

# CETACEAN SOCIETIES

Field Studies of

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Dolphins and Whales

Edited by

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# 11

## FUNCTIONAL ASPECTS OF CETACEAN COMMUNICATION

PETER L. TYACK

MY GOAL for this chapter is to present studies of cetacean communication from the functional perspective of behavioral ecology and ethology. This may involve a view of communication that is not familiar to readers from other disciplines. For example, the mathematical theory of communication usually frames communication between one signaler and one recipient (fig. 11.1A). The signaler is presumed to know something that the recipient may not know, and it is assumed to produce a signal to communicate information to the recipient. The information in the signal is defined by the ability of the signal to reduce uncertainty in the recipient (Shannon and Weaver 1949; Bradbury and Vehrencamp 1998). This classic idea of communication involving reduction of uncertainty is superficially similar to our typical usage regarding human communication transmitting knowledge by language.

By contrast, the functional view I follow in this chapter attempts to look at communication from a much broader perspective (fig. 11.1B–F). The following list describes several non-mutually exclusive features of communication that may not be captured in the classic view:

*Advertisement.* A signaler may produce an “advertisement” signal more to influence a decision of the recipient than to exchange information. This view emphasizes the role of communication in manipulating the receiver, possibly to its detriment (Dawkins and Krebs 1978; Krebs and Dawkins 1984). Receivers that are predictably bombarded by advertisements may develop sales resistance.

*Tonic communication.* The classic view of communication uses a model in which one signal transmits

information to a receiver, often evoking an immediate response (see fig. 11.1A). In some situations, though, signalers produce long strings of signals without an obvious response from a receiver (fig. 11.1B). Receivers may monitor signals for a long time before making a choice, as when a female chooses a male based upon advertisement displays. There are other situations in which changes in the rate of signaling may convey information (Schleidt 1973).

*Deception.* A signaler may signal to mislead or to increase uncertainty in the receiver. A variety of theoretical analyses of situations in which the interests of animals conflict suggest that rather than signaling to allow an opponent to predict future behavior, animals might produce signals that either minimize predictability (Maynard Smith 1974) or that actively deceive the opponent (Cheney and Seyfarth 1990; Whitehead and Weilgart, chap. 6, this volume). The classic view of fighting assessment emphasizes the role of threats in predicting future attacks or retreats, while the deception view emphasizes the possibility of bluffs or feints (fig. 11.1C).

*Environment.* Most signals are modified as they pass through the environment from sender to receiver. This modification need not represent only degradation of the signal, but may provide information to the receiver. For example, songbirds may estimate the range of a singer by assessing degradation of the signal (McGregor et al. 1983; McGregor and Krebs 1984b; Morton 1982, 1986; Naguib 1998). Animals such as bats and dolphins are well known to learn about their

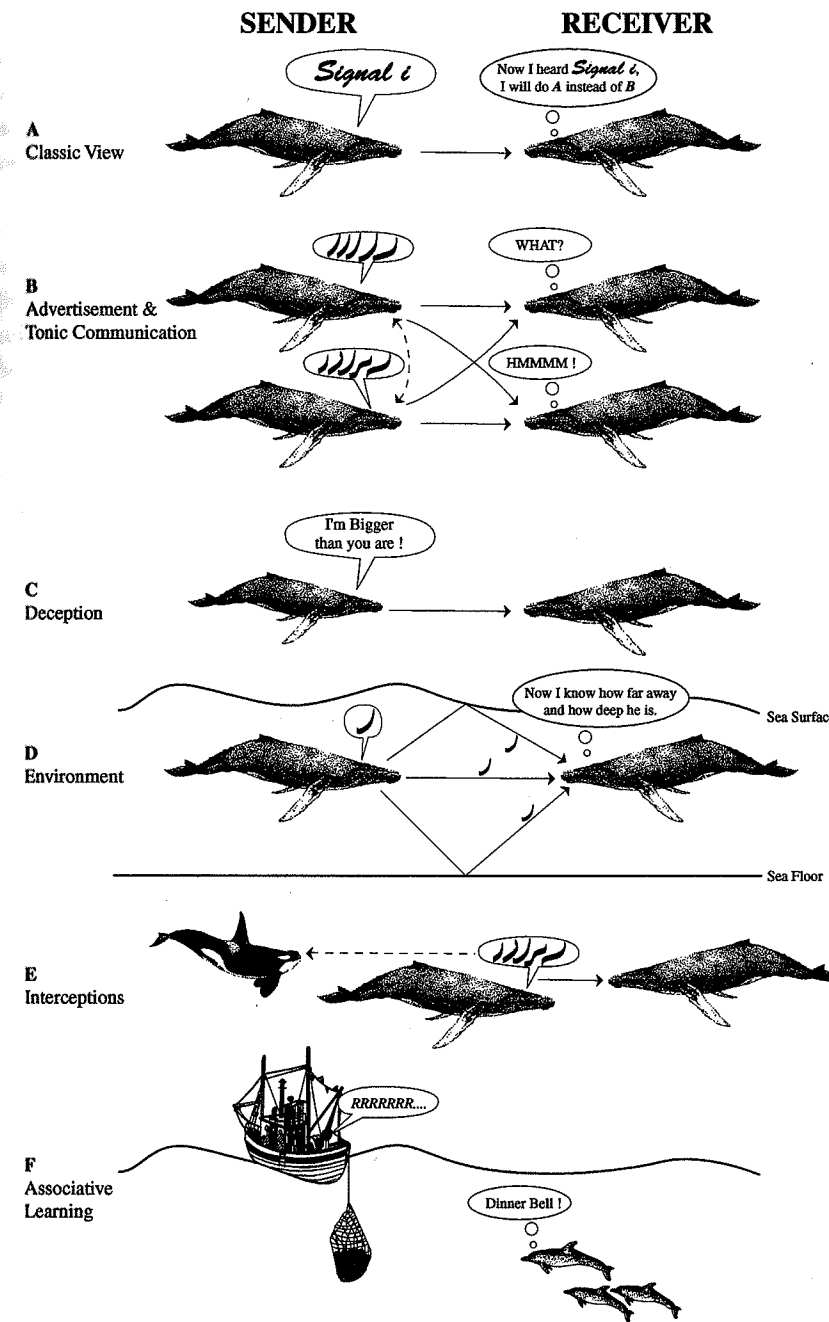


Figure 11.1. Comparison of classical “reduction of uncertainty” view of communication (A) with the ecological view of communication presented in this chapter. This view includes the concepts of advertising and tonic communication (B): viewing communication as a potentially manipulative process, potentially involving many parties and many signals. It does not assume that all signals are “honest,” but entertains the possibility of deception (C). It acknowledges that signals change as they pass through the environment, and that this can inform the receiver about both the signaler and the physical environment (D). There may be multiple intended recipients of a signal, and others may intercept the signal, using information to their own advantage (E). Unintended recipients may even learn beneficial responses to signals from other species (F), as when dolphins suddenly appear at a fishing vessel when a winch that releases fish is turned on.

environment by listening to echoes of sounds they themselves have made. Animals may also learn about their environment from sounds they use for communication and from the sounds of other animals as well (Tyack 1997).

*Interception.* A signaler may produce a signal to communicate with one specific class of receivers, but

other receivers may detect the signal and respond to it, to their advantage and to the detriment of the signaler (Myrberg 1981). These interceptors may be predators (Ryan et al. 1982) or parasites (Cade 1975) of the signaler, or they may be competitors, such as satellite males that may seek out females attracted by the advertisement displays of a territorial male (Cade 1979). Risks of interception may influence the active

range of a signal: a signaler may limit the intensity of a signal so it cannot be detected beyond the expected range of the intended recipient. Risks of interception may also influence the frequency range or sensory mode of a signal, or influence the evolution of displays that can be directed toward the intended recipient in such a manner that they are difficult to detect from different directions.

*Associative learning and interspecific communication.* Akin to interception is the situation in which a receiver may learn the contexts in which a signaler may produce a signal intended for some other recipient. For example, vervet monkeys may respond appropriately to the alarm calls of a bird and may even recognize that the mooing of cows is associated with the presence of a human predator, the Masai (Cheney and Seyfarth 1985).

I will develop an analogy to illustrate the difference between the classic and functional ecological views of communication. During the past few decades, while behavioral ecologists and ethologists have developed the functional view of communication in animals, a human communication system has actually changed from a simple classic mode of operation to a more complex form of communication involving many aspects of the functional perspective I have described above. Starting in the 1960s, the U.S. Department of Defense funded the development of an early version of the Internet, called the ARPANET, to link computers by phone lines to allow more efficient use of limited computer resources (Hafner and Lyon 1996). It quickly became obvious that electronic mail using this network could speed up communication of commands and questions and answers between the military, defense contractors, and academics. While each message typically had one originator and one intended receiver, a complex distributed network for sending these messages was developed on the ARPANET. Some of the design features of this distributed network were developed by a consultant concerned with the vulnerability of centralized communication systems in case of a nuclear attack (Hafner and Lyon 1996). Each computer was linked to several others, so that if one node of the network stopped functioning, the message could immediately be rerouted along the best new path. Now, in the 1990s, this network has opened up to a much broader world. While the initial Internet was designed for classic models of information exchange between two individuals for mutual benefit, cyberspace is now a completely different landscape. One person may send a message to thousands of recipients with ease. Internet users may be

attacked by spam—mass advertisements indiscriminately sent to unwilling receivers. Malicious computer programmers devote enormous ingenuity to designing computer viruses—sequences of code not designed to transfer information to the receiving computer, but rather to take over some of its resources or to interfere with its operation. A message may be sent through one computer not to communicate with it, but rather to obscure the actual identity of the signaler.

The world in which animals communicate is more like cyberspace than like the original ARPANET. Over the long course of evolutionary time, animals have evolved adaptations to take advantage of any opportunity provided by communication systems, and this exploitation has stimulated countermeasures. The fullest view of communication is not limited to educational messages between cooperating partners, but also includes competition, advertisement, parasitism, and predation. What we observe today is the product of complex balances of the costs and benefits of many of these relationships. In this chapter, I present a functional view of cetacean communication in this broad ecological context.

Many recent reviews of animal communication emphasize elements of this functional perspective (e.g., Alcock 1998; Bradbury and Vehrencamp 1998; Krebs and Davies 1993), but it is less common in previous reviews of cetacean communication (e.g., Herman 1980) or of vocal behavior and hearing in cetaceans (e.g., Richardson et al. 1995b). One reason for this contrast is that it is often easier for a human to study the functions of communication in animals that share our own terrestrial environment than to work in a foreign environment, which often requires special methods. When humans study communication in terrestrial animals, we naturally can rely upon our own senses, which are adapted for the terrestrial environment, to detect communicative displays. We also draw upon our familiarity with the terrestrial environment to infer the intended recipient of a display. For example, when a cricket calls or a bird sings, we usually have an intuitive sense of how far away an animal might sense the display. The senses of marine animals are adapted to a very different environment, one that is more difficult for biologists to sense directly and to understand intuitively.

When we monitor terrestrial animals, we also can integrate information from all of our senses as we follow an interaction, often tapping skills from our own species-specific communication system. For example, when a nonhuman primate calls, it may also direct its gaze toward the intended recipient of the call. Since the human primate also uses gaze in this way, it is relatively simple for a biologist to interpret the interaction. Direction of gaze has even proved

a powerful response measure for playback experiments with wild primates (Cheney and Seyfarth 1980). All of these factors make it easier for us to understand the communicative context of displays by terrestrial animals than by marine animals such as cetaceans.

Phylogenetic similarities between human observers and their nonhuman primate subjects have costs and benefits for the observer. To the extent that displays such as facial expressions are homologous, the observer may more easily be able to understand and interpret the display. On the other hand, this similarity raises the potential for unquestioned or unwarranted anthropomorphism. When humans observe a chimpanzee, they may be more susceptible to anthropomorphic interpretation than when watching an animal as foreign as a dolphin. One can seldom study wild cetaceans simply by watching and listening to them and inferring what is happening, as is possible with some terrestrial animals. Biologists who study cetaceans in the wild have needed to develop a suite of novel methods and study designs (see Whitehead et al., chap. 3, this volume). Difficulties in identifying which cetacean produces a particular vocalization have been an obstacle to teasing apart the patterns of signal and response that make up a system of communication. In order to overcome these difficulties, studies of communication in cetaceans have used an unusually diverse array of methods. While this has taken extra time and effort, the results ultimately may be less subjective and more valid than those of studies relying upon easier but more subjective methods. Some of the methods initially developed for cetacean research, such as acoustic localization, are now being used with other taxonomic groups to answer questions where the simpler methods are inadequate (McGregor et al. 1997).

However, the evolutionary distance between cetaceans and primates has not prevented anthropomorphism from influencing our understanding of cetacean communication. John Lilly was one of the first scientists to discover the remarkable imitative abilities of dolphins. Marine mammals do stand out as radically different from most nonhuman terrestrial mammals in this ability. Since humans also use vocal imitation, Lilly jumped to the conclusion that if dolphins have large brains and can imitate, they must possess a communication system very similar to human language:

All of dolphin culture may be transmitted in somewhat the way primitive human tribes transmit knowledge from one generation to the next with long folk tales and legends. . . . (Lilly 1975: 17)

I believe that rather than leaping to analogies with human language, it is a more profitable research strategy to study

how cetaceans actually use communication to solve specific problems in their natural environment (Tyack 1993). I will present cetacean results in a broad comparative perspective, including examples from many different animal groups. My presentation of these results in the functional framework of behavioral ecology is designed to highlight the many areas of commonality with studies of communication in terrestrial animals. The basic theories of behavioral ecology are equally applicable in the sea and on land. I will also highlight areas in which cetaceans differ from terrestrial animals, areas of particular interest from a comparative perspective. Some of these differences stem from the physical properties of seawater versus land (Tyack 1998); others, such as the effect of diving upon vocalization, depend upon the interaction of biology with the physical properties of the environment (Janik and Slater 1997).

The phylogenetic distance from cetaceans to many other mammalian groups makes convergent characters particularly interesting. For an example harking back to Lilly's comparisons with humans, while vocal imitation is critical for human language and music, most nonhuman terrestrial animals appear unable to modify their vocal repertoire based upon what they hear (Janik and Slater 1997). Several groups of marine mammals, including seals, whales, and dolphins, have highly developed skills for vocal learning. If their terrestrial ancestors did not have these skills, then this means that vocal learning evolved independently in at least two mammalian taxa that independently entered the sea: seals and cetaceans. This provides two independent groups for analyzing the selective pressures leading to the evolution of vocal learning. By comparison, if such a skill were found in chimpanzees, it would be difficult to determine whether this similarity with humans arose from a shared ancestor with the trait or through independent evolutionary events.

The basic questions I will address include "What are the functions for which cetaceans evolved particular signals?" and "What are the factors that cause these signals to have particular design features?" The structure of the problems and the features of communication described above are very important for deciphering what a communication signal is designed for and why it has particular physical features. Here are some examples of new results using a variety of methods to study cetacean communication, followed by some of the kinds of questions on communicative functions that will be addressed in this chapter:

*Mechanisms of sound production.* The sperm whale (*Physeter macrocephalus*) devotes about a quarter of its body length to the spermaceti organ, which appears



to function primarily to produce loud clicks (see Whitehead and Weilgart, chap. 6, this volume). The vocal repertoire of sperm whales involves variations in these clicks.

- What justifies such a massive investment in such a unique sound production organ?
- What are the critical features of sperm whale clicks driving the evolution of this organ?

*Correlations between structure and function of songs.* Humpback whales sing complex series of sounds that may last for tens of minutes before repeating (Payne and McVay 1971). These songs sound so musical to our human ears that recordings of them have become commercial best-sellers.

- Why do humpbacks sing these songs?
- Why does humpback song have such a complicated acoustic structure?

*Vocal learning.* Humans are the only terrestrial mammal with well-developed abilities of vocal learning, yet many marine mammals, including whales, dolphins, and seals, are exceptional vocal mimics. These unusual imitative abilities form the basis of the popular stories that dolphins have a "language."

- What are the functions of vocal learning in the natural communication systems of marine mammals?

*Echolocation and communication.* Dolphins have a remarkable system for echolocation using high-frequency clicks (Au 1993), and they also produce a diverse array of sounds used in social communication. Biologists often appear to assume that echolocation and vocal communication are independent abilities.

- Might some echolocation signals also transmit information to other animals?
- Might the evolution of skills for echolocation influence the evolution of vocal communication, or vice versa?

*Long-range communication.* Biologists using technology initially designed to track submarines have been able to hear loud low-frequency vocalizations of fin and blue whales from hundreds or even thousands of kilometers away (Costa 1993; Clark 1994, Clark 1995).

- Do the whales themselves communicate over such long ranges?
- What can a fin whale near Iceland need to know from a fin whale near Bermuda?
- The sounds of fin and blue whales produce echoes

from the seafloor and distant seamounts. Do whales use these echoes to orient or navigate? Might these sounds function both for communication and for echolocation?

This chapter attempts to put what we know about cetacean communication into its ecological and social context. The marine environment presented ancestral cetaceans with a new set of selection pressures for each modality of sending and receiving signals. I will briefly discuss how the marine environment influences communication in each sensory modality: chemical, tactile, electrical, visual, and acoustic. The rest of the chapter focuses on acoustic communication in terms of the different kinds of communication problems faced by whales and dolphins. This analysis asks how communication works as a system: for example, who are the intended recipients of a signal? Are there unintended recipients who intercept the signal to their own advantage? This question includes the potential for interspecific communication, particularly in predator-prey relations. I close the chapter by comparing echolocation and communication, by discussing the role of vocal learning in mammals, and by relating patterns of communication in different species of cetaceans to differing problems posed by the social systems of each species.

### Sensory Modalities for Communication in Cetaceans

Tens of millions of years ago, the ancestors of cetaceans gradually evolved from a terrestrial existence to living in the sea for their entire lives. These terrestrial mammals, most closely related to modern ungulates (see Eisenberg 1981 for a general review), underwent enormous changes as they adapted to the marine environment. Not only did their bodies have to change to allow them to swim more efficiently, but their sensory systems and vocal apparatus had to adapt to functioning in the dense water medium. The physical characteristics of the ocean environment also greatly modified the usefulness of different sensory modalities for achieving particular communicative ends. For example, vision is important among terrestrial animals for sensing objects at long ranges. Of all the ways to transmit information through the sea, however, sound is the best for communicating over a distance. Whales may hear one another at ranges of up to hundreds of kilometers, but they see one another underwater at ranges of no more than tens of meters. This means that hearing may be more important than vision as a distance sense for marine animals, and that vocal communication

may be used preferentially for rapid long-distance communication.

