphatic human conversation" (Ridgway et al. 1985). One beluga named "Logosi" was reported to produce clear imitations of his name (Eaton 1979). Captive bottlenose dolphins of both sexes are highly skilled at imitating both human-made pulsed sounds and whistles (Caldwell and Caldwell 1972b, Herman 1980); in fact, they may imitate sounds spontaneously within a few seconds after the first exposure (Herman 1980) or after only a few exposures (Reiss and McCowan 1993). Dolphins can also be trained using food and social reinforcement to imitate human-made whistle-like sounds (Evans 1967, Richards et al. 1984, Sigurdson 1993). The only other non-human animals with such highly developed skills of vocal imitation are the most accomplished avian mimics such as parrots and mynahs (West and King 1990).

Why have marine mammals evolved such unusual abilities to modify their vocalizations based on what they hear? As discussed earlier in this chapter, some baleen whales, like many songbirds (Marler 1970, Catchpole and Slater 1995), appear to use vocal learning to increase the complexity, and

perhaps the attractiveness, of their reproductive advertisement songs. The rapid change of humpback song coupled with convergence of singers within a population can only be achieved with well-developed abilities of vocal learning. Vocal imitation appears to function in dolphins both in the development of individually distinctive whistles and in maintaining individual-specific relationships among adults (Tyack and Sayigh 1997). Therefore, there is a diversity of evolutionary functions for vocal imitation among marine mammals. In general, vocal imitation allows the development of remarkably open systems of vocal communication, in which adults and young can learn new signals with new associations.

One of the ironies of animal language research with marine mammals is that Lilly actually was one of the first to discover vocal imitation in dolphins (Lilly 1965). At that early stage of animal language research, Lilly jumped to the conclusion that, if animals were capable of vocal imitation, they must also have most other skills that humans use for language. It also turned out to be more difficult to train imitation of speech signals than other sounds that are more like the natural sounds dolphins produce. The more recent animal language studies with marine mammals selected a very controlled experimental approach in which the subjects primarily responded to human commands in part because of Lilly's overinterpretation of very limited data. Yet Savage-Rumbaugh (1986) emphasizes the need for animal language training to incorporate two-way communication to develop more languagelike performance. No animal language studies with dolphins have fully exploited their imitative abilities.

Motor Imitation

Marine mammals also produce novel postures and movement patterns in imitation of other animals, a skill called motor imitation. Several different trainers at different marine zoological parks have described how a dolphin that had only observed show behaviors of other dolphins would be able to perform the entire show flawlessly (Caldwell and Caldwell 1972a, Pryor 1973). Other examples of playful imitation include bottlenose dolphins imitating distinctive swimming, self-grooming, and sleeping behaviors of fur seals and postures and swimming behavior of animals as diverse as fish, turtles, and penguins (Tayler and Saayman 1973). Perhaps the most striking example of playful imitation concerned a bottlenose dolphin calf that would watch humans who had gathered to watch her through an underwater viewing window. One day the calf swam off immediately after a human exhaled a large cloud of tobacco smoke. She went directly to her mother, suckled, swam back to the window, and squirted a mouthful of milk toward the smoker (Tayler and Saayman 1973).

Motor imitation by observational learning is more com-

plex than first meets the eye. For an animal to imitate the act of another, it must be able to relate parts of the body of the performer to the appropriate parts of its own body. It must then somehow map its perception of the movements and configuration of these parts onto motor commands to perform similar movements. These abilities are quite mysterious. How did the young calf map the mouth of the smoker to her own mouth? How did she come up with the idea of using milk to simulate in water the motion of smoke in air? Motor imitation remains controversial both because of lack of repeated experimental demonstrations and because the cognitive processes leading to the skill are so poorly understood. However, the adaptive significance of this skill is obvious for marine mammals.

Many mammals appear to use social learning to learn how to select and handle prey (Zentall and Galef 1988). Many marine mammals are generalists, feeding on a variety of prey in diverse habitats. Marine mammals show remarkable flexibility in learning how to exploit feeding opportunities created by human fisheries. Seals, dolphins, and whales are often reported to learn how to take fish off hooks or remove them from nets. Even when they feed on the same kinds of prey, wild bottlenose dolphins from different areas typically use different foraging techniques. For example, dolphins may catch fish by chasing them down and catching them in the mouth, by striking them with their tails, or by washing them out of the water on a mud flat (see Wells, Boness, and Rathbun, Chapter 8, this volume). Lopez and Lopez (1985) suggest that young killer whales learn how to strand on a beach to capture seals by imitating adults. Norris and Prescott (1961) report that two captive-born bottlenose dolphins were clumsy at handling large prey items that were handled with ease by two wild-caught animals. This difference led them to suggest that this handling behavior was learned. Novel feeding behaviors have also been reported to spread through humpback whale populations with a pattern suggesting that young learn the feeding method by observation (Weinrich et al. 1992).

Observation of both wild and captive marine mammals clearly demonstrates the importance of learning and imitation in the development of foraging behavior and communicative displays. This is a promising area for future research—conducting carefully controlled tests of whether social learning, especially observational learning, is involved in the acquisition of these behaviors.

Brain Size in Cetaceans and Possible Functions

The review of cognition in the last two sections has relied on data from the behavior of animals. Different kinds of insights can derive from training captive animals and from observing

wild ones. Cognition is more than just behavior, however. Cognition is typically defined as information processing within the organism, which means within the nervous system. Neurobiologists have made great progress in using neurophysiological methods to study how sensory systems convert external stimuli into neural signals, how these signals are analyzed within the brain, and how this may lead to structured patterns of muscular activity to generate a behavioral response. Neuroethological investigations of information processing in animals have had great success in explaining, for example, how bats echolocate and how birds learn their songs. Unfortunately, we know much less about how marine mammals actually process information in the brain. The development of noninvasive techniques to image activity within the nervous system of alert animals offers hope for the future, but for now we must rely on more gross comparisons of brain size and anatomy.

Worthy and Hickie (1986) compared the relationship between brain size and body size in 648 species of mammals, and they derived an equation to define this relationship for all mammals. They found that pinnipeds had brain-to-body weight ratios that were very similar to those predicted from the equation calculated from all mammals. Sirenians, mysticetes, and the sperm whale had smaller brains than would be predicted from their body size, using the equation from all mammals. O'Shea and Reep (1990) suggest that the small brain-to-body weight ratios of sirenians are correlated with their low-quality diet and low metabolic rate. Sirenians are specialized to eat tropical sea grasses, a food that is abundant but low in quality. Grazing on these plants does not appear to require complex foraging strategies or sensory adaptations, but does require a relatively large gut size to process larger quantities of low-quality food. O'Shea and Reep (1990) suggest that the foraging pattern of sirenians selected for an increase in body size without a corresponding increase in brain size.

The baleen whales and sperm whales are much larger than any other mammals. Big terrestrial mammals must support their body mass, but the weight of a large whale is supported by the water, and this may free them from some mechanical constraints. These differences in size and mechanical constraints on the bodies of big whales may cause problems in extrapolating a brain-to-body relationship derived from animals tending to weigh around 1 kg to animals weighing tens of thousands of times more. For example, the size of the head in these large whales seems less constrained than in their terrestrial counterparts; the whale head is much larger than is typical of mammals, between one-quarter to one-third of the entire body length (Clarke 1978, Lockyer 1982). Animals with large blubber stores, such as baleen whales, may also require a correction in body size to account for this relatively inert tissue.

Primates and most other odontocete cetaceans have brains that are larger than predicted from their body size (Worthy and Hickie 1986, Marino 1998). Humans have the highest brain-to-body weight ratios among primates. It has been known for centuries that some dolphins with bodies a little larger than those of an adult human have brains roughly the same size. Adult humans with bodies weighing from 36 to 95 kg have brains weighing from 1100 to 1540 g (Jerison 1973). An adult dolphin of the genus *Lagenorhynchus* weighing 100 kg might have a brain weighing more than 1250 g (Ridgway and Brownson 1984). Adult bottlenose dolphins weigh more than humans, with a typical range cited in Ridgway and Brownson (1984) of 130 to 200 kg. Their brains weigh on the order of 1600 g, comparable to that of a human.