### Chemical Communication

Chemical communication is common among terrestrial mammals and many marine organisms. Chemical communication was almost certainly an important mode of communication among the terrestrial ancestors of cetaceans, but it appears to be limited among cetaceans. The olfactory bulbs and nerves, which function in terrestrial mammals for sensing airborne odors, are reduced in mysticetes and absent in odontocetes (Breathnach 1960; Morgane and Jacobs 1972). Little is known about how whales and dolphins may sense waterborne chemicals (Kuznetsov 1979). Most experiments on the chemical senses of cetaceans have tested responsiveness to basic tastes such as sweet, sour, salty, or bitter (Friedl et al. 1990), and the sensitivity of dolphins to taste appears to be about an order of magnitude less than that of humans. There have been some suggestions of use of pheromones among cetaceans (e.g., Norris and Dohl 1980b). M. C. Caldwell and D. K. Caldwell (1972b, 1977) point out the presence of pores from anal glands in bottlenose dolphins, and they suggest that these might release a pheromone. Norris (1991b) speculates that male spinner dolphins (*Stenella longirostris*) use chemical cues to sense the reproductive state of adult females. Little is known about how cetaceans might detect pheromones, and more experimental research is needed to test for pheromones and for specialized abilities to sense them. If cetaceans have only limited use of chemical communication, this may in part stem from the limited ranges of diffusion in water compared with the mobility of these animals.

### Tactile Communication

Touch is important for communication at short range in most cetacean species (e.g., Chapters 4–7, this volume). As they evolved a streamlined, hydrodynamically efficient body, most cetacean species lost external sensory hairs or vibrissae. However, most cetaceans retain a few residual hair follicles on the rostrum or upper jaw, and well-innervated hair follicles are present in the Amazon River dolphin, *Inia geoffrensis* (Simpson and Gardner 1972). The skin of cetaceans is well innervated and is very sensitive to touch. Nerve endings are particularly dense in the dermis near the eyes, blowhole, jaw, flukes, vulva, and perineum (Simpson and Gardner 1972; Kolchin and Bel'kovich 1973). Ridgway and Carder (1990) used somatosensory evoked potentials to assess the sensitivity of bottlenose dolphins to vibratory skin stimulation. They suggested that the most sensitive areas are at the angle of the gape of the

jaw and around the eyes, snout, melon, and blowhole. These areas are about as sensitive as human skin on the lips or fingers.

Dolphins and whales may rub or caress one another with their flippers or other parts of the body. Up to one-third of the members of an active school of wild spinner dolphins have been estimated to engage in caressing at any one time (Johnson and Norris 1994). Gentle rubbing seems to play an important role in maintaining affiliative relationships in some dolphin species, perhaps analogous to that of social grooming in primates (Norris 1991b; Samuels et al. 1989).

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 (e.g., Newman 1976 for gray whales), and copulation is commonly observed between animals that are not sexually mature (Connor et al., chap. 4, this volume). D. K. Caldwell and M. C. Caldwell (1972a) report that infant male bottlenose dolphins in captivity attempt to mate with their mothers within a few weeks of birth. Brodie (1969) has suggested that nursing in toothed whales may not only function in nutrition, but may also take on an affiliative communicative role, reinforcing the mother-calf bond.

Cetaceans 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 finding raises an important distinction that illustrates the usefulness of the concept of information for communication researchers: If an animal is said to be responding to a communicative signal, then it must be responding to the information sent, rather than to the physical effects of the signaling action.

### Electrical Communication

Many groups of freshwater and marine fish are able to sense electrical signals that can propagate over limited distances in water (Hopkins 1977). Some species, such as the electric eel, are also well known to be capable of producing electrical discharges powerful enough to stun predators or prey. Other groups of freshwater fish, such as the gymnotid fishes of South America and the mormyrid fishes of Africa, produce complex electrical signals that are used for social communication. Electrical communication is characterized by signals that travel very rapidly, fade out quickly, and have ranges typically limited to less than a meter or so in water. Since so few aquatic organisms are highly sensitive to electrical signals, they also form a relatively private channel for communication, reducing the risk that predators or prey will detect a signaling animal. Cetaceans are like most mammals in not being particularly sensitive to electric

fields. They are unlikely to use electrical signals themselves, and would be relatively insensitive to such signals from prey organisms.

Even though cetaceans do not use electrical signaling, there is one area where comparisons with electric fishes are useful. This involves potential interactions between using signals to communicate and using signals to learn about the environment. Many fish that have both electric organs and electroreceptors can detect objects in their environment by sensing distortions in the electric field emitted by their own bodies. Some fish can also detect the electric fields generated by other organisms, such as prey. The same abilities to send and receive electrical stimuli may be used by these fish either for communication or to learn about their environment. Some cetacean species have a similar ability to use sound either to communicate or to learn about their environment through echolocation, and this ability creates the potential for evolutionary interactions between these two functions.

### Visual Communication

Most marine cetaceans have a well-developed sense of vision, but several species of dolphins living in turbid riverine environments have eyes with reduced capabilities for forming optical images. The platanistid river dolphins, *Platanista minor* and *Platanista gangetica*, have no lens in the eye at all, and the transparency of the cornea is limited because it is vascularized (Dawson 1980). While visual acuity is reduced in these species, they may be able to form crude images using the narrow aperture of the pupil in a manner analogous to a pinhole camera. Most other cetaceans have transparent and colorless lenses and corneas, but the Amazon river dolphin, *Inia geoffrensis*, has a lens that is deep yellow in color (Dawson 1980). It has been suggested that in the brown waters typical of most of the Amazon, this yellow filter might function as well as a clear one.

The eyes of many cetaceans have specific adaptations for underwater vision. Terrestrial eyes rely upon refraction as airborne light enters the aqueous cornea, but this effect is greatly reduced in aquatic animals, and the optics of cetacean eyes have been modified as a result. Deep-diving cetaceans enter a cold and dark environment in which blue-green light penetrates the best. The photopigments of cetaceans are shifted toward the blue end of the spectrum compared with those of terrestrial mammals, and they also have a tapetum lucidum that reflects light and increases the sensitivity of the retina at low light levels (Mobley and Helweg 1990). Cetacean eyes also must be protected against the strong fluctuations in temperature and pressure that occur during dives. A few hundred meters below the

sea surface, the water temperature hovers only a few degrees above 0°C.

Anyone who has observed a captive bottlenose dolphin leaping 5 m into the air to catch a small object would not be surprised to hear that these animals have in-air vision that is nearly as acute as their vision underwater (Herman et al. 1975). Many species of toothed whales clearly can be seen to observe objects in the air when their heads are out of the water. Baleen whales and some odontocetes engage in a specific behavior, called spyhopping, that is thought to be used for inspection of objects in air (Madsen and Herman 1980). It has been suggested that in-air vision may play a role in foraging, surveillance, and orientation among cetaceans (Mobley and Helweg 1990).

Mobley and Helweg (1990) discussed evidence that cetaceans have adaptations favoring motion detection, which might select for moving versus static visual stimuli. They also presented evidence that bottlenose dolphins are excellent at estimating the distance to an object. The visual skills that dolphins display when catching a ball in a show are likely to be equally useful for detecting, tracking, and capturing prey. These visual skills may complement the echolocation skills of odontocetes, and are likely to be particularly useful during daylight at close range. For example, some bottlenose dolphins in the wild hit fish so hard with their flukes that they knock the fish into the air (Wells et al. 1987). After hitting a fish, the dolphin can track the fish in the air and catch the fish in its mouth as the fish hits the water.

Most cetacean species are reported to use some visual signals as communicative displays. Both aggressive and sexual interactions often involve visual signals at close range. Many aggressive visual signals in cetaceans follow patterns that are common among other mammals, including vigorous movements of the head toward another animal, jerking the head, opening the mouth, or even making threats that resemble biting actions (Overstrom 1983; Samuels and Gifford 1997). Some behaviors appear to function to increase the apparent size of a male, and these behaviors may function as visual displays (see Clapham, chap. 7, this volume). 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. Several observers have suggested that this may function to increase the apparent size of a competitor (Tyack and Whitehead 1983; Baker and Herman 1984). Other male cetaceans may have thickened areas of callused skin. While these secondary sexual features may function as weapons or armor during fights between males, they may also function as a visual signal to either potential competi-

tors or potential mates (Payne and Dorsey 1983). Some cetaceans retain white pigment where they have tooth rakes from fights (sperm whales: Best 1979; *Grampus griseus* and *Mesoplodon carlhubbsi*: Leatherwood et al. 1983). This might function in a similar way as a visual badge of fighting experience or fighting ability. Visual signals that have been identified in submissive interactions among dolphins include flinching, looking away, and orienting the body away from another animal (Samuels and Gifford 1997). 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 Pryor (1991) suggests that gaze cues may be important for cetaceans in clear water as well as in air.

Many cetacean species have distinctive pigmentation patterns (e.g., Yablokov 1963; Mitchell 1970; Perrin 1997). Most biologists have emphasized the role of pigmentation patterns as camouflage or disruptive coloration against visually hunting predators (e.g., Madsen and Herman 1980; Würsig et al. 1990). Biologists find these pigmentation patterns to be very useful for identifying species and even individual animals, but little is known about whether cetaceans use them as signals in their own social interactions. Variation in pigmentation and morphology is correlated with age-sex classes among dolphins of the genus *Stenella* (Perrin et al. 1991). The pigmentation patterns among species such as the humpback whale are highly individually distinctive (Katona et al. 1979), so animals that swim within visual range would certainly have sufficient cues to discriminate a large number of individuals.

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 whistle vocalizations (D. K. Caldwell and M. C. 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 during the breeding season (see Clapham, chap. 7, this volume). In competitive groups, they emit streams of bubbles typically in a line as long as 30 m (Tyack and Whitehead 1983). A male escorting the female in such a group may place a bubble stream between a challenging male and the female, perhaps as a visual screen. Pryor (1991) reports that a young male spotted dolphin (*Stenella attenuata*) used a cloud of bubbles created by a breach as a visual screen to facilitate escape. Humpback whales are also reported to use bubbles in an unusual form of interspecific communication. In certain circumstances, feeding

humpbacks produce a series of large bubbles. Their prey seem to respond to these bubbles, and the humpbacks appear to use these bubble "nets" to increase the concentration of prey before they engulf a mouthful (see Clapham, chap. 7, this volume). As was discussed with aggressive contact behaviors, the concept of communication is usually limited to signals that evoke a response through information transfer, rather than through the physical effects of the signal. It is not known whether bubble nets act as a signal to fish or whether the bubbles act as an obstacle or physically concentrate the fish prey.

With the exception of bubbles, which are unique to aquatic animals, the visual signaling of marine mammals seems similar to that of their terrestrial relatives. Terrestrial animals also have male secondary sexual characteristics such as ornaments or weapons, they have visual agonistic displays that appear to be ritualized from fighting behavior, they use gaze cues, and they use pigmentation for camouflage. However, the range of vision is much more limited in water than in air, with daytime vision usually limited to a few meters in the sea.

### Acoustic Communication and Echolocation

Communication using the auditory modality is emphasized throughout the rest of this chapter. In this section, auditory processing and echolocation will be discussed. An understanding of auditory processing is important for evaluating which acoustic features of a vocal communication signal may be most salient to the recipient of the signal. Echolocation is an important vocal and auditory adaptation for many dolphins and toothed whales.

*Adaptations of cetaceans for sound production and hearing underwater.* The basic mechanisms for sound production are similar in cetaceans and terrestrial mammals: both make sound by passing air under pressure past membranes that vibrate. However, the differing densities of air and water make for some differences, as do the special needs of animals that dive while vocalizing. When a terrestrial animal vocalizes, it usually must open its mouth to propagate sound into the surrounding air. When cetaceans vocalize underwater, sound vibrations in their soft tissues, which are about the same density as seawater, transfer well to the surrounding medium. This means that cetaceans do not need to open their mouths or blowholes when they vocalize underwater. When terrestrial animals vocalize, they usually simply do so while exhaling, and fill their lungs on the next inhalation. However, many cetaceans vocalize underwater when they cannot breathe again for tens of minutes. For example, humpback whales may sing for 10–20 minutes

without surfacing to breathe and without emitting air bubbles. This observation suggests that if sound production involves the flow of air in the vocal tract, this air may need to be stored in the upper respiratory tract and recycled in between vocalizations.

Cetaceans have an auditory anatomy that follows the basic mammalian pattern, with some modifications to adapt to the demands of hearing in the sea. The typical mammalian ear is divided into three sections: the outer ear, the middle ear, and the inner ear or cochlea. The outer ear is separated from the inner ear by the tympanic membrane, or eardrum. In terrestrial mammals, the outer ear, eardrum, and middle ear function to transmit airborne sound to the inner ear, where the sound is detected in a fluid. Since cetaceans already live in a fluid medium, they do not require this matching, and cetaceans do not have an air-filled external ear canal.

The inner ear of cetaceans shares the same basic design with that of terrestrial mammals. The inner ear is where sound energy is converted into neural signals that are transmitted to the central nervous system via the auditory nerve. Sound enters the inner ear, or cochlea, via the oval window. This acoustic energy causes a membrane, called the basilar membrane, to vibrate. The motion of the membrane creates a shear force on hair cells, generating acoustically stimulated neural signals. The key to how the mammalian inner ear operates involves the mechanical tuning of the basilar membrane. This membrane is stiff and narrow at the basal end, near the oval window, causing it to vibrate when excited by high frequencies. Farther into the cochlea, at the apical end, the basilar membrane becomes wider and floppier, making it more sensitive to lower frequencies. Sensory cells at different positions along the basilar membrane are excited by different frequencies, and their rate of firing is proportional to the amount of sound energy in the frequency band to which they are sensitive. Thus the mammalian ear basically measures sound energy in a series of frequency bands.

The ability of mammals to discriminate different frequencies appears to be related to the density of neurons receiving input from sensory cells on the basilar membrane. The density of these ganglion cells is expressed as the number of cells per millimeter along the basilar membrane. Humans and the greater horseshoe bat (*Rhinolophus ferrumequinum*) are mammals with excellent hearing. They average about 1,000 ganglion cells per millimeter (humans: Schuknecht and Gulya 1986; bat: Bruns and Schmieszek 1980; reviewed in Ketten 1990). The greater horseshoe bat has an area along the basilar membrane that is particularly sensitive, corresponding to the frequency of its echoloca-

tion calls. This "acoustic fovea" has a density of 1,750 ganglion cells/mm (Bruns and Schmieszek 1980). As might be expected for animals that rely so heavily upon hearing, cetaceans have an unusually high density of these ganglion cells (Ketten 1990). Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, and spotted dolphins, *Stenella attenuata*, have about 2,000 ganglion cells/mm. The bottlenose dolphin has about 2,500 ganglion cells/mm. The harbor porpoise averages 2,750 cells/mm, and Ketten (1997) suggests that porpoises may also have an acoustic fovea at the frequency of their echolocation calls. Among mammals, dolphins have extraordinary abilities of discriminating different frequencies, and can detect a change of as little as 0.2% in frequency (Thompson and Herman 1975). This is roughly equivalent to the abilities of humans revealed in similar psychoacoustic tests.

*Hearing ranges in cetaceans.* The hearing ranges of animals can be estimated anatomically. The resonant frequencies of the basilar membrane can be estimated by measuring its dimensions. Ketten (1994) has analyzed inner ears from twelve cetacean species and suggests that there are three basic patterns. The baleen whales have inner ears that appear to be specialized for low-frequency hearing. The apical end is unusually wide and floppy, probably allowing these whales to hear sounds best in the range of approximately 20–200 Hz. All of the toothed whales studied by Ketten (1994) had inner ears that were specialized for high frequencies rather than very low frequencies. All of the smaller odontocetes had measurements from the basal end of the basilar membrane that were consistent with an upper limit of hearing well above 100 kHz. There appeared to be two basic odontocete inner ear types. The inner ears of animals such as *Tursiops* appeared to be consistent with a generalist adaptation for high-frequency hearing with best frequencies ranging from 40–70 kHz, while the inner ears of porpoises and the platanistid dolphins appeared to be particularly specialized for hearing above 100 kHz.

For cetaceans that are held in captivity, hearing ranges can be measured directly by training these animals to respond to tones. Audiograms plot the level of sound that is just detectable by a subject as a function of frequency. The lower a sound level a subject can detect, the more sensitive its hearing. Audiograms thus typically have a U-shaped curve, with low thresholds (best hearing) in a central frequency range and higher thresholds (less sensitive hearing) at higher or lower frequencies. Figure 11.2 presents audiograms for a range of toothed whales that have been tested in this way. All of these odontocetes have hearing that is specialized for sensitivity at frequencies well above what

Definitions of Acoustic Terms

**Frequency (Hz, kHz), wavelength, and bandwidth.** A sound that we perceive as a pure tone has a sinusoidal pattern of pressure fluctuations. The *frequency* of these pressure fluctuations is measured in cycles per second. The modern name for the unit of frequency is the *Hertz*, and just as 1,000 meters are called a kilometer, 1,000 Hertz are called a *kiloHertz*, abbreviated kHz. The *wavelength* of this tonal sound is the distance from one measurement of the maximum pressure to the next maximum. Sound passes through a homogeneous medium with a constant speed, *c*. The speed of sound in water is approximately 1,500 m per second, or roughly five times the value in air, which is 340 m/second. The speed of sound *c* relates the frequency *f* to the wavelength  $\lambda$  by the following formula:  $c = \lambda f$ . Not all sounds are tonal. Sounds that have energy in a range of frequencies, say in the frequency range between 200 and 300 Hz, would be described as having a *bandwidth* of 100 Hz.

**Sound intensity, sound pressure; decibel, dB; microPascal,  $\mu$ Pa.** Sound *intensity* is the amount of energy per unit of time (power) flowing through a unit of area. The intensity of a sound equals the acoustic pressure squared, divided by a proportionality factor that is specific for each medium. This factor is called the specific acoustic resistance of the medium and equals the density of the medium,  $\rho$ , times the speed of sound, *c*.

$$Intensity = \frac{Pressure^2}{\rho c} \quad (11.1)$$

If *I* and *I*<sub>ref</sub> are two intensities, then their difference in decibels (dB) is calculated as follows:

$$Intensity\ difference\ (dB) = 10 \log \frac{I}{I_{ref}} \quad (11.2)$$

For the intensity levels and pressure levels to be comparable in dB, the difference in sound pressure is defined as follows:

$$Pressure\ difference\ (dB) = 20 \log \frac{P}{P_{ref}} \quad (11.3)$$

This maintains the appropriate proportionality of intensity and pressure (if  $I \propto P^2$  then  $\log I \propto 2 \log P$ ) for sounds in the same medium. As an example, take a

sound measured to be 10 times the pressure reference. This would be a pressure difference of 20 dB re *P*<sub>ref</sub> by equation (11.3). Since intensity is proportional to pressure squared, the intensity of this sound would be 10<sup>2</sup> or 100 times the intensity of the reference. This would still be 20 dB re the reference intensity, by the definition of intensity in equation (11.2).