Brains this large are extremely rare, in part because brain tissue is metabolically expensive (Parker 1990). The 1400-g brain of a human weighing 70 kg can account for about 20% of the basal metabolic rate (Sokoloff 1977). This investment in large brains may slow growth and development significantly. Holliday (1978) extrapolates from data on children 5 years old or older to estimate that a newborn human infant may devote 87% of its basal metabolic rate to the brain. Holliday (1978) estimates that the brain of a 1-year-old may still consume more than half of the basal metabolism, and data from 5-year-olds indicates that their brains still consume as much as 44% of basal metabolism. Large developing brains drain resources that could otherwise increase the number of offspring of the mother or reduce the time between generations (Parker 1990). Compared to most other mammals, odontocete cetaceans have both larger brain-to-body weight ratios and slow reproductive rates. Cetaceans rarely have more than one young at a time, and gestation periods are nearly 1 year. Some species do not reach sexual maturity until 8 to 10 years or more, and the interval between calves may be more than 5 years in some species. This focus on the costs of large brains immediately raises questions about why dolphins have invested so heavily in brain tissue. What are the potential benefits that might outweigh these formidable costs?

Several different functions have been suggested for the large brains of some cetaceans. Many researchers focus on the well-developed auditory system, especially the need for rapid auditory processing of high frequency echolocation pulses (Wood and Evans 1980, Ridgway 1986, Worthy and Hickie 1986). Many of the nuclei involved in processing auditory information are highly enlarged in dolphins compared to other mammals. The auditory cortex also appears to cover large areas in the dolphin (Bullock et al. 1968, Bullock and Ridgway 1972), but the question of how the dolphin cortex is organized to process auditory information is much less well understood than in echolocating bats (e.g., Suga 1977)

or in owls specialized for passive acoustic localization (Knudsen 1982). The extraordinary echolocation abilities of the bat are achieved with such radically smaller brains that I find it hard to believe that echolocation per se requires such a large investment in neural tissue by dolphins. Brain size within marine mammals also does not appear to correlate well with what we know of echolocation abilities. For example, the harbor porpoise (*Phocoena phocoena*) and platanistid river dolphins appear to have well-developed echolocation systems, but have smaller brains than delphinids of the same size (Jerison 1978, Marino 1998).

As we have seen vocal learning is another vocal/auditory skill that is well developed in marine mammals, but rare in other non-human mammals. As was true for echolocation, however, small birds achieve comparable vocal learning abilities with much smaller brains, and what we know of the vocal learning abilities among marine mammals again does not appear to correlate well with brain-to-body size ratios. For example, baleen whales show impressive vocal learning capabilities, such as is seen in humpback song, but have low brain-to-body ratios (Jerison 1978, Worthy and Hickie 1986). Harbor seals are also capable of excellent vocal imitation (Ralls et al. 1985), but have brain-to-body ratios typical of most mammals (Worthy and Hickie 1986).

We are only beginning to understand the auditory processing abilities of marine mammals, and it is possible that they achieve processing qualitatively more complex than that of the bat or bird (Worthy and Hickie 1986). Not even results from the animal language research, however, provide strong evidence for processing abilities that would justify such a large investment in neural tissue compared to other mammals. Sea lions with brain-to-body ratios typical of most mammals have a performance in animal language experiments that is similar to that of dolphins with much higher investments in neural tissue.

These kinds of concerns have led some to argue that the cetacean brain retains some primitive and inefficient structure, which means that cetaceans need large brains to do the same things that land mammals achieve with much smaller brains (Glezer et al. 1988). Fossils suggest that cetaceans have had enlarged brains for many tens of millions of years, however, much longer than hominids had equivalent brain sizes (Jerison 1978). The high energetic demands of these large brains would have created a strong selective pressure for changes to improve the so-called primitive structure of cetacean brains to render them more efficient. Although cetacean brains do differ from those of most terrestrial mammals, I find it hard to believe that cetaceans have been constrained to retain for tens of millions of years inefficiencies that demand such a large metabolic cost.