The primary definition of the decibel is as a ratio of intensities. The decibel always compares a pressure or intensity with a reference unit. The standard underwater reference *I*<sub>ref</sub> is the intensity of a sound having a pressure level of 1  $\mu$ Pa (Urlick 1983). The microPascal is a unit of pressure: 1  $\mu$ Pa = 10<sup>-6</sup> Pascal = 10<sup>-6</sup> Newtons/m<sup>2</sup>. Both intensities and pressures are referred to a unit of pressure, 1  $\mu$ Pa, in a form of shorthand. When an *intensity* is referred to *pressure* of 1  $\mu$ Pa, it really means referred to the intensity of a continuous sound of pressure equal to 1  $\mu$ Pa. Confusion about decibel references and pressure versus intensity can have significant practical consequences (Chapman and Ellis 1998).

**Doppler.** When echoes from a moving source bounce off a moving target, the frequency of the echo is shifted by the Doppler effect. The change in frequency  $\Delta f = (2vf)/c$ , where *v* is the difference in velocity between source and target and *c* is the speed of sound.

**Hydrophone.** A hydrophone is an underwater microphone that converts the pressure fluctuations of a sound into voltage fluctuations.

**Received Level and Source Level.** If you measure the pressure of a sound at some location with a calibrated hydrophone, you can report the received level of that sound in decibels, simply as 20 log *P*<sub>measured</sub>/*P*<sub>ref</sub>. If *P*<sub>ref</sub> = 1  $\mu$ Pa, then this would be expressed as Received Level = XX dB re 1  $\mu$ Pa. However, if this was measuring a specific sound source, and you want to report how loud it was, it is conventional to report the source level as measured one meter from the sound source. Source levels are expressed as Source Level = XX dB re 1  $\mu$ Pa at 1 m. If you measure the sound farther away, and you know how sound energy was lost as it propagated from 1 m to where you measured it, you can correct the received level to give an estimated source level.



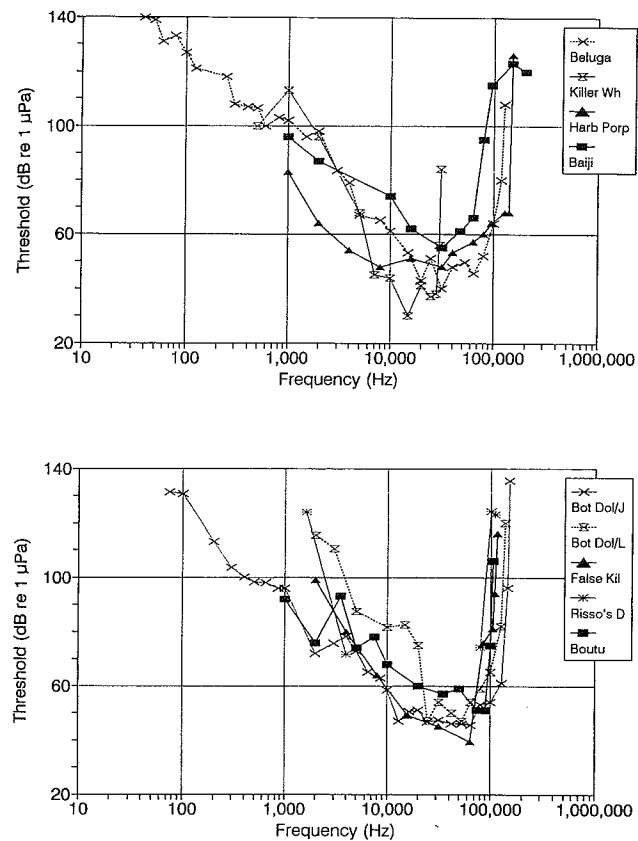


Figure 11.2. Audiograms of a variety of toothed whales tested in captivity. (From Richardson et al. 1995b.)

humans hear (reviews in Au 1993 and Richardson et al. 1995b). Their best frequencies extend from about 20 kHz, the upper limit of human hearing, to about 70 kHz. The upper limit of hearing in most toothed whales that have been tested extends above 100 kHz, or more than five times the upper limit of human hearing. Ambient noise levels are usually low in this high-frequency region (Urick 1983). In such a low-noise environment, the ability to detect a faint signal may depend upon having hearing that is sensitive compared with the typical noise levels. Noise levels tend to be much higher at lower frequencies, lowering the benefit of such sensitive hearing in this frequency range. The sensitivity of hearing in most of these toothed whales drops off at frequencies below about 10 kHz. Hearing has not been well studied below 1 kHz, but these animals appear to be relatively insensitive to low-frequency sounds (Richardson et al. 1995b). Hearing is still important at these low frequencies, however; many odontocetes produce vocal signals with dominant energy below several kHz (e.g., Connor and Smolker 1996; Overstrom 1983).

The frequency range of hearing has never been tested in baleen whales. Hearing is usually tested with trained ani-

mals, and baleen whales are so big that only a few have been kept for short periods in captivity. However, as mentioned above, the frequency tuning of the inner ear suggests they are specialized for low-frequency hearing (Ketten 1994). As we shall see, the vocalizations of baleen whales concentrate sound energy well below 1 kHz, and some species, such as fin and blue whales, produce sounds with dominant energy below 20 Hz, well below the frequencies humans can hear well. There tends to be a rough correlation between the frequencies at which most animal species can hear best and the frequencies typical of their vocalizations, so these low-frequency vocalizations of baleen whales also suggest the importance of low-frequency hearing.

**Echolocation.** Echolocation, defined as the ability to produce high-frequency clicks and to detect echoes that bounce off distant objects, is highly specialized in some odontocete species. Echolocation has been studied most in the smaller toothed whales that can be kept in captivity (Au 1993). Several distinct kinds of echolocation signals have been reported for different species. For example, figure 11.3 shows two examples of odontocete echolocation pulses, one from the bottlenose dolphin (*Tursiops truncatus*) and one from the harbor porpoise (*Phocoena phocoena*). The *Tursiops* pulse has a sudden onset, increasing to its peak level in tens of microseconds. The maximum peak-to-peak sound source level is quite high, >220 dB re 1  $\mu$ Pa at 1 m (see Box 11.1 for an explanation of how acousticians measure intensity of sound in decibels, or dB). These louder levels tend to be recorded from animals in open waters echolocating on distant objects. Peak-to-peak source levels as low as 150–160 dB re 1  $\mu$ Pa at 1 m have also been reported, typically from captive animals in tanks (Evans 1973). The *Tursiops* pulse in figure 11.3A was recorded from a trained dolphin as it was echolocating in open waters on a distant artificial target. When wild bottlenose dolphins are recorded as they echolocate, their pulses are typically reported to have energy in a broad range of frequencies from about 100 to 130 kHz (Au 1993). The *Tursiops* pulse in figure 11.3A has a peak frequency of 117 kHz and a bandwidth of 37 kHz. The echolocation pulses of harbor porpoise (fig. 11.3B) are quite different from those of bottlenose dolphins. They have a high-frequency component in the frequency band of 120–150 kHz, with sound source levels around 150–160 dB re 1  $\mu$ Pa at 1 m (Goodson et al. 1995; Møhl and Anderson 1973; Kamminga and Wiersma 1981). These porpoise pulses have a longer duration (hundreds vs. tens of microseconds), lower level, and narrower bandwidth (10–15 kHz vs. 30–60 kHz) than pulses from bottlenose dolphins (Au 1993). The

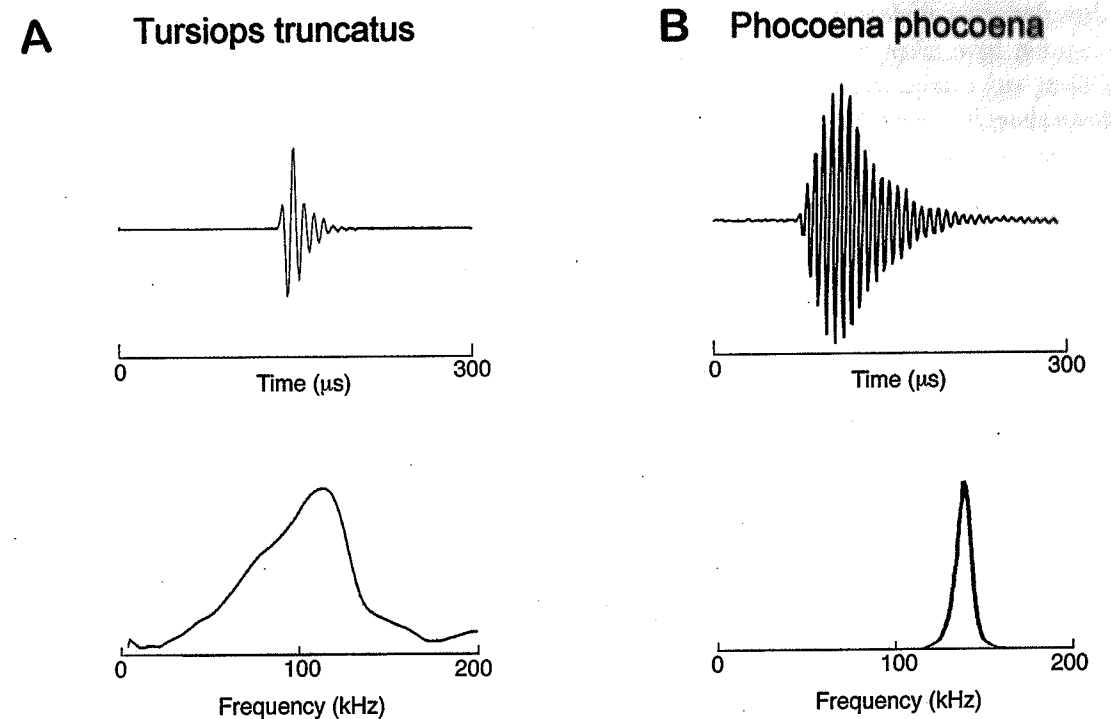


Figure 11.3. Waveforms (top) and spectra (bottom) of clicks from the bottlenose dolphin, *Tursiops truncatus* (A) and the harbor porpoise, *Phocoena phocoena* (B). The bottlenose dolphin figure is an average from an entire click train (adapted from Au 1980). The harbor porpoise figure is from a single click from a young animal (adapted from Kamminga 1988).

high-frequency hearing abilities of these small toothed whales are typically related to the need for these animals to detect faint echoes from their high-frequency echolocation clicks (Au 1993).

Odontocetes can vary their echolocation clicks depending on background noise. For example, the echolocation clicks of a beluga whale, *Delphinapterus leucas*, tested in San Diego had peak energy in the frequency band 40–60 kHz (Au et al. 1985). When the beluga was moved to Kaneohe Bay, Hawaii, where there is a high level of noise in these frequencies, it shifted the frequency of its clicks upward to mostly above 100 kHz. Moore and Pawloski (1991) investigated whether dolphins could be trained to modify the loudness or peak frequencies of their clicks. They successfully trained a bottlenose dolphin to produce clicks that were either high or low source level (>205 vs. <195 dB re 1  $\mu$ Pa at 1 m) or that had high or low peaks in frequency (>105 kHz vs. <60 kHz). Echolocating dolphins can discriminate the shape or composition of targets (e.g., Kamminga and van der Ree 1976), but there is little evidence of dolphins modifying their echolocation signals for different kinds of targets.

Many echolocation tasks involve ranges of less than several meters. Dolphins often inspect objects with echoloca-

tion at ranges as close as a few centimeters away. Bottlenose dolphins usually wait to hear the echo from a target before they produce the next click, and as these dolphins close in on the target, the interval between pulses usually decreases (Au 1993). This sounds to our ears like individual clicks blending into a buzz sound, but the dolphins are capable of much better temporal resolution in their hearing, and can resolve the individual clicks.

Dolphins do not use echolocation only at short ranges, but can detect objects at much greater distances than they can typically see them. An echolocating dolphin can detect a 2.5 cm metal target about 72 m away (Murchison 1980). The greater potential range of echolocation compared with vision may make it particularly useful for detecting obstacles or prey at a distance. If a cetacean were swimming rapidly in murky water, at depth, or at night, it seldom could see an obstacle rapidly enough to avoid it, but echolocation could be used to detect an obstacle far enough away to give even fast-swimming animals plenty of time to respond. Many cetaceans also feed in turbid water, at depth, or at night when there is little downwelling light from the sky. Some of these animals may visually detect luminescent prey nearby, but there are many circumstances in which 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. Little is known about how wild dolphins use echolocation to perform tasks such as obstacle avoidance or prey detection, prey selection, or prey capture.

The problems of studying how cetaceans use echolocation to forage are particularly difficult for deep-diving animals such as sperm whales, because it is so difficult to observe them feeding at depths of many hundreds of meters. When sperm whales dive and forage, they tend to produce series of click sounds with relatively stable interpulse intervals of 0.5–2.0 seconds (Whitehead and Weilgart 1990, 1991). This association of what Weilgart and Whitehead (1988) call "usual clicks" with diving and feeding has led most biologists to hypothesize that these regular click trains function for echolocation (Backus and Schevill 1966; J. C. D. Gordon 1987a; Whitehead and Weilgart 1990). Watkins (1980), on the other hand, argued that sperm whale clicks were not suited to echolocation of prey. For example, the clicks of sperm whales are lower in frequency, longer in duration, and much less directional than the high-frequency clicks of dolphins (Au 1993). These observations led Watkins to argue that usual clicks are social signals used by diving whales to maintain contact with one another.

The echolocation hypothesis for the usual clicks of sperm whales has not been definitively tested. However, Goold and Jones (1995) have used acoustic models to evaluate the potential range at which the clicks of sperm whales might be used to detect their squid prey. These calculations necessarily involve assumptions and rough estimates of some parameters, but they suggest that sperm whales might detect squid at a range of 200–680 m. This range is consonant with the low end of the interpulse intervals observed in usual clicks, assuming the whale waits to make a new click until it hears an echo return. The speed of sound in seawater is near 1,500 m/sec, so the round-trip travel time to a target 750 m away would be about one second. If sperm whales producing usual clicks are waiting for potential echo returns before producing the next click, then the 0.5–2.0-second intervals between usual clicks would suggest maximum working ranges between about 375–1,500 m. While the shortest intervals correspond to the estimated detection range, the longer intervals involve much longer round-trip travel times.

Unfortunately, Goold and Jones (1995) did not correct for the bandwidth of hearing in their application of the sonar equation, and this inflated their estimated range of detection. They defined the threshold at which sperm

whales are just able to detect echoes from their clicks as occurring when the echo level equals the ambient noise level. To make a biologically realistic estimate, it is critical to match the noise and echo levels in equivalent bands, optimally ones that are appropriate for the hearing of the animal. Goold and Jones did not do this, but rather compared a broadband estimate of the source level of sperm whale clicks across a frequency range of thousands of Hz to a spectral level of noise in 1 Hertz band. Most mammals integrate sound energy over frequency bands roughly about one-third octave in breadth. If the spectral noise estimates used by Goold and Jones are corrected to third-octave band levels, leaving all other aspects of the calculation the same, the estimated detection range drops from 200 m to 68 m at 2 kHz and from 680 m to 108 m at 10 kHz. These reduced ranges match the round-trip travel time much less well than those resulting from the unrealistic echo:noise comparisons.

The only way to find out whether sperm whales do use their clicks for echolocation is to conduct empirical tests. Sperm whales have seldom been held in captivity for long enough to conduct the kind of tests that have been so successful with dolphins. Tags that can record sounds at the whale are important new tools for conducting this kind of research with free-ranging animals (e.g., see Fletcher et al. 1996 and Burgess et al. 1998 for acoustic recording tags for deep-diving elephant seals). If such a tag had sufficient dynamic range, it ought to be able to record clicks of individual sperm whales throughout the dive cycle, as well as detect the hypothesized echo returns at the whale. If echoes were detected, and if they were followed by specific responses such as pursuit and capture of prey or avoidance of obstacles, then this would provide much stronger evidence for echolocation.

The only echolocation system that has been demonstrated in cetaceans involves the use of high-frequency clicks by small odontocetes. These animals clearly have evolved a highly specialized system for echolocation. However, sound may be used to explore the environment even among cetaceans that are not specialized for high-frequency echolocation. Several biologists have suggested that whales might be able to sense echoes of low-frequency vocalizations from distant bathymetric features to orient or navigate (Norris 1967b, 1969; Payne and Webb 1971; Thompson et al. 1979). Some baleen whales produce loud low-frequency sounds that are particularly well suited for long-range propagation. For example, finback (*Balaenoptera physalus*) and blue whales (*B. musculus*) produce series of loud sounds well below the lowest frequencies humans can hear, centered around 10–30 Hz. The sounds of blue

whales last several tens of seconds (Cummings and Thompson 1971a; Edds 1982), while the most common sounds reported from finbacks comprise series of one-second pulses (Watkins et al. 1987). Biologists have recently used bottom-mounted hydrophones to locate and track whales over long ranges, including one blue whale tracked for >1,700 km over 43 days (Costa 1993). These results have confirmed the predictions of Payne and Webb (1971) and Spiesberger and Fristrup (1990), who used acoustic models to estimate that these low-frequency whale calls could function for communication or orientation over very long ranges. Payne and Webb (1971), Watkins et al. (1987), and McDonald et al. (1995) conclude that these signals have better design features for communication than for listening for echoes from features on the seafloor. On the other hand, Clark (1993) has suggested that the low-frequency calls of finback or blue whales would produce easily identifiable echoes from seamounts hundreds of kilometers away. Even if these sounds are used primarily for communication, echoes from these signals could be very useful for orientation of migrating animals. If these uses of sound to explore the environment met an important biological need, they could influence the further evolution of cetacean signals.

None of these suggestions that whales may use low-frequency sounds to echolocate on bathymetric features have been tested, but there is suggestive evidence that migrating bowhead whales, *Balaena mysticetus*, use echoes from their calls to detect ice obstacles. Vocalizing bowhead whales avoid floes of deep ice at ranges much farther than the limit of underwater visibility (Clark 1989; George et al. 1989). Ellison et al. (1987) used acoustic models to show that deep-keeled ice may produce strong echoes from the low-frequency calls of migrating bowhead whales, and they suggested that bowhead whales may use these echoes to sense and avoid deep ice.

### Functional Categories of Acoustic Communication Signals in Cetaceans

A signaling animal incurs costs such as the energy and time required to produce the signal and the risks of attracting predators or alerting prey. Some animals that are not the intended recipients of the signal may overhear it and respond to it to their own benefit, and often to the detriment of the signaler. Myrberg (1981) calls these unintended recipients "interceptors" of the signal. Interspecific communication often includes interactions in which predators or prey may intercept signals. This risk of detection by an interceptor may represent a significant component of the

cost of signaling in many settings. If production of the signal is to confer a selective advantage, then these costs must be offset by a benefit to the signaler induced by changes in the behavior of a recipient of the signal. There are a variety of benefits associated with different potential recipients. Common forms of intraspecific communication involve signaling to potential mates or potential competitors. In species with parental care, communication is often required between parent and offspring. In social species, animals often communicate to maintain contact with other members of the group. In species with individual-specific social relationships, signals are required for individual recognition and for maintaining these relationships.

### Interspecific Communication and Interception

*Interception by prey.* One potential problem with producing echolocation sounds for detecting prey is that an echolocating predator runs a risk of the prey intercepting the echolocation signal. This advance warning may help the prey escape or avoid detection. Odontocete predators may be able to alter their echolocation strategies to reduce the probability that acoustically sensitive prey (including seals and other cetacean species) will intercept their echolocation signals. For example, in the Puget Sound area of the Pacific Northwest, there are two populations of killer whales, *Orcinus orca* (see Baird, chap. 5, this volume). One population feeds on marine mammals, a prey that is sensitive to the frequencies of killer whale clicks; the other population feeds on salmon, a prey that is likely to be much less sensitive. Barrett-Leonard et al. (1996a) report that mammal-eating killer whales vary the intensity, repetition rate, and spectral composition within their click trains, apparently making these clicks more difficult for their acoustically sensitive prey to identify than the regular click series of fish-eating killer whales.

There is suggestive evidence that even some species of fish may have special abilities to intercept the high-frequency echolocation sounds of their odontocete predators (Mann et al. 1997). Fish such as American shad (*Alosa sapidissima*), alewives (*Alosa pseudoharengus*), herring (*Alosa aestivalis*), and cod (*Gadus morhua*) are able to detect intense sounds of frequencies much higher than is typical of their own vocalizations (Astrup and Møhl 1993; Dunning et al. 1992; Mann et al. 1997; Nestler et al. 1992). Some of these species are prey for echolocating odontocetes. The only known natural sources of sounds with the intensity and frequency of these ultrasonic stimuli are the clicks of echolocating toothed whales. Clupeid fishes have an unusual specialization for hearing: an air-filled chamber that abuts the inner ear and is thought to increase the sensitivity

of hearing (Blaxter et al. 1981). This auditory specialization is shared by all living clupeids, suggesting an origin in early clupeids, which date well before the origin of echolocating cetaceans. If this auditory specialization not only enhances sensitivity at low frequencies, but also enables ultrasonic hearing in clupeids, then this ultrasonic sensitivity may be a preadaptation (Mann et al. 1997), rather than having evolved specifically to enable interception of odontocete predators. Several clupeids respond with escape behavior when they hear ultrasonic pulses, and this response may represent an adaptation for escaping odontocete predators.

*Responses of cetaceans to their own predators.* Animals may produce signals to confuse or startle an approaching predator. For a visual example, dwarf sperm whales of the genus *Kogia* release a cloud of opaque reddish anal fluid when they are disturbed (Scott and Cordaro 1987). As with squid ink, this release of opaque fluid is thought to act as a visual screen, giving the whale better odds of concealment or escape. Whales and dolphins may also intercept the signals of their predators and respond to avoid detection or capture. One of the most common predators of many cetaceans is another cetacean, the killer whale (Jefferson et al. 1991). Killer whales often vocalize while foraging (Ford 1989), providing their cetacean prey the opportunity to intercept these signals and avoid capture. When potential prey intercept the calls of a dangerous predator, they often show strong responses. These strong, easy-to-observe responses make this a good phenomenon to study using playback experiments. For example, when Fish and Vania (1971) played killer whale calls to beluga whales, *Delphinapterus leucas*, that were feeding on salmon in an Alaskan river, the beluga whales showed a strong avoidance response. Gray whales migrating along the coast of California responded to playback of killer whale calls by swimming rapidly inshore into beds of kelp (Cummins and Thompson 1971b; Malme et al. 1983).

### Intraspecific Communication and Interception

This section is organized around the potential intraspecific recipients of a signal, along with the problem(s) that the signaling is designed to resolve. These categories include the following signaling functions:

- increase one's chances of mating
- agonistic relationships or fighting assessment
- parent-offspring recognition

- maintaining the coordination and cohesion of individuals within a group
- maintaining individual-specific social relationships

The "communication-as-manipulation" view discussed at the beginning of this chapter treats signals as advertisements designed to manipulate the choices of recipients, and leads one to expect that the recipients may be selected to develop a certain amount of sales resistance. Just as the signaler balances costs and benefits when deciding whether to signal, the receiver may balance the costs and benefits of responding at all to a signal or of selecting any of several potential responses. The structure of these displays cannot be understood unless one considers how the signal is designed to manipulate the choices of animals that receive the display. For example, when we think of an animal responding to a signal, we usually think of an immediate response, such as the avoidance responses of animals hearing the sounds of a predator. However, one animal may produce a long series of signals to modify the outcome of one choice by a receiving animal. The receiver may make its choice only after hearing hundreds or thousands of advertisements from many different signalers. If our model of communication was limited to expecting immediate responses based upon transfer of information from a single signal, we would have a hard time understanding these kinds of advertisements.

### Signals for Improving Chances of Mating

A common form of animal advertisement is the reproductive advertisement display made by an animal that is seeking to improve its chances of mating. Charles Darwin (1871) coined the term sexual selection to describe the evolutionary selection pressures for traits that are concerned with increasing mating success. Darwin described two basic modes of sexual selection: those that increase the likelihood that an animal will outcompete a conspecific of the same sex for fertilization of or by a member of the opposite sex (intrasexual selection), and those that increase the likelihood that an animal will be chosen by a potential mate (intersexual selection). More recent reviews have included a third mode, in which a male may attempt to limit the choice of a female by coercing her to mate with him and not with other males (Smuts and Smuts 1993; Clutton-Brock and Parker 1994).

Sexual selection can create different selection pressures for reproductive advertisement displays than for signals designed for simpler exchanges of information. Selection is likely to favor these other signals being quieter and more

difficult to detect to avoid the costs of interception. Reproductive advertisement displays are typically designed to be attention-getting. This involves potential risks, such as attracting a predator, but the intended receiver may use the advertisement in part to evaluate how well the displaying animal can deal with these risks. Since the biologist is more likely to observe advertisement signals than other, more-difficult-to-intercept signals, advertisements are better known than many other kinds of animal signals, such as the quiet interchanges of mother and young when they are close together, predator alarm calls, or the nighttime flight calls of migrating birds.

Examples of reproductive advertisement displays include the songs of birds and whales. Songs are usually defined as acoustic displays in which sequences of discrete sounds are repeated in a predictable pattern.

*Songs of humpback whales.* The songs of humpback whales are the best-known advertisement display in the cetaceans. Humpback songs have a hierarchical structure that was described by Payne and McVay (1971). Each song is made up of three to nine themes that tend to be sung in a particular order, and it often takes about ten to fifteen minutes before a singer returns to the initial theme. Each theme is made up of phrases that repeat a variable number of times before a new theme is heard. Each phrase lasts about fifteen seconds and contains a series of sounds. Figure 11.4 shows a spectrogram of a humpback song recorded in waters near the Hawaiian Islands and made during a period when songs contained up to nine themes.

Humpback song is so loud and distinctive that it is relatively easy to record, and biologists now have recordings of song from many humpback breeding areas over periods of many years. There appears to be a strong force for vocal convergence in the songs of humpback whales on a breeding area at any one time, coupled with progressive change in all aspects of the song over time (K. B. Payne et al. 1983; Payne and Payne 1985). Recordings of humpback song made from different whales in the same breeding area at the same time are quite similar. At any one time, all of the singers within a breeding area sing the same themes in the same order, and the individual sounds that make up the song are quite similar. However, the song changes dramatically from month to month and from year to year. For example, theme 3 from figure 11.4 was on its way out in March of 1977. In hundreds of recordings made later that spring and for years afterward, it was never heard after the end of March 1977. There is no indication that these changes in the song reflect changes in the message, for the

whales appear to be engaged in similar interactions even as the song changes.

Humpback song is usually recorded during the winter in the tropical breeding grounds of these whales (see Clapham, chap. 7, this volume). This observation led Schevill (1964: 310) to suggest that the song "may be an audible manifestation of more fundamental urges." The primary reason that we can discuss the social functions of humpback song at all rests on the ability of biologists to identify and follow singing whales at sea, and to track their interactions with other whales. Singing humpback whales often surface to breathe once per song during a particular theme, "blowing" or breathing during the silent intervals between notes (Tyack 1981). Biologists can deploy a hydrophone from a small boat to listen for singers. If they can get close enough to one singer that it is louder than the others in the background, they can often locate the singer by careful visual scanning during this part of the song. Once a singer has been identified in this way, its sex can be determined by underwater photography of the genital slit (Glockner 1983) or by taking a small tissue sample for genetic determination of sex (Baker et al. 1991; Palsbøll et al. 1992; see Whitehead et al., chap. 3, this volume). The continuous vocalizations and predictable surfacing behavior of singers allow biologists to follow them for hours. These observations have shown that almost all singing humpbacks are lone adult males, and that their songs are repeated in bouts that can last for many hours.

Observation from elevated shore stations has been important for studying species, such as humpbacks, that concentrate in coastal waters. Observers on land can use a surveyor's theodolite to pinpoint the location of each whale surfacing, and can communicate by radio with vessels that can obtain more detailed behavioral and acoustic data by following whale groups (Tyack 1981). This combination of shore- and ship-based observations has revealed interactions of singing whales with groups nearly 10 km away (Tyack and Whitehead 1983), and is well suited to observing whales for periods up to ten hours. These visual locations can also be linked to acoustic locations from arrays of hydrophones (Frankel et al. 1995). This acoustic location technique provides some evidence suggesting that singers tend to be evenly spaced. The interactions of whales are so much slower than our own pace that it is often necessary to make a plot of movement patterns and behavioral displays to make sense out of an interaction that took many hours to unfold.

A variety of results have encouraged biologists to suggest that humpback song plays a role in male-male competition:



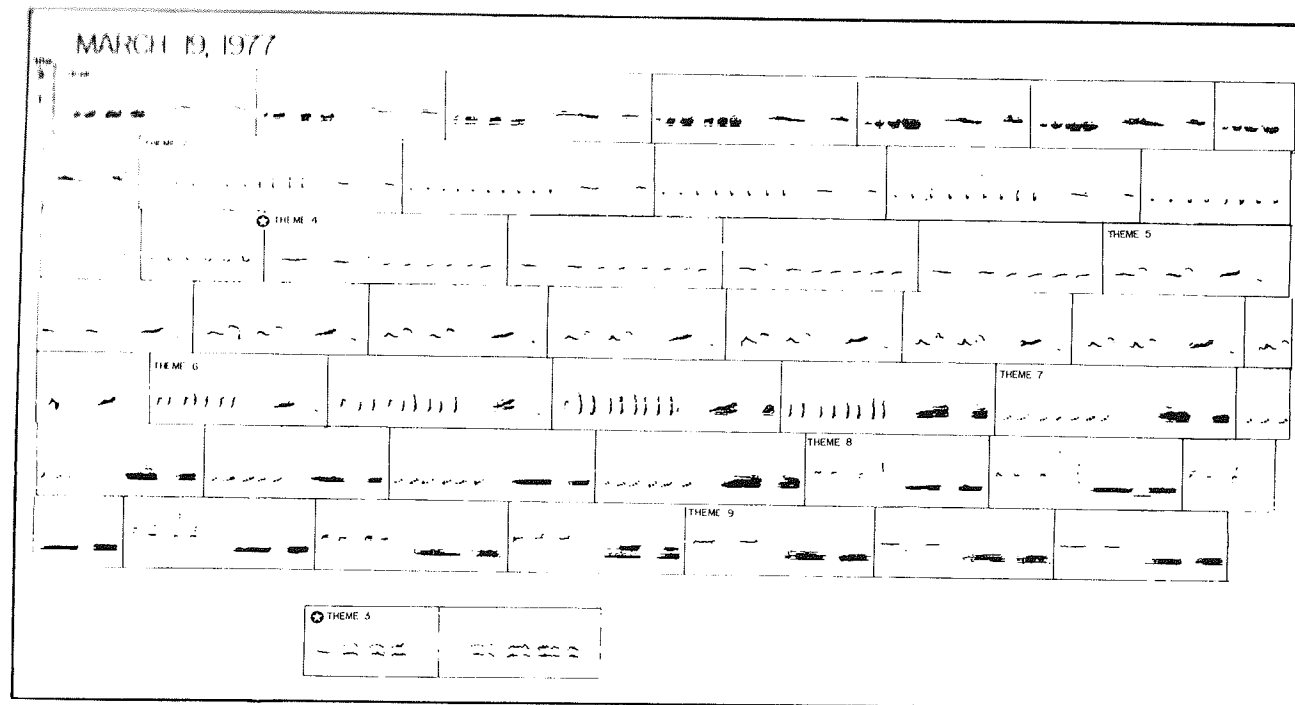


Figure 11.4. Spectrogram of the song of a humpback whale, *Megaptera novaeangliae*. This song was recorded from a lone humpback on 19 March 1977 in the Hawaiian Islands. Each line represents 120 seconds; this song took seven lines, or fourteen minutes, before repeating the initial theme. The phrase boundaries are marked by vertical lines. The x-axis indicates time; the y-axis indicates frequency in kHz. The third theme was not included in this song, but was in the next song of this whale, as indicated by the star in the spectrogram. (From K. B. Payne et al. 1983; courtesy Roger Payne.)

- Song appears to maintain distance between singers (Tyack 1981; Frankel et al. 1995; Helweg et al. 1992).
- No known females were attracted to playbacks of song (Tyack 1983; Mobley et al. 1988).
- 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; Darling 1983).

These behavioral observations are clearly consistent with the idea that song plays a role in mediating male-male interactions.

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 (see Catchpole 1982 for a discussion regarding bird song). The use of songs to mediate spacing among 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 fea-

tures 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 common and 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 and rarer responses of females to singers are not biologically significant. The critical question here is whether females choose a mate based upon his song. Copulation has never been observed in humpback whales, so little evidence has been collected to address this question. However, genetic analysis of paternity is a much more direct indicator of male reproductive success. Extensive efforts to biopsy humpback whales now make genetic analysis of paternity a realistic option for this species (Clapham and Palsbøll 1997).

In the absence of direct data on the relative function of song in male-male competition versus female choice, there may be some indirect evidence from the acoustic structure of the song. Much more is known about relationships between acoustic structure and social function in the songs of birds than in whales. In the next few paragraphs, I will

apply some of these songbird results to humpback song. Several ornithologists have attempted to relate specific acoustic features of the songs of birds to the relative importance of intra- versus intersexual selection. Catchpole and Slater (1995) suggest that songs used to attract females may be selected to be long, complex, and continuous, while songs used for intrasexual competition are likely to be shorter, simpler, and sung with gaps, so that a singer can listen for rival males. Catchpole (1982) 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, and they do not respond to the song of another male by immediately matching the sounds produced by that male, nor do they respond to song playbacks by singing themselves. All of these features are consistent with the hypothesis that humpback males sing in part to influence the mating choices of females.

There are also some acoustic features of humpback song that have been associated with intrasexual selection. Baker and Cunningham (1985) suggest that intrasexual selection tends to select for rapid song change and convergence in the songs of neighboring males. The basic idea is that young males may benefit from mimicking the songs of territorial neighbors with greater attractiveness to females, and the more attractive males may then have to change their song to avoid this competitive mimicry. Humpback males on the breeding grounds are not thought to be territorial, and there is no evidence that this kind of arms race occurs with humpback whales, but both rapid change and convergence between individuals are striking features of humpback song.

There are problems with extrapolating from models of bird song to singing whales, because whales live in an environment with significant differences from those of most songbirds. In particular, while birds must lay eggs in a nest, whales are not bound to a fixed site, but meander at will. During the breeding season, females with young may seek out clear, protected waters, but humpbacks do not stay in one site for long, nor does either sex appear to defend territories on the breeding ground. Tyack (1981, 1982) followed interactions between singers and other whales within 5–10 km of a shore station, and the same individual whales were seldom sighted across days within this site. If males do not have small territories and consistent neighbors, then they would be unlikely to form the subdialects described by Baker and Cunningham (1985) for birds. Also, sound propagates so far in the ocean that the songs of whales have a much longer range than those of most birds. These differ-

ences may help account for the unusual pattern of vocal convergence and continual change in the songs of entire populations of humpback whales, a pattern that differs from that of most songbirds.

In summary, there is evidence suggesting that humpback song plays a role in both male-male competition and female choice. Observations of interactions between humpbacks emphasize the role of song in mediating interactions between males, but females may also monitor, approach, and join with singers. The acoustic structure of humpback song clearly has attributes associated with both intra- and intersexual selection, and is more complex than would be expected for a signal used only in male-male interactions (Helweg et al. 1992).

*Songs of bowhead whales.* In addition to humpback whales, several other species of baleen whales are reported to produce songs that are thought to be reproductive advertisement displays. However, the behavioral contexts of song production are not as well understood in these species as in humpback whales. Bowhead whales spend their winter breeding season in Arctic waters, where biologists have few opportunities to observe them. The songs of bowhead whales have been recorded in the spring as they migrate past Point Barrow, Alaska (Ljungblad et al. 1982). Bowhead songs are simpler than those of humpbacks, consisting of a few sounds that repeat in the same order for many song repetitions. Like humpback songs, bowhead songs appear to change year after year (Clark and Johnson 1984; Clark 1990; Würsig and Clark 1993). However, little is known about behavior concurrent with singing, and there are few reports of bowheads observed during their winter breeding season in Arctic waters.

*Long-range communication in finback whales.* In the section on echolocation, I described low-frequency vocalizations of finback and blue whales that appear to be adapted for long-range propagation in the ocean. As described in that section, there has been speculation that these signals may function for long-range echolocation of large-scale geographic targets such as seamounts, which might be used for orientation and navigation. However, it has also been suggested that the long series of low-frequency pulses produced by finback whales may also be a reproductive advertisement display produced by males (Watkins et al. 1987). Finback whales produce pulses with energy in a range roughly between 15 and 30 Hz (Watkins et al. 1987), near the lowest frequencies that humans can hear. Each pulse lasts on the order of one second and contains twenty cycles. The source level of the pulses ranges from about 170 to 180 dB re 1

$\mu\text{Pa}$  at 1 m (Patterson and Hamilton 1964). Particularly during the breeding season, finbacks produce series of pulses in a regularly repeating pattern. These bouts of pulsing may last for longer than one day (Watkins et al. 1987). The seasonal distribution of these pulse series has been measured near Bermuda, and it matches the breeding season quite closely (Watkins et al. 1987). This correlation has been used to suggest that the pulse series may function as reproductive advertisement displays (Watkins et al. 1987). However, finback whales are common in waters near the latitude of Bermuda only during the winter breeding season, so few would be likely to be heard there at other seasons even if they did vocalize at that time. Similar recordings in more polar waters will be required to test how frequently these whales produce these series of pulses outside of the breeding season.