I have just reviewed suggestions that cetaceans have large

brains either to accomplish particularly complex auditory processing or to make up for an inefficient and primitive brain. A very different perspective comes from primatologists who emphasize the social functions of intelligence (e. g., Humphrey 1976). Think of the cognitive demands of a game like chess where players can use their intelligence to come up with new strategies to beat an opponent. Players must also be on guard against their opponents coming up with new strategies. Such a game could create positive feedback for the evolution of more and more sophistication. This is fundamentally different from the evolution of a specific sensory ability such as echolocation or a motor ability such as learning to manipulate an object. Once a neural system is constructed that can achieve, for example, a certain speed and precision of auditory processing, there need not be any selection for a more complex system. Competition between conspecifics for innovation of complex behavioral strategies could, on the other hand, create an arms race for any improvements in the cognitive abilities used to generate these strategies.

Now imagine a species in which the young are dependent for a large fraction of their lives on care from parents and possibly from other members of their group. Suppose that adults depend on one another for social defense from predators and for efficient foraging. At the same time, animals within these groups compete for access to food, mates, and other important resources. Individuals that lose in a one-on-one competition may form an alliance with other individuals to improve their competitive advantage. This kind of society puts a premium on animals that can recognize other individuals, understand how they interact with others, and remember the history of interactions. Any individual that can modify how she or he interacts with another depending on the history of their interaction has a significant advantage in obtaining benefits from cooperation and reducing risks and losses from competition. The young animals can spend years honing their social skills for the times when they become necessary.

This kind of picture has been drawn of the evolution of human social behavior and has been related to the evolution of human social intelligence, called Machiavellian intelligence by Byrne and Whiten (1988), in honor of an Italian Renaissance master of political advice. Descriptions of the complexities of political intrigue are not limited to human primates; complex dynamics of cooperation and competition in chimps at a zoo led Frans de Waal (1982) to title a book "Chimpanzee Politics." Are there marine mammal species where social politics of this sort might have a significant enough impact on reproductive success to justify the investment? We do not know much about such fine-grained interactions in societies of marine mammals, but many more gen-

eral parallels are obvious. Some odontocete cetaceans have extended parental care and rely on conspecifics for social defense from predators and for efficient foraging. Some species with fluid social groupings provide particularly clear evidence for individual-specific social bonds. For example, bottlenose dolphins have a very fluid fission–fusion society in which group composition only remains stable over intervals of minutes to an hour or so. Yet within these fluid groupings different individuals usually remain together. Male bottlenose dolphins form stable alliances with one or two other males to defend females from other males, and groups of two alliances may temporarily cooperate to compete against a third (Connor et al. 1992). Evidence from social communication, such as the signature whistles of dolphins, suggests the importance of individual recognition, not just between parents and offspring but between animals of both sexes at each stage of life. Both the social structure and these communication signals suggest the importance of individual-specific social relationships of the sort implicated in the evolution of social intelligence.

Discussion of the social functions of intelligence emphasize particular kinds of societies involving balancing cooperation and competition within individual-specific social relationships (Cheney et al. 1986, Byrne and Whiten 1988). Species such as the bottlenose dolphin, for which there is the best evidence of these relationships, also have some of the highest brain-to-body weight ratios (Ridgway and Brownson 1984). There is little evidence for strong individual-specific social relationships in species with the smallest brain-to-body weight ratios such as the sirenians and baleen whales (O'Shea and Reep 1990). Most discussions of the social functions of intelligence have been limited to primates. Marine mammals are phylogenetically distant from primates and evolved in such a different environment that they will make a particularly interesting comparison (Marino 1996).

The remarkable diversity of social behavior, life history, ecology, and patterns of communication among marine mammals make them excellent subjects for studying the evolution of communication and cognition. Further neurobiological and behavioral studies offer great promise for comparative studies on the evolution of large-brained animals, what cognitive processes these brains support, and how they function in the natural behavior of marine mammals. Broad comparisons of communication and cognition across diverse mammalian taxa will help us to understand the evolution of these traits in many species including our own.

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