Finback whales disperse into tropical oceans during the mating season, unlike other species such as humpback and gray whales, which are thought to congregate in well-defined breeding grounds. The functional importance of a signal adapted to long-range communication is obvious for animals that disperse over ocean basins for breeding. However, even though biologists can hear finback pulses at ranges of hundreds of kilometers by listening at appropriate depths, the effective range of these signals for finbacks themselves is not known. Until very recently, marine bioacousticians have had few methods that would allow us to detect whether a whale was responding to the calls of another whale more than several kilometers away. The longest range over which whales have been observed to respond to the sounds of other whales is approximately 10 km (Tyack and Whitehead 1983; Watkins and Schevill 1979).

The U.S. Navy has recently made networks of bottom-mounted hydrophone arrays available to biologists (Costa 1993). These arrays will allow biologists to track vocalizing whales hundreds of kilometers away, and may help us to ascertain whether whales actually communicate in vocal exchanges over these long ranges. Just because biologists can detect these signals over such long ranges, however, does not mean that the intended recipients are that far away. If the signals are used in competitive interactions, for example, and if the louder vocalizer has an advantage, then selection could favor the evolution of signals much louder than required to be just detectable at the typical range of the intended recipient.

*Mate guarding in bottlenose dolphins.* The discussion above of reproductive advertisement displays emphasizes female choice and competition between males. There are also species in which males may adopt a strategy of attempting to

preempt female choice by guarding a receptive female and preventing her from mating with other males (Smuts and Smuts 1993; Clutton-Brock and Parker 1994). As described by Connor et al. (chap. 4, this volume), groups of two or three adult male bottlenose dolphins in Shark Bay, Western Australia, may form consortships with an adult female. A coalition of males may start such a consortship by chasing and herding a female away from the group in which they initially find her. Some of these consortships appear to be attempts by the males to limit choice of mate by the female, who may try to escape from the males.

Males in these coercive consortships produce distinctive trains of low-frequency clicks, called "pops" (Connor and Smolker 1996). These pops have peak frequencies of 300–3,000 Hz, far below the clicks typically reported for echolocation. They occur at rates of about 6–12 per second in trains of about 3–30 pops. When a herded female hears these pops, she shows a strong tendency to turn toward the popping male and to approach him within seconds. A male may produce aggressive displays toward a female who fails to approach after he pops. These may include head jerks, chases, or physical contact. Much of this aggression is also typically associated with the production of pops by males. Connor and Smolker (1996) argue that males that are consorting with and guarding a female produce these pops to induce her to remain close.

#### Signals to Competitors: Predictive Signaling or Fighting Assessment

Animals often find themselves in a situation in which they must compete with a conspecific for access to a critical resource. Competitors often confront one another in a contest in which there will be a winner and a loser. In most of these contests, it will be worth a competitor's while to gather some information on the willingness and ability of its opponent to fight. Both competitors often have a shared interest in gaining this information, and many contests start with a ritualized phase of exchanging displays (see chapter 21 of Bradbury and Vehrencamp 1998 for a review of threat display contests). While competitive contests sometimes involve physical contact and injury, they may be settled prior to such escalation through a series of displays. If one contestant concludes from this initial assessment phase that it would be likely to lose a fight, or that the potential cost of injury outweighs the potential benefit of winning, then it may gain by breaking off and leaving the contest (Krebs and Davies 1993). In this case, it may benefit from producing a submissive display to signal an end to the contest to the opponent.

The communicative signals used in agonistic interac-

tions have several functions. Some features of signals may correlate with attributes that are good predictors of fighting ability, such as age, physical condition, or size. These basic attributes cannot be changed without considerable cost. If a contestant is using a signal to estimate the fighting ability of an opponent, then the signal need not necessarily predict an immediate behavioral response by the signaler, but it is critical that the signal involve features that are reliable indicators of fighting ability. Other agonistic signals may be used to assess the willingness of an opponent to escalate or to predict its next actions. Some theoretical analyses of fighting emphasize the costs of producing signals that help an opponent to predict one's behavior (e.g., Maynard Smith 1974). These analyses highlight the potential benefit of bluffing or of tailoring signals so they do not allow an opponent to predict immediate responses. However, there is evidence of predictive signaling from a diverse array of species. The potentially high risks of making a mistake in assessing an opponent in an all-out fight may encourage a more or less "honest" assessment phase (Hauser and Nelson 1991). For example, male African elephants (*Loxodonta africana*) produce vocal, chemical, and postural cues about their willingness to fight other males during the breeding season (Poole 1987). Poole (1987, 1989) argues that these cues provide accurate signals that males frequently use in deciding whom and when to fight. If the competitors are closely matched, they may escalate to more costly displays, which may serve the functions of more accurate assessment of the competitor or increasing the likelihood that the competitor will stand down.

The best description of agonistic interactions and displays in cetaceans stems from observation of captive bottlenose dolphins, *Tursiops truncatus*. Samuels and Gifford (1997) conducted a quantitative assessment of agonistic interactions among bottlenose dolphins. Their analysis focused on a specific set of aggressive or submissive behaviors. Following earlier work with primates (Hausfater 1975), a dolphin was said to have lost an interaction if and only if it produced a submissive response to either a neutral or an aggressive behavior from its opponent. This use of submissive behaviors to define which animal won or lost the interaction differed from most previous work on dominance in dolphins, which focused more on aggressive than on submissive behaviors. The submissive behaviors involved either fleeing from an opponent and leaving the contest or "flinching." This "flinching" behavior, which was previously little noted, involves an immediate recoil in response to an action by the opponent.

Most of the aggressive behaviors defined by Samuels and Gifford (1997) were behaviors that are directly involved in

a fight; these included chasing, pinning, ramming, hitting, or biting an opponent. However, they also included threat displays. A graded series of threat displays has been defined by Overstrom (1983) for captive bottlenose dolphins (fig. 11.5). Overstrom suggests that the earliest stages of a threat may involve one dolphin simply directing pulsed sounds toward another. The dolphin may escalate the threat by producing an open mouth threat display while emitting distinctive bursts of pulses. Overstrom suggests that the longer in duration or the louder in sound intensity these burst-pulses are, the stronger the threat. As another step in the escalation, the animal may accentuate this display with abrupt vertical head movements. This is similar to the head jerk display that Connor and Smolker (1996) associate with the pop vocalizations produced by wild male dolphins when they are aggressively herding an adult female. The jaw clap is a commonly cited aggressive display in dolphins, and is interpreted by Overstrom as one of the most intense threat displays. A dolphin starts the jaw clap display with an open mouth. The jaw clap consists of a rapid and abrupt closure of the gaping jaw, accompanied by an intense pulsed sound (fig. 11.6). Overstrom seldom recorded a dolphin producing a jaw clap when it had not already produced some burst-pulsed sounds, and the probability of an animal producing a jaw clap increased as the duration of the burst-pulsed sounds increased. Overstrom's framework for describing a graded series of threats in bottlenose dolphins should be viewed more as a hypothesis than as a definitive result, pending further analysis of how these displays function in agonistic interactions.

Many of the agonistic visual displays used by bottlenose dolphins are related to movements used to inflict injury. For example, the open mouth display looks like the first step in preparing to bite. Norris and Møhl (1983) suggested that some click sounds used by dolphins and toothed whales may be so intense that they could be used to stun or threaten conspecifics. Overstrom (1983) suggested that the loudest burst-pulsed sounds or the jaw clap may be intense enough to produce tactile or auditory irritation. If these suggestions were true, then lower-intensity pulsed calls might be used as a direct threat, similar to the way an open mouth display may threaten a bite. However, there is no evidence that these calls do function as weapons, so these interpretations remain speculative.

Most of the examples of agonistic signals described above involve "predictive signaling," in which a signal may reliably indicate future behavior, such as whether a competitor is ready to escalate (Hauser and Nelson 1991). The escalating series of aggressive displays described by Overstrom (1983) fit this "predictive signaling" model. The

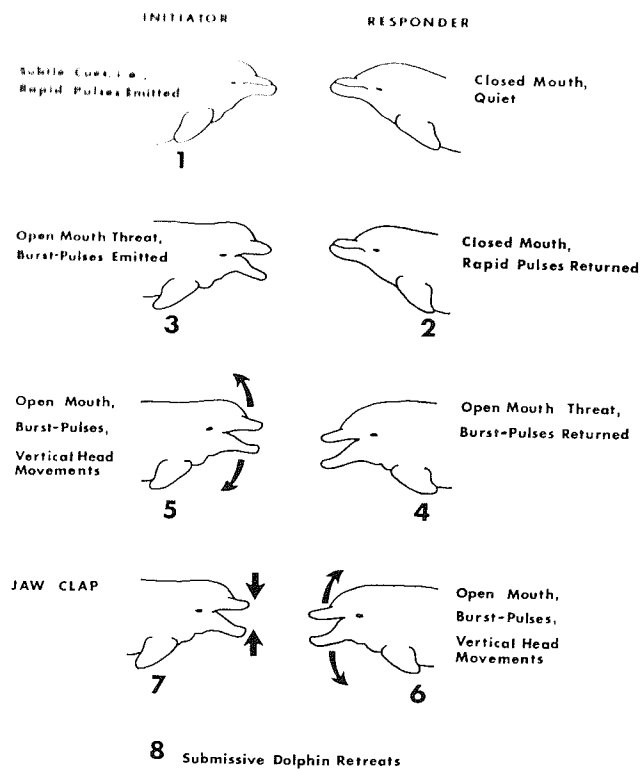


Figure 11.5. Visual and acoustic threat displays of the bottlenose dolphin, *Tursiops truncatus*. (From Overstrom 1983.)

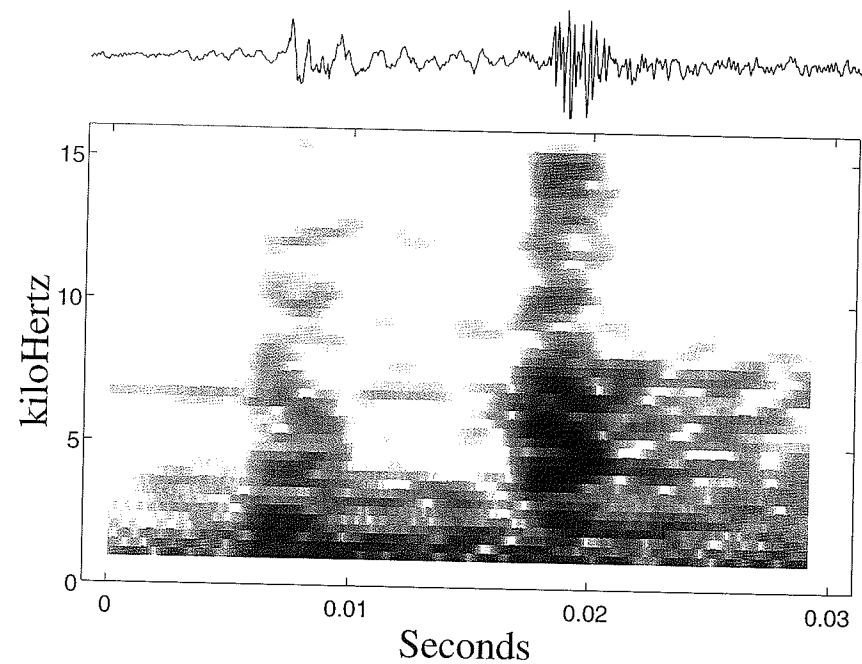


Figure 11.6 Spectrogram of a jaw clap from a bottlenose dolphin, *Tursiops truncatus*.

pops described by Connor and Smolker (1996) also may be interpreted as early stages of a threat to escalate aggression if the consorting female does not approach the popping male. The pop vocalization may reliably indicate the readiness of the male to attempt to herd the female more aggressively.

Let us now switch focus from predictive signaling to signals that allow animals to assess the fighting ability of opponents. Body size is a good predictor of the outcome of fights in many animal species (Krebs and Davies 1993). A variety of animal species assess the lowest frequency of vocalization as an indicator of body size (e.g., Davies and Halliday 1978 for anurans; Clutton-Brock and Albon 1979 for a terrestrial mammal). There is clear evidence for such an effect in some marine fishes. Myrberg et al. (1993) demonstrated a strong correlation between the body size of the bicolor damselfish, *Pomacentrus partitus*, and the fundamental frequency of a chirp sound produced by males. They suggested that differences in the peak frequency of chirps result from differences in the volume of the swim bladder. The basic principle here is that if a sound is made by a resonant cavity, then the frequency of the sound will be lower for an animal with a larger resonator. If males judge the size of opponents by listening to the lowest peak frequency of their calls, then this will create selection pressure for males to make the lowest-frequency sounds they

can. However, if the minimum peak frequency a male can produce is constrained by the volume of a resonating cavity, and if the resonator volume correlates with body size, then males may be constrained to produce an honest advertisement of their body size.

However, the link between frequency of vocalizations and body size depends upon how the sounds are produced. In fishes such as the toadfish, *Opsanus tau*, the fundamental frequency of the call is affected more by the contraction rate of sound-producing muscles than by the volume of the swim bladder (Fine 1978). In this case, the frequency of the vocalizations may not reliably indicate the size of the displaying fish, as was suggested for the bicolor damselfish. A small toadfish might be able to slow the rate of contraction of its sound-producing muscles to make a call lower in frequency than that of a larger competitor. This could be interpreted as the weaker contestant making a bluff by faking a display that inflates its apparent size and abilities. If an animal can use a signal to bluff about its motivation or ability, then it will pay the opponent to call the bluff. In many situations, it may even pay the opponent to ignore this kind of signal. This kind of logic has led biologists to emphasize the importance of signals that cannot be faked because they are inherently linked to an attribute associated with fighting ability.

While the frequency of a resonator is inversely proportional to its size, the comparison between damselfish and toadfish shows that the association between frequency of vocalizations and body size depends upon how the sounds are produced. The same issue is important in mammals. In some terrestrial mammals, there is little correlation between body size and the fundamental frequency of vocalizations (Fitch 1997). It appears for some primates that a different acoustic feature, the separation between formants, is a better indicator of size. Unfortunately, there are few models of sound production in cetaceans sufficiently detailed to predict which acoustic features of a signal are inherently related to attributes of the animal that may be relevant for mate choice or fighting assessment. The sperm whale is the cetacean species for which we have a model of vocal production that is relevant to this issue. As mentioned by Whitehead and Weilgart (chap. 6, this volume), an enormous fraction of the volume of the sperm whale body is devoted to an unusual organ called the spermaceti organ. The spermaceti organ lies dorsal and anterior to the skull and can have a length up to 40% of the length of the whale. Norris and Harvey (1972) argue that the spermaceti organ may function to generate the clicks that are the dominant vocalization of sperm whales. The clicks usually recorded from sperm whales are made up of a burst of pulses with

very regular interpulse spacing (Backus and Schevill 1966; Gould and Jones 1995). Norris and Harvey (1972) suggest that this regular spacing may result from reverberation within the spermaceti organ. They suggest that the spermaceti organ has an efficient reflector of sound at the posterior end and a partial reflector of sound at the anterior end. They propose that the source of the sound energy in the click comes from a strong valve in the nasal passage, called the *museau du singe*, at the anterior end of the spermaceti organ. They suggest that the first pulse within the click is produced as the initial sound made by this valve is transmitted directly into the water, while the remaining pulses within the click result from reverberation of the posteriorly directed component of the initial sound between the posterior and anterior reflectors within the spermaceti organ. Each time the sound arrives at the anterior reflector, some of the sound energy passes out into the ocean medium, while some reflects back within the spermaceti organ. If this hypothesis is correct, then the interpulse interval (IPI) could represent an accurate indicator of the length of the spermaceti organ. Gordon (1991) measured the length of sperm whales in the wild, along with the IPI of their clicks, and found a clear relation between IPI and estimated size of the spermaceti organ.

Mature male sperm whales produce a distinctive click vocalization, called slow clicks because of the long interclick interval (Weilgart and Whitehead 1988). Males can produce both slow clicks and usual clicks, and one solitary maturing male switched between slow clicks and usual clicks with no intermediate forms (Weilgart and Whitehead 1988). Slow clicks differ from usual clicks not only in their longer interclick interval, but also in their increased loudness, longer duration, and lower-frequency intensity peaks, near 2 kHz (fig. 11.7). Slow clicks tend to have a "ringing" sound near 2 kHz, perhaps indicating a structure in the sound production apparatus that resonates at this frequency. Sperm whales are sexually dimorphic, with adult males growing to 16 m in length, while females grow to about 12 m (Best 1979). The spermaceti organ also takes up a greater proportion of body length in adult males than in females or smaller males (Nishiwaki et al. 1963). If some of the acoustic features of slow clicks necessarily scale to the size and condition of adult sperm whales, then these may qualify as honest advertisements that may be used by males for fighting assessment or by females in mate choice.

Other acoustic features may be directly related to the condition of a male in other cetacean species. For example, Chu and Harcourt (1986) suggest that humpback females may select singing males based upon how long they can stay underwater and hold their breath. As described above,



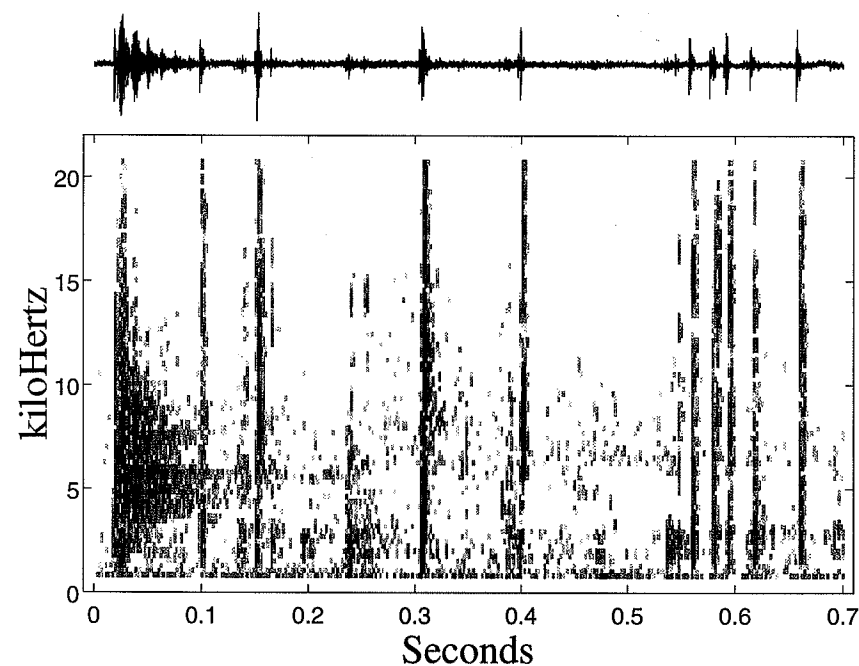


Figure 11.7. Spectrogram comparing one slow click (between 0 and 0.1 sec) and a series of usual clicks (to right of slow click) of sperm whales. The *x*-axis indicates time; the *y*-axis indicates frequency in kHz. Recordings are from a sperm whale group near Dominica, West Indies. (Data from William Watkins, Woods Hole Oceanographic Institution.)

most singers surface once per song cycle, and when they do, there are distinctive changes in the song. As a singing whale nears the surface, the lowest frequencies of the song drop out. This is due to the physics of underwater acoustics: as a sound source comes within a fraction of a wavelength of the surface, the sound does not propagate as well as it would at greater depth. This makes it difficult for a singing whale to come to the surface to breathe without broadcasting a reliable cue of his surfacing. Chu and Harcourt (1986) argue that breath-holding ability may be a good indicator of a male's stamina and physical condition. Breath holding may be particularly important for diving mammals. The problem with this argument is that, as described above, song duration changes as humpbacks slowly evolve every feature of their song. In the beginning of one year, the song may average seven minutes, whereas four months later it may have doubled in length (K. B. 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 he was singing a few months earlier or later (Guinee et al. 1983). If humpbacks were using song to advertise their breath-holding ability, then each individual would be expected either to always 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. These predictions do not match 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.

*Recognition systems and contact calls.* When one animal interacts with another, the appropriate behavior often depends upon the identity of the other animal. Almost every species faces this problem when selecting a mate: an individual must find a mate from the other sex of the same species. The reproductive isolating mechanisms used to reduce inappropriate mating can be thought of as a recognition system. Other socioecological settings require other kinds of recognition systems. If a mother hears a begging call from an infant, the proper response may depend upon whether it is her own infant or not. If an animal becomes separated from its group and hears sounds of conspecifics, it may be critical to determine whether the sounds are coming from its own group or from a different one.

All animals have evolved recognition systems to discriminate conspecifics from animals of other species. Depending upon the social system typical of a species, they may evolve systems for discriminating kin, mates, neighbors, strangers, and individual companions. As Beecher (1989) points out, the resolution of these recognition systems depends upon the within-class and between-class variability of the signals used and upon the level of detail that

can be sensed by the perceptual system. We do not yet know much about variation in the perceptual abilities used by cetaceans for resolving recognition signals, but there are a variety of cetacean acoustic signals that appear well designed to allow recognition between parents and young, between different social groups, and between specific individuals.

The need for recognition systems is particularly acute when animals meet after a separation. For example, if a human mother gives birth to an infant in a room and stays with the infant in that room, there is little need for a recognition system. However, in many hospitals, the infant is taken away from the parents into a nursery with many other infants. As soon as this happens, there is a serious danger of mixups unless the infant is carefully tagged and identified. A variety of features of cetacean life in the marine environment may require more frequent exercise of recognition mechanisms. Cetaceans have no nests or central places where specific individuals or groups can reliably be found. Cetaceans are highly mobile, and show great variability in their movement patterns. For many cetacean species, location cues are much less useful than they are for many terrestrial animals. Cetaceans within a group frequently swim out of sight of one another, causing increasing likelihood of separation unless the animals exchange signals using the acoustic modality, which is the only modality capable of rapidly transmitting information over the ranges at which these animals routinely separate.

The term "contact call" is used for sounds that function to help an animal keep in touch with its group. "Isolation calls" are a kind of contact call produced when animals are losing or have lost contact with one another, and they typically elicit immediate approach. Contact calls need not necessarily elicit an immediate reaction. When members of a group are separated but within acoustic range of one another, they may regularly call in order to keep in touch with at least one other member of the group, without otherwise altering their activity or movement pattern. The terms "contact" and "keep in touch" are unfortunate because they imply close physical proximity. This is not the case for contact calls; rather, these calls are used to keep an open communication channel between animals that are staying within the effective range of the communication signals. In the ocean, this range can extend over many kilometers. As might be expected for calls of mutual benefit to sender and receiver that pose a risk of interception, contact calls are often relatively short in duration and faint if the animals are not separated by great distances. For example, the flight calls of migrating passerine birds are shorter and fainter than their songs. Isolation calls of primates are often longer

and louder than contact calls of the same species (Robinson 1982).

If animals can use contact calls to track one another continuously from the time they separate to the time they rejoin, then these calls may reduce the need for recognition at reunion. Much of the time, however, contact calls may function in a recognition system by containing enough information to allow the listener to recognize the caller. The relevant information may vary depending upon the social setting. In the parent-offspring context, the parent may need to distinguish its own offspring from other young in the area. In species with stable groups, an animal may simply need to maintain contact with other members of its group, while discriminating them from members of other groups. In species in which individuals share strong bonds within fluid groupings, it may be necessary for each individual to recognize and track the contact calls of specific individuals within a group. In the next three subsections, I will describe vocal signals that appear to play a role in mediating recognition between parents and their offspring, between members of a group, and between specific individuals.

For all three of these recognition problems, there is a clear pattern of correlation in which those species with the most obvious examples of each kind of signal live in socioecological settings with high demands for that signal function. While the discussion will separate these three different kinds of recognition, they all share a similar framework in which the communication signals function to make or regain contact between animals who must recognize and discriminate between different individuals or classes of individuals.

*Signals for parent-offspring recognition.* In many mammalian and avian species, parents invest heavily in their own offspring, spending significant amounts of time and energy to feed their young and to maintain an appropriate physical environment for them. All mammalian young are born dependent upon the mother. Most need to suckle frequently, and many species depend upon the mother for thermoregulation and for protection from parasites and predators. Mammals have sophisticated systems for chemical communication during pregnancy so that a fetus obtains the appropriate nutrients and physical environment. Once the young are born and the direct umbilical communications are broken, they still need to signal the mother to maintain homeostasis and to receive appropriate levels of nutrients. When the young are in contact with the mother, they may produce a "distress" call if they require immediate care, or a "begging" call to request food.

If dependent young are mobile and might be separated from a parent, they need to be able to signal their location to the parent so they can rapidly be reunited. In most mammalian species, when mother and offspring are separated, the young produce "isolation" calls that are used for regaining contact. These isolation calls are produced by infants within days of birth and are particularly elicited by separation from the mother. Most mammalian isolation calls are frequency-modulated tonal calls, and are longer and louder than other infant calls. These calls appear to represent a widespread and basic mammalian adaptation. Examples come from a variety of terrestrial taxa, including primates (Newman 1985), felids (Buchwald and Shipley 1985), bats (Balcombe 1990), and ungulates (Nowak 1991).

The investment that a parent puts into its offspring presents an opportunity for other animals of the same or different species to parasitize the parent. Parasitism of parental care is best documented for birds, in which a parasitic bird may lay an egg in the nest of a conspecific (Brown and Brown 1998; Lyon 1998; Petrie and Møller 1991) or of another species (Payne 1998). Young birds that are receiving inadequate parental care may parasitize the parental care of unrelated adults. They may seek care from unrelated adults temporarily, or they may actually be adopted by these adults until they are independent (Pierotti and Murphy 1987; K. M. Brown et al. 1995). This kind of parasitism, in which the young parasitize adults, has also been reported for some marine mammals. For example, Trillmich (1981) reports that young Galápagos fur seals, *Arctocephalus galapagoensis*, may attempt to suckle from females other than their mother.

Among some primate species, infants run a risk of being taken by an animal other than the mother. While these other animals may be highly attracted to infants, unrelated animals seldom provide as much care as the mother. The chances of survival for such an infant may be low unless it is reunited with its biological mother. Similar cases of animals other than the mother associating with a young infant have been reported for several species of odontocetes (see Whitehead and Mann, chap. 9, this volume), both in the wild and in captivity.

The risks described in the preceding paragraphs may create selection pressures either for parents to isolate their offspring from conspecifics or for a system for mothers and young to recognize one another. Among some mammals, there appears to be a two-part process by which a mother finds and then recognizes her offspring. For example, a ewe uses visual and auditory cues at a distance to learn that a lamb may need care (Alexander 1977; Alexander and Shil-

lito 1977). However, once she has approached a lamb, she relies upon olfactory cues before letting it suckle (Alexander 1978). Similarly, when a female Galápagos fur seal arrives at the beach after feeding, both she and her pup may exchange calls to find one another (Trillmich 1981). Before actually allowing the pup to suckle, however, she sniffs the pup, apparently using olfactory cues for final recognition. While olfaction was probably important for individual recognition among the terrestrial ancestors of cetaceans, the sense of olfaction has been either lost or greatly reduced among modern cetaceans (see the section above on chemical communication). Vision functions over much shorter ranges underwater than in air. This leaves acoustic signals as the primary ones for individual recognition in cetaceans.

Most birds also have a poorly developed sense of olfaction and rely upon acoustic signals for parent-offspring recognition. In many cases, the calls used by the young to beg for food or by parent and young to reunite contain sufficient information for individual recognition. The ability of different bird species to recognize individuals using these signals appears to correlate with the likelihood of misallocation of parental care. For example, barn swallows (*Hirundo rustica*) raise their young in nests that are far from other broods, so location is a good predictor of kinship throughout the period of parental care. Young cliff swallows (*Petrochelidon pyrrhonota*), on the other hand, intermingle within a colony while still being fed by their parents. There is evidence from these closely related species that animals evolve systems to recognize their own young if the ecological setting involves a sufficient risk of providing care to the wrong offspring or of withholding care from the correct one. The chicks of barn swallows make a begging call, but their parents do not distinguish between the calls of their own and unrelated chicks (Medvin and Beecher 1986). 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 a more distinctive begging call in the young and also a more rapid discrimination of begging calls by adults (Loesche et al. 1991). Similar results suggest that colonial birds switch from location cues to identifying the calls of their own offspring at the time when the young from different broods intermix (Beer 1970; Miller and Emlen 1975). These results suggest that evolution favors investment in parent-offspring recognition if the risk of misallocation of care outweighs the cost of the recognition system.

The young of many dolphin and other odontocete species are born into groups made up of many adult females with their young, and they rely upon an unusually extended mother-young bond. Bottlenose dolphin calves typically re-

main with their mothers for three to six years (Wells et al. 1987). Sperm whales and short-finned pilot whales (*Globorhynchus macrorhynchus*) suckle their young for up to fifteen years (Best 1979; Kasuya and Marsh 1984). Dolphin calves are precocious in sensory and locomotor skills, and they swim out of sight of the mother within the first few weeks of life (Mann and Smuts 1993). Sperm whale calves may not be able to stay with their mother on deep foraging dives, and may remain separated from her nearer the surface for tens of minutes (Weilgart and Whitehead 1986; Whitehead and Weilgart, chap. 6, this volume). Young calves often associate with animals other than the mother during these separations. This combination of early calf mobility and prolonged dependence would appear to select for early development of a mother-offspring recognition system in these species. The prevalence of alloparental care in these species (see Connor et al., chap. 4; Whitehead and Weilgart, chap. 6, this volume) may favor a more generalized caregiver-calf recognition system.

Some baleen whales show a pattern different from this prolonged and highly social period of dependence in the young. In the seasonally migratory baleen whales, a young calf must migrate thousands of kilometers within months of birth, and the young of most species are weaned within one-half to one year (Tyack 1986a). When an adult female humpback whale has a calf, she seems to avoid other mother-calf pairs (Tyack 1982). Very few groups of humpbacks with more than one calf are ever sighted on the breeding grounds. Some baleen whales may have an ecological setting more like that of barn swallows than cliff swallows, in which a mother and calf may stay away from other mothers with young during most of the period of dependency. This reduces the potential for misallocation of parental care. In these cases, there may be reduced selection for parent-offspring recognition. One caveat about these conclusions concerns our ignorance of how mothers and calves maintain contact on the migration, and the social setting for migration. This is an important setting for further behavioral research.

In the beginning of this section, I mentioned that in many terrestrial mammals, infants produce frequency-modulated tonal "isolation" or "distress" calls. A very similar call is produced by dolphin species in which the young are raised within a social group or school. In most of these species, dolphin infants produce frequency-modulated tonal calls, called whistles, within the first few days of life. Not only the acoustic structure of dolphin whistles, but also the context in which they are produced, is very similar to the isolation or distress calls of many terrestrial mammals. Dolphins of all ages often whistle when alarmed or

distressed, leading to some early descriptions of alarm or distress whistles (Lilly 1963b; Busnel and Dziedziec 1968). While dolphins do tend to whistle in these contexts, there is little evidence for a species-specific alarm or distress whistle with a particular acoustic structure that differs from that of whistles produced in other contexts (Caldwell et al. 1990).

Observations of captive dolphins suggest that whistles function to maintain contact between mothers and young calves (McBride and Kritzler 1951). When a mother and her young calf are forcibly separated in the wild, both whistle at high rates (Sayigh et al. 1990). During voluntary separations between wild mothers and calves in Shark Bay, Western Australia, whistling can be heard after the calf turns toward the mother (Smolker et al. 1993). This observation suggests that mothers and calves can keep track of each other's general location during normal separations, and that they use whistles to reunite as they approach each other.

The ecological and social settings of sperm whales would suggest a premium on early development of a communication system for mothers to find and recognize their calves after separations. Newborn calves appear unable to dive as deep as their mothers must dive to feed. In one of the few published observations of a sperm whale birth, Weilgart and Whitehead (1986) report that a calf was left on the surface for twenty minutes as the mother dove. Yet sperm whales have not been observed to produce whistles, and they primarily produce click sounds. Newborn sperm whales have been recorded making relatively unstereotyped sequences of clicks (Watkins et al. 1988). Tonal sounds have also been recorded in settings where a calf was present, and this is the only setting in which tonal sounds have been reported for sperm whales (J. C. D. Gordon 1987a; Watkins et al. 1988). Further research is required to test whether these tonal calls are used in a fashion similar to the isolation calls of other mammals, or whether sperm whale calves might use clicks to meet the same functional need to reunite after separations.

There are some hints among cetaceans of the same kind of matching between social setting and parent-offspring recognition system as has been shown for some bird species (Beer 1970; Miller and Emlen 1975; Stoddard and Beecher 1983; Medvin and Beecher 1986; Loesche et al. 1991). I mentioned above that humpback whale mother-calf pairs remain close together in clear tropical waters. They also appear to isolate themselves from other mothers and calves, and this may reduce the importance of a system to find and recognize each other (Whitehead and Mann, chap. 9, this volume). The vocalizations of humpback whales have

been well studied on the breeding grounds. Biologists have followed and recorded thousands of social groups. While vocal patterns have been well documented from lone males (song) and from groups of males competing for access to a female (so-called social vocalizations: Silber 1986), there are no reports of vocalizations from mothers and calves. I have spent tens of hours listening within range of mother-calf pairs and have never heard a vocalization from them. If their use of vocal signals to maintain contact was as frequent as that of bottlenose dolphin mother-calf pairs, then this level of monitoring effort would have recorded such signals. Herman and Tavorga (1980) have argued that among the odontocetes, the species not known to produce whistles are more solitary than those that do whistle. Mothers with young of non-whistling species may be solitary enough to have reduced needs for a vocal system to recognize their own offspring. However, further studies of communication between mothers and infants, and of the social settings of mothers and infants, will be needed to test whether cetaceans show the same kind of matching between social setting and individual recognition systems that has been shown for many bird species. In particular, studies need to be designed for unbiased estimates of call rates and the behavioral contexts of vocalizations in different social groups (see Mann, chap. 2; Whitehead et al., chap. 3, this volume). This is particularly important for the poorly studied platanistid river dolphins and phocoenid porpoises, which have been described as solitary based upon fragmentary data. Herman and Tavorga (1980) categorized platanistid river dolphins as "non-whistling," but whistles have been reported for several platanistid species (Mizue et al. 1971; Jing et al. 1981; Wang et al. 1995). Further research on the vocalizations of this group is also urgently needed.

*Signals for maintaining coordination and cohesion of groups.* Individual animals that live in social groups may need to remain with a particular group to obtain the fullest benefits of group living. If these animals are mobile, they may need a communication system allowing them to maintain or regain contact with members of their group at the distances over which they separate. There are two cetacean species for which there is strong evidence for stable groups. These two species, killer whales and sperm whales, are described by review chapters in this volume. As Baird (chap. 5, this volume) points out, the most stable groups documented among mammals occur among fish-eating killer whales studied in the inshore waters of the Pacific Northwest. Neither sex disperses from its natal group; the only way group composition changes is by birth, death, or rare fissions of

very large groups (Bigg et al. 1990b). Adult female sperm whales live in matrilineal family units that are stable for years (Whitehead and Weilgart, chap. 6, this volume).

Both sperm whales and killer whales tend to aggregate while they are socializing, but individuals often disperse out of sight of other group members while feeding. Groups of sperm whales near the Galápagos Islands tend to spend about three-quarters of each day diving and foraging in small dispersed clusters and about one-quarter of the day aggregated in large social groups (Whitehead and Weilgart 1991). While killer whales in the inshore waters of British Columbia tend to be sighted in stable pods, these pods break up during foraging into small subgroups that disperse over areas of several square kilometers (Ford 1989). In both species, individuals would appear to need some mode of communication to allow animals separated by several kilometers to maintain contact or to reunite on a daily basis.

This problem would easily be solved by vocal contact calls. Loud calls of sperm and killer whales can be heard over ranges of 5 km or more under normal circumstances. However, a single species-specific contact call could cause problems for maintaining group cohesion. In areas of high whale density, several groups might swim within acoustic range of one another, and individuals that are dispersed while foraging might be confused by calls from several groups coming from different directions. Individual sperm and killer whales also face a problem in that their pod or family unit may join with any of a large number of other groups, and when these larger groups split up, each individual must find its own pod or family unit. This problem would seem to call for a group-distinctive contact call to act as a badge of group membership. In fact, killer and sperm whales are the only cetacean species for which group-specific vocal repertoires have been reported.

Killer whales produce a variety of vocalizations, including echolocation clicks, whistles, and pulsed calls. Ford (1989) separates the pulsed calls into two general categories of discrete and variable calls. The discrete calls can easily be further broken down into stable call types, while the variable calls cannot be sorted into such well-defined categories (Ford 1989, 1991). Figure 11.8 shows spectrograms of several stereotyped discrete calls from killer whales recorded in the waters off British Columbia. These spectrograms show the slight variations that define different subtypes of two common discrete calls from this community, N7 and N8. Individual pulses can be seen as vertical lines in the beginning of each of the N8 calls. In other parts of these spectrograms, the interval between pulses is usually less than the window size for spectral analysis. This creates a pattern that may look like the multiple harmonics of a

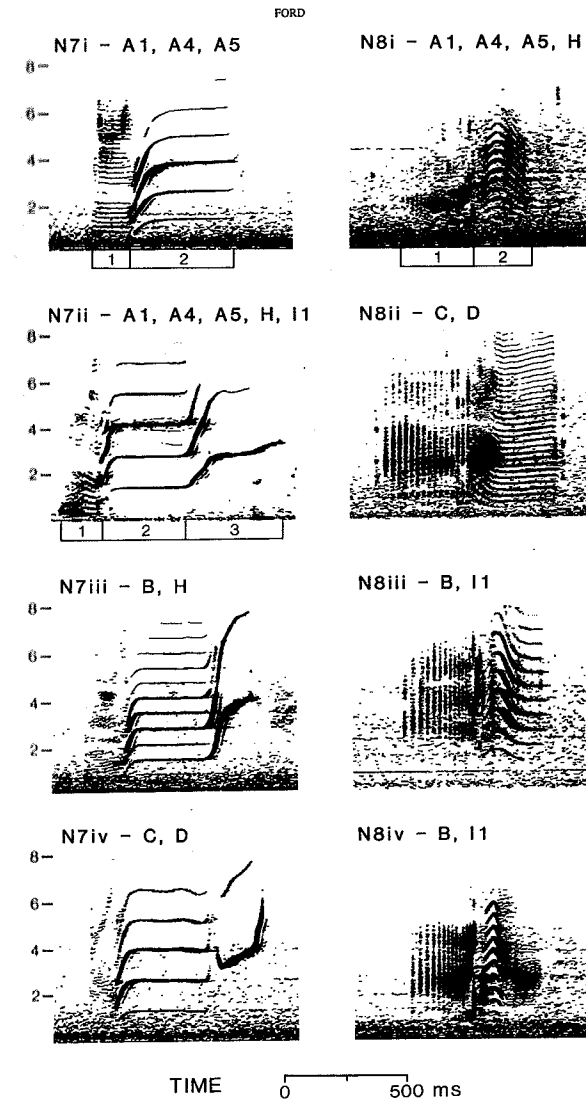


Figure 11.8. Spectrograms of discrete calls N7 (left column) and N8 (right column) from killer whales of the northern resident community in waters off British Columbia. Each of the spectrograms represents a repeated subtype of the basic N7 or N8 call. This is labeled above each spectrogram, along with the pods that have been recorded producing this call. The x-axis indicates time; the y-axis indicates frequency in kHz. (From Ford 1991.)

tonal signal, but the apparent harmonics actually represent the frequency proportional to the period of the interpulse interval (Watkins 1967). As long as one uses the same settings for spectrographic analysis, the apparent harmonics cause no problems for categorizing these discrete calls. Ford (1989) points out that these signals are relatively broadband and contain abrupt frequency shifts, which enhance their potential for detection in noise and for localization.

While all of the pulsed calls of killer whales are thought to function primarily in social communication, the discrete calls are most associated with foraging and traveling, and

the more variable pulsed calls are associated with socializing (Ford 1989). When killer whales are foraging, each pod usually breaks up into subgroups, and often several different pods will feed in the same area (Ford 1989). A foraging killer whale will often produce a series of the same discrete call, or two or more whales will exchange series of the same call. Discrete calls are also produced at high rates when two different pods meet and temporarily join.

Each pod of killer whales has a group-specific repertoire of discrete calls that is stable for many years (Ford 1991; Strager 1995). Figure 11.9 illustrates the presence or absence of different discrete calls within the northern resident community of killer whales. Each pod has been recorded producing between eight and fourteen of these calls. No two pods have the same repertoire of these calls. These group-specific repertoires are thought to indicate pod affiliation, maintain pod cohesion, and coordinate activities of pod members. Ford (1989) argues that these repertoires function to maintain the spacing and coordination of foraging and traveling whales. Production of discrete calls would allow dispersed subgroups of foraging whales to keep track of each other's location. After several pods have finished foraging together, they may use their group-specific repertoires to regroup to form the original pods. Ford (1989: 743) argues that these "repertoires of multiple discrete calls have evolved in killer whales to increase the reliability and efficiency of intrapod communication and to maintain the integrity of the pod."

The only other cetacean species in which group-specific dialects have been reported is the sperm whale (Weilgart and Whitehead 1997). Sperm whales make a variety of click sounds. So far, I have discussed the usual clicks produced during foraging dives and the slow clicks produced by adult males. When sperm whales are socializing, they tend to repeat series of clicks, lasting 0.5–1.5 seconds, that follow a precise rhythm. Each of these distinct rhythmic click patterns is called a coda (Watkins and Schevill 1977c). As with the discrete calls of killer whales, codas can be easily classified into discrete categories based on the number of clicks they contain and the timing of the intervals between clicks (Moore et al. 1993; Weilgart and Whitehead 1993). Figure 11.10 illustrates examples of codas from sperm whales recorded in waters near Dominica, West Indies.

Individual sperm whales often repeat a particular coda pattern several times in a row (Backus and Schevill 1966; Watkins and Schevill 1977c). Watkins and Schevill (1977c) used an array of hydrophones to locate where each coda was produced. They reported that over periods of tens of minutes, each coda pattern appeared to come from one direction, and different coda patterns came from different



Call	Pod							
	A1	A4	A5	B	C	D	H	I1
N1								
i	x							
ii				x				x
iii					x	x		
iv							x	x
v		x						
N2	x	x	x					
N3	x	x	x	x	x	x	x	x
N4	x	x	x					
N5								
i	x	x	x	x			x	x
ii				x			x	x
N7								
i	x	x	x					
ii	x	x	x				x	x
iii				x				x
iv					x	x		
N8								
i	x	x	x				x	
ii					x	x		
iii				x				x
iv				x				x
N9								
i	x							
ii		x						
iii			x					
N10	x	x	x					
N11								
i	x	x	x	x				
ii				x	x	x	x	
N12	x	x	x	x	x	x	x	x
N13		x	x					
N16								
i				x				
ii					x	x		
iii							x	x
iv								x
N17			x					
N18				x	x			
N19		x						
N20				x	x	x		x
N21				x				
N27	x							
N47	x							
Total	14	14	13	14	9	8	9	13

Figure 11.9. Patterns of production of discrete calls by eight pods of killer whales in the northern resident community. An X in the column of a pod means that the call has been recorded from that pod; a blank space means that the call has not been reported. (From Ford 1991.)

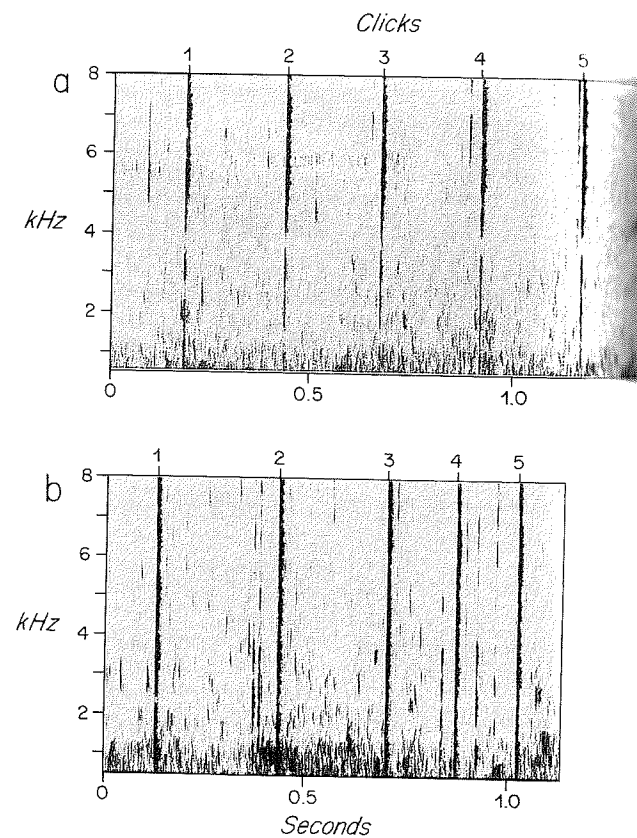


Figure 11.10. Spectrograms of coda vocalizations recorded from sperm whales in waters near Dominica, West Indies. The timing of intervals from Dominican sperm whales can usually be categorized as regular (A) or by a series of long intervals followed by a series of short intervals (B). (From Moore et al. 1993.)

directions. This observation led them to suggest that each sperm whale produces an individually distinctive coda. Whales that are close together—say, within a few hundred meters—often exchange codas (Watkins and Schevill 1977c). Sperm whales that are exchanging individually distinctive codas may match the coda typical of the other whale (Watkins and Schevill 1977c).

Later research on sperm whale codas has revealed that in each geographic area, the most common codas are shared by different individuals in different groups. The two most common codas from Dominican sperm whales involve five equally spaced or "regular" clicks (fig. 11.10A) and a series of two long intervals followed by a series of two short intervals (fig. 11.10B). Codas involving equally spaced click intervals are similar in different oceans. For example, the regular codas from Dominican sperm whales are similar to those reported from sperm whales in the Galápagos (Weilgart and Whitehead 1993). By contrast, irregular codas from sperm whales in the Galápagos differ from those from

Dominica, tending to start with short intervals followed by long intervals (Weilgart and Whitehead 1993). Weilgart and Whitehead (1997) have analyzed coda repertoires by recording session, date, group, place, area, and ocean. They find strong similarities in coda repertoires recorded from the same group of whales over periods of several years, along with a weaker pattern of geographic variation. This finding leads them to describe sperm whale codas as group-specific dialects. As with the discrete calls of killer whales, the weakest link in this argument is the lack of data on the vocal repertoires of individual sperm whales within these groups.

Weilgart and Whitehead (1997) suggest that codas function primarily for intragroup communication. The clicks that make up codas appear to be less intense than usual or slow clicks. Weilgart and Whitehead (1997) argue that codas may have an effective range that does not extend beyond 600 m, limiting communication to within groups. However, this is almost certainly an underestimate of the effective range of codas, and sperm whales have been seen to react to codas of other groups. Sperm whales sometimes abruptly silence their own vocalizations after distant codas from some other group of sperm whales are heard (Watkins et al. 1985). The impression this gives to a listener is that the whales cease vocalizing to listen for the faint codas of distant whales. Adult female sperm whales with young tend to form temporary groupings of two matrilineal units (Whitehead and Weilgart, chap. 6, this volume). This means that sperm whales within a unit frequently join or split with other units. When they detect a distant unit, they face a problem of deciding whether to join or avoid that unit. Weilgart and Whitehead (1997) show that groups within one area tend to have more similar coda repertoires than more distant groups. Sperm whales may listen to the similarity of call repertoires to assess a group within acoustic range; for example, to decide whether or not to challenge strangers, to affiliate with a neighboring group, or to avoid a group altogether. While these intergroup interactions may not be as common as intragroup responses to codas, more research is needed to define the effective range of codas and to evaluate whether interception of codas from other groups influences interactions between groups.

Whitehead and Weilgart (1991) systematically recorded vocal and visually observable behaviors as they followed groups of sperm whales in the Galápagos. They found that usual clicks were strongly associated with periods when the whales were diving and foraging in dispersed subgroups, and that codas were strongly associated with periods when the whales were socializing in tight aggregations at the sur-

face. This pattern differs from the usage of discrete calls in killer whales, which predominate during foraging, but Weilgart and Whitehead (1993) have an interpretation of the function of codas similar to that proposed by Ford (1989) for discrete calls in killer whales. Weilgart and Whitehead (1993) hypothesize that codas function to maintain the cohesion of groups of sperm whales as they aggregate following dispersed foraging. It is also possible that the different coda repertoires of different groups could result from cultural or genetic drift, with no adaptive function. Testing these hypotheses about the possible functions of codas will require more detailed observations of call usage by individual killer and sperm whales as they come together after dispersal. There is an urgent need to study the fine-grained patterns of communication using methods that can link data on acoustic location of calls with follows of individual whales.

If an engineer were designing a system to identify group membership, she might assign one distinctive call as a badge for each group. Sperm and killer whales have a more complex system in which individual calls may be shared between groups, but the entire call repertoire of each group is distinctive. One reason for this apparent complexity may involve difficulties in evolving a system where each group develops a distinctive call. In addition, if the number of distinctive features in one call is limited, then a larger repertoire might allow for a larger number of groups to be distinguished. However, this system has the potential disadvantage that an individual may need to monitor a series of calls for some time before being able to distinguish between some groups.

Current research on calls for maintaining cohesion in cetacean groups suggests a correlation between the presence of and the need for such calls. However, there is a paucity of data describing how sperm or killer whales use these calls as members of a group reunite, or as members of one group detect a distant group and make a decision about whether or not to join with it. The main reason for this lack of data stems from a methodological difficulty. It is relatively easy to follow a group of killer or sperm whales in the wild and to record sounds in their presence. However, it is extremely difficult to identify which animal produces a call. This problem forces one to analyze the data by group and prevents one from studying patterns of signal and response of individuals within a group. Miller and Tyack (1998) report the development of an array of hydrophones that can be towed behind a boat and used to locate where killer whale sounds are coming from. This kind of system can be integrated with individual-focused follows of visual behavior

to identify which individual produces a call. This technique may allow observers to better define the contexts in which an individual whale produces a call as well as the vocal and behavioral responses of other individuals. Such an approach holds great promise for better defining functional usage of these calls.

*Signals for maintaining individual-specific social relationships.* A common theme runs through many chapters of this book, suggesting that individual-specific social relationships may be important elements of the social behavior of many dolphins and toothed whales. If animals are to maintain these individual-specific relationships, they must be able to recognize and differentiate between different individuals. Another mammalian taxon in which individual-specific social relationships are important is the primates, and the mechanisms of individual recognition by primates have been well studied. Some primates can recognize individuals by voice cues (e.g., Cheney and Seyfarth 1980), but visual recognition of the face is of primary importance for individual recognition in many primate species. Primates appear to have evolved a system for recognizing and differentiating between many different individuals using special mechanisms for processing individually distinctive features of the face (Gross 1992; Tovee and Cohen-Tovee 1993).

If some cetaceans also rely upon individual-specific social relationships, then they will require mechanisms for individual recognition. Many cetacean species have enough individual variation in visual features, such as pigmentation or scars and notches, that human biologists can discriminate between many individuals (Hammond et al. 1990). However, as described above, vision is much less valuable as a distance sense under the sea than in many terrestrial environments. If cetaceans are to broadcast a signal of their identity or recognize individuals at ranges of greater than 10 m or so, they must rely upon acoustic signals.

The whistle vocalizations described for dolphins in the context of mother-infant recognition provide one of the most striking cases of individually distinctive vocalizations. Most early papers on dolphin whistles tried to associate specific whistle patterns with a particular behavioral context, such as alarm or distress, and they appeared to assume that all or most of these whistle patterns were shared by all members of a species (Dreher and Evans 1964; Lilly 1963b). However, Caldwell and Caldwell (1965) recorded whistles from five recently caught wild bottlenose dolphins in a variety of captive contexts, and they reported that each individual dolphin tended to produce its own individually distinctive whistle, which they called a signature whistle. Signature whistles have also been reported for the common

dolphin, *Delphinus delphis* (Caldwell and Caldwell 1968), the Pacific white-sided dolphin, *Lagenorhynchus obliquidens* (Caldwell and Caldwell 1971), and the spotted dolphin, *Stenella plagiodon* (Caldwell et al. 1973). Caldwell et al. (1990) reviewed whistle repertoires from 126 captive bottlenose dolphins of both sexes and a wide range of ages. The primary method of identifying which dolphin produced a whistle was recording dolphins when they were isolated, and signature whistles made up about 94% of each individual's whistle repertoire in this context. These signature whistles were distinctive between individuals and stable over many years.

Caldwell et al. (1990) also reported that bottlenose dolphins produce an extremely variable array of whistles that are not individually distinctive. These non-signature whistles are called variant whistles. While variant whistles made up only about 6% of the whistles in the Caldwell et al. (1990) data set, which emphasized isolated animals, they are more common in other contexts. For example, Tyack (1986b) reported that variant whistles made up 23% of the repertoire of two dolphins that were interacting socially, and Janik et al. (1994) reported that variant whistles were much more common when a dolphin was being trained than when it was isolated. The increased tendency of dolphins to produce signature whistles in isolation supports the hypothesis that dolphins use signature whistles to maintain contact with individuals from which they have been separated (Janik and Slater 1998). Variant whistles can be very diverse, but there can also be considerable overlap in the repertoires of variant whistles from different individuals. Tyack (1986b) and Janik et al. (1994) identified several classes of variant whistles, such as rise, flat, or down whistles, that were repeated by each individual and appeared to be shared across different individuals in different studies.

Additional evidence for signature whistles comes from a study of free-ranging bottlenose dolphins in inshore waters near Sarasota, Florida. Approximately a hundred free-ranging dolphins have been the focus of this long-term field study of population biology and behavior, which has involved extensive observations and censuses (Scott et al. 1990a; Wells et al. 1987; Wells 1991). This study also includes, on a more or less annual basis, a temporary capture-release component, in which dolphins are briefly held in a net corral and are then released. During the period when they are restrained and isolated from other dolphins in the net corral, the vocalizations of individual dolphins can be recorded with suction cup hydrophones placed directly on the head of each animal. A library of 398 recording sessions, most containing hundreds of whistles from an identified individual, has been obtained from 134 known indi-

viduals. Many of these dolphins were first recorded at one or two years of age and have been recorded over spans of ten to twenty years. All but a very few individuals have shown a stable and distinctive signature whistle over the entire time span during which they have been recorded (Sayigh et al. 1990), similar to the pattern reported by Caldwell et al. (1990) for captive dolphins. Figure 11.11 shows spectrograms of the signature whistle of an adult female over a period of eleven years and of one of her calves at one and three years of age. These whistles were recorded in an unusual setting, when the dolphin was restrained and separated from other dolphins. However, there is evidence that these whistles are similar to whistles recorded under more normal circumstances. Sayigh (1992) followed groups of free-ranging Sarasota dolphins (average group size of three to seven animals) and found that the signature whistles recorded during these follows matched those recorded previously from the same individuals using suction cup hydrophones.

There are several details of analyzing the acoustic structure of whistles that are crucial to the categorization of signature whistles. When biologists analyze the song of a bird, what is defined as a song is not limited to signals with continuous energy. If these continuous signals, called syllables, are seldom produced in isolation and usually produced in

a regular and predictable series, then it is the series, called the song, that becomes the primary unit of analysis. Biologists who have had the opportunity to study large repertoires of whistles from identified individual dolphins have tended to define the acoustic structure of signature whistles in a manner similar to that of bird song, as opposed to syllables. For example, the signature whistles of mother 16 and calf 140 shown in figure 11.11 are each made up of three continuous elements, which are called "loops" by Caldwell et al. (1990). Since these are typically produced as a unit with regular interloop spacing and highly variable spacing between the three-loop units, they are analyzed as one three-loop whistle instead of as three separate whistles. Even if a dolphin varies the number of loops in a signature whistle, as long as the variation involves repetition of the same loop with regular spacing, it is categorized as one signature whistle (Tyack and Sayigh 1997). Dolphins sometimes appear to produce incomplete sections of a signature whistle. If such a whistle precisely matches a portion of a signature whistle, Tyack (1986b) would categorize it as a segment of a signature whistle. Inspection of the whistles of mother 16 in figure 11.11 reveals how precisely dolphins can repeat the frequency-time contour of a loop over more than a decade.

McCowan (1995) proposed an alternative way to ana-

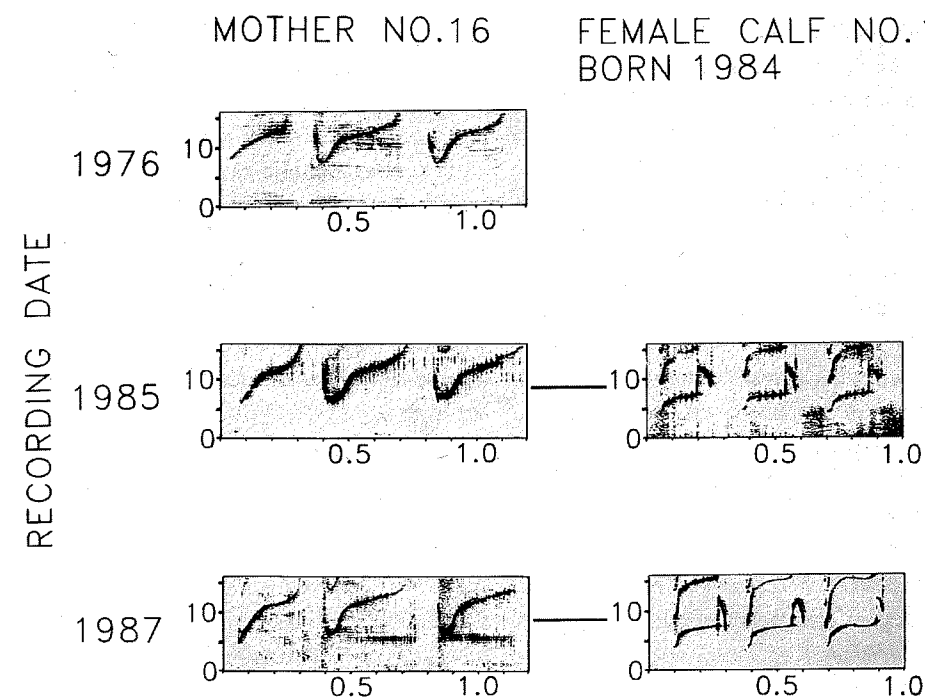


Figure 11.11. Spectrograms of signature whistles from one wild adult female bottlenose dolphin recorded over a period of eleven years, and from her daughter at one and three years of age. Note the stability of both signature whistles. The x-axis indicates time in seconds; the y-axis indicates frequency in kHz. (From Sayigh et al. 1990.)

lyze dolphin whistles. The basic unit of her analysis is a continuous trace of whistle energy in a spectrogram. This would split many signature whistles into their component loops, a modification that would affect later analysis as much as if one compared an analysis of bird song with an analysis of the same data broken up into each song syllable. Furthermore, most analyses of signature whistles compare the detailed changes in frequency with time that make up the loop and whistle. McCowan instead used a technique that assigns little weight to the actual durations and frequencies of the whistle, but rather compares the relative changes in frequency across twenty evenly spaced segments of each whistle. These are then fed into a cluster analysis, which, as might be expected, yields quite different whistle categories from those derived by the typical approach (Janik 1999). McCowan and Reiss (1997) used this method to categorize whistles of captive dolphins and reported results similar to those of "studies published before the advent of the 'signature whistle hypothesis'—a large whistle repertoire within social groups, sharing of whistle types across social groups, and a predominant but not individualized whistle type" (180).

These differing results from different methods of categorizing whistles can be resolved only by testing how dolphins themselves perceive whistles. The hypothesis that dolphins use signature whistles to broadcast individual identity assumes that dolphins can use acoustic features of whistles to recognize different individuals. McCowan and Reiss (1995, 1997) appear to be arguing that most whistles do not contain individually distinctive features. Some studies have been conducted that are germane to this issue. Captive dolphins have been trained to categorize a sample of whistles from the same individual as similar and samples of whistles from different individuals as different, even if these are novel whistles from dolphins with which they have not interacted. A captive male bottlenose dolphin was able to discriminate signature whistles from two different males, in a design using a large sample of whistles from both individuals (Caldwell et al. 1969). Recall of this discrimination remained high for as long as the animal was retested, up to twenty-two days. Experimental playbacks with wild bottlenose dolphins have also demonstrated that mothers and offspring can recognize each others' signature whistles even after calves became independent from their mothers (Sayigh 1992; Sayigh et al. 1999).

Quantitative signal processing also indicates that signature whistles provide sufficient information to distinguish individuals. The question of whether the interindividual variability of signature whistles is greater than their intra-individual variability was tested analytically by Buck and

Tyack (1993), who developed a computer algorithm to compare the similarity of pairs of whistle contours. This algorithm measures differences in absolute frequency while allowing different segments of the whistle to vary their time axis to maximize fit in the fundamental frequency of the whistle. It was used to sort three randomly chosen signature whistles recorded from each of ten wild bottlenose dolphins of the Sarasota population during temporary captures. Five dolphins produced signature whistles without repetitive loops, and the other five produced multi-loop whistles. The algorithm correctly matched fifteen of fifteen of the whistles without repetitive loops and fourteen of fifteen central loops from multi-loop whistles.

Bottlenose dolphins appear to develop a highly stable signature whistle within the first year or so of life, yet observations of dolphins that are interacting socially and/or acoustically suggest that imitation may play an important role in the natural communication system of dolphins. Janik (1998) found whistle matching in 24% of 188 whistle interactions among wild bottlenose dolphins in the Moray Firth, Scotland. In one study of two captive adult dolphins, Tyack (1986b) found that each dolphin imitated the signature whistle of the other at rates of about 25% (i.e. 25% of all occurrences of each signature whistle were imitations produced by the other dolphin). Other studies have reported rates of signature whistle imitation near 1% among captive dolphins that were in acoustic but not physical contact (Burdin et al. 1975; Gish 1979; Janik and Slater 1998). These imitated signature whistles are not just produced immediately after the partner makes its signature whistle, but can become incorporated into a dolphin's whistle repertoire. For example, after a period of silence, one dolphin might produce a copy of another dolphin's signature whistle. The two animals in the Tyack (1986b) study were first housed together at about five years of age, well after signature whistles are developed. This ability of adult dolphins to add new whistles to their vocal repertoire through imitation of auditory models has been well established in experimental studies in which dolphins were trained to imitate novel synthetic whistle-like sounds (e.g., Richards et al. 1984).

If one dolphin can produce precise imitations of another dolphin's signature whistle, then this raises questions about whether a dolphin hearing a signature whistle can reliably predict which individual made the whistle. We do not know whether dolphins can discriminate imitated whistles from the original signature whistle, but many imitated whistles have acoustic features that allow biologists to discriminate them from the original (Tyack 1991b). Little is known about the precise functions of whistle imitation. If

the intended recipient of an imitated whistle is the animal that typically produces that whistle, then that animal is unlikely to be confused about whether it is an imitated whistle or not. In this context, imitated whistles may function to initiate an interaction with the animal whose signature whistle has been imitated (Tyack 1993). Among songbirds, call matching appears to provide a competitive advantage for young males (R. B. Payne 1982, 1983). The deceptive mimicry hypothesis suggests that call matching might allow a young bird to deceive a mate or competitor into accepting it as an experienced resident (McGregor and Krebs 1984a). While dolphins do not have the same pattern of territoriality, a dolphin could use an imitated whistle to attempt to deceive another dolphin about the identity of the whistler. In order to succeed, such deception would have to be rare enough not to interfere with the usual reliability of individual recognition by signature whistles. All of these considerations suggest that imitation of signature whistles is not likely to interfere with their role in individual recognition.

McCowan and Reiss (1997) raised a different set of questions about the proportion of whistles produced by captive dolphins that are unique to individuals. They recorded whistles from small groups of captive dolphins held together in small pools. Their methods differed from earlier studies of signature whistles, both in the categorization scheme described above and because they limited their whistle sample to occasions when the individual producing the whistle could be identified because the whistle was accompanied by a stream of bubbles from the blowhole. Emission of bubbles allows one to identify whistles from dolphins that are interacting closely, but is so rare that Caldwell et al. (1990) raised questions about its reliability and effectiveness.

McCowan and Reiss (1997) categorized 185 bubble-stream whistles from ten adult dolphins in three social groups. Their categorization method identified twenty-eight whistle types, 29% of which were shared across groups, 25% of which were shared only within groups, and 46% of which were unique to individuals. Differences in the methods used to categorize whistles make it difficult to compare the McCowan and Reiss (1995, 1997) data to other analyses of signature whistles. The percentage of whistles unique to individuals reported by McCowan and Reiss (1997) was lower than the 70–90% typically reported for signature whistles, but if they recorded imitated signature whistles, those would probably have been scored as whistles shared within a group. The most common whistle was a simple upsweep produced by all of the adults. This is similar to the rise whistle reported by Tyack (1986b), who identified whistles from two captive dolphins using

small telemetry devices, called vocalights, attached to each dolphin's head. However, the upsweep accounted for 97 of 185 bubble-stream whistles, but only 17 of 284 vocalight whistles. Janik et al. (1994) found that rise whistles were the second most common whistle type (305/1743), after the signature whistle (1098/1743) of the subject.

The primary results of McCowan and Reiss (1997) are that they observed fewer whistles unique to individuals, and many more upsweeps, than has been reported in other whistle samples. Janik and Slater (1998) studied whistles of four captive bottlenose dolphins and found that these differences may relate to the social context in which the whistles were recorded. They reported that each dolphin produced its signature whistle when in a separate pool from the other three, but that rise whistles were most common when all the dolphins were swimming together in one group. When these captive dolphins were undisturbed and together in one pool, only 2.4% of their whistles were signature whistles. These results make sense in terms of the signature whistle hypothesis, which suggests that dolphins use signature whistles to maintain contact with specific individuals when they are separated or isolated.

The Janik and Slater (1998) results emphasize how important it is to study variation in whistle repertoires within a behavioral context. Most work on signature whistles has emphasized recordings from the isolation context, so it might be expected to overestimate the percentage of signature whistles compared with other contexts. On the other hand, bubble-stream whistles may also represent a biased sample of whistles. As mentioned in the section on visual displays, bubble streams may be used as a display by cetaceans. If a dolphin chooses to add a visual display to a whistle, the intended recipient may be likely to be within view, so this context may be particularly different from the isolation setting, where other dolphins are out of view. In addition, the highly unusual addition of bubble streams to a whistle does not necessarily occur at random, but may be more likely for some whistle types, such as upsweeps. Their rarity, unreliability, and potential for bias led Caldwell et al. (1990) to consider bubble streams a method of last resort for identifying whistles from captive bottlenose dolphins.

Resolution of these alternative interpretations of dolphin whistles will depend upon several directions for future research. Experiments on how dolphins perceive whistles are urgently needed to test which methods of categorizing whistles most closely match how dolphins categorize whistles themselves. In addition, new methods are required to identify whistles unbiased by the activity or context in which the dolphins are engaged. A promising start in this



direction was provided by Janik (1997), who located individual wild dolphins from a shore station and used an array of hydrophones to locate the whistles of wild dolphins. He was able to link the acoustic locations of whistles to the sightings of specific individual dolphins being followed from shore, and neither observation method affected the behavior of the dolphins in any way.

Another cetacean species reported to have individually distinctive signals is the sperm whale. In the first paper to define the codas of sperm whales, Watkins and Schevill (1977c) suggested that each individual sperm whale may produce an individually distinctive coda. Since that time, both Moore et al. (1993) and Weilgart and Whitehead (1993) have reported that many sperm whales within a geographic area may share several common coda types, such as those illustrated in figure 11.10. Weilgart and Whitehead (1993) reject the hypothesis that codas are individual identifiers, except over short time periods, because many individuals produce more than one coda type, and there are many fewer coda types (as classified by Moore et al. 1993 and Weilgart and Whitehead 1993) than individuals in the population. Weilgart and Whitehead (1997) interpret codas as group-specific dialects. However, the existence of shared codas does not rule out the existence of individually distinctive codas as well. Weilgart and Whitehead (1997) partitioned variance in codas from the large scale of ocean and area down to the group, and found that codas within a group were similar over several years. However, they were not able to compare coda repertoires of individual whales within a group. Their results are consistent with either group-specific dialects or a repertoire combining shared codas and individually distinctive codas. The small number of coda types does not rule out the possibility of an individual identification function among subsets of the population. Codas are categorized by humans rather broadly by timing and number of clicks. It is likely that sperm whales can achieve finer distinctions among codas. Bradbury and Vehrencamp (1998) point out that it is common for signals to have hierarchical levels of variation, in which a mean pattern might indicate species or group identity, and small deviations from the mean may indicate individual identity.

A broad range of communication and echolocation functions has been hypothesized for sperm whale clicks. These different functions are by no means mutually exclusive, especially for different click patterns such as slow clicks, regular clicks, and codas. I cannot help but feel that our understanding of sperm whale codas is like that of the blind men feeling small parts of the elephant—each individual study has had such a limited view that different studies of codas can easily be expected to have come to different

conclusions. I feel that our most important task is to determine the coda repertoires of individual sperm whales within a variety of behavioral contexts. Further research using acoustic recording tags or acoustic location to identify codas from known individuals over days, weeks, and years may provide a new perspective on this problem.

### Echolocation May Influence Communication in Cetaceans

Many cetaceans use their vocal and auditory systems for echolocation as well as communication. Many treatments of vocal behavior in cetaceans suggest that high-frequency clicks are used exclusively for echolocation and that all other sounds are used exclusively for social communication. While this assumption of a rigid dichotomy between echolocation and communication is often implicit, it may overly restrict our hypotheses about the functions of cetacean vocalizations. Some cetaceans may use low-frequency sounds for biosonar, sounds that are typically thought of as serving a communicative function. For example, while humpback song appears to function as a reproductive advertisement display (Tyack 1981), whales may also learn about their environment from listening to echoes of bottom reverberation from sounds used in song (Tyack 1997). I have discussed how different biologists have argued that the 20 Hz pulses of finback whales may function either as a low-frequency echolocation system (e.g., Norris 1967, 1969; Payne and Webb 1971; Thompson et al. 1979) or for social communication (Payne and Webb 1971; Watkins et al. (1987); McDonald et al. 1995), perhaps as a reproductive advertisement display (Watkins et al. 1987). On the other side of this issue, there are several dolphin species that appear to use "echolocation" clicks for social communication. Several of the species that specialize in high-frequency hearing, including the phocoenid porpoises and dolphins of the genus *Cephalorhynchus*, are not known to produce any of the sounds typically associated with social communication in other dolphins (Amundin 1991; Dawson and Thorpe 1990). The clicks they use in echolocation may also function in social communication (Amundin 1991; Dawson 1991; Dawson and Thorpe 1990). Amundin (1991) associated relatively stereotyped patterns of repetition rate of "echolocation" clicks with specific social contexts in the harbor porpoise. Dawson (1991) also found in Hector's dolphin, *Cephalorhynchus hectori*, that specific kinds of complex clicks were associated with large groups and specific group activities. High repetition rates of Hector's dolphin clicks were associated with aerial and aggressive behavioral contexts rather than feeding. If preda-

tors of these species, such as killer whales, cannot hear the high frequencies of these clicks, then it may be advantageous to use them for communication as well as echolocation. Sperm whales also have a vocal repertoire limited primarily to clicks, and biologists have argued that these clicks are used for echolocation (Backus and Schevill 1966; Goold and Jones 1995; J. C. D. Gordon 1987a; Whitehead and Weilgart 1990) as well as communication (Watkins and Schevill 1977c; Whitehead and Weilgart 1991).

Tyack (1997) has argued that research on the evolution of echolocation in cetaceans suffers from a dearth of studies of ecological function and from a lack of broad comparative reviews. If studies of cetacean sonar included more analysis of the problems for which sonar may have evolved, we might have a much broader view of echolocation in cetaceans. For example, low-frequency sound is better suited than high-frequency sound for long-range sonar in the sea, and many targets of great importance to cetaceans, such as large bathymetric features, are also well suited to low-frequency sonar. Clark (1993) suggests that the low-frequency calls of baleen whales that are so well suited for long-range propagation in the sea, such as those described for blue and finback whales, may function for long-range orientation through detecting echoes from large distant features such as seamounts. Even if these signals have a primarily communicative function, these whales may also detect and respond to reverberation from bathymetric features. This possibility has been little studied, but there is suggestive evidence that bowhead whales migrating through the ice may use low-frequency calls to detect large areas of ice where they may not be able to surface to breathe (Ellison et al. 1987; Clark 1989 and George et al. 1989).

These examples blend features typically associated with the separate domains of sonar and communication. I would like to suggest that auditory and vocal skills evolved to function in one of these domains may preadapt animals for developing abilities in the other domain.

### Vocal Learning

Most of this review has suggested parallels between communication in cetaceans and in other taxa. There is one area, however, in which cetaceans show pronounced differences from their terrestrial mammalian relatives. Janik and Slater (1997) review evidence for vocal learning among mammals. Their definition of vocal learning concentrates on "production learning": evidence that the acoustic morphology of an animal's signals is modified by auditory exposure. Very few nonhuman terrestrial mammals have been shown to have an ability for production learning. Janik and

Slater (1997) further divide evidence for vocal learning into modification of the timing of vocalizations, which may involve simple modification of the timing of exhalation, versus modification of frequency parameters, which is more likely to involve complex coordination of the entire vocal apparatus. The only nonhuman mammals for which they find convincing evidence of vocal learning of frequency parameters are the following:

- Greater horseshoe bat, *Rhinolophus ferrumequinum*
- Harbor seal, *Phoca vitulina*
- Humpback whale, *Megaptera novaeangliae*
- Beluga whale, *Delphinapterus leucas*
- Bottlenose dolphin, *Tursiops truncatus*

Some of the strongest evidence for vocal learning comes from species that have been reported to imitate man-made sounds in captivity. A few individual harbor seals (Ralls et al. 1985) and beluga whales (Eaton 1979) have been reported to imitate the sounds of human speech. Many bottlenose dolphins have been shown to imitate man-made whistle-like sounds (Caldwell and Caldwell 1972c; Herman 1980). Dolphins can also be trained using food and social reinforcement to imitate man-made whistle-like sounds (Evans 1967; Richards et al. 1984; Sigurdson 1993). Evidence of vocal learning in the other two species stems from observations of natural behavior. The echolocation call of horseshoe bats rises in frequency over the first year or two of life and then has a decreasing frequency with increasing age. The echolocation calls of young with older mothers are lower in frequency than the calls of young with younger mothers, suggesting that young horseshoe bats match the call of their mother (Jones and Ransome 1993). The vocal convergence at any one time within a population of singing humpback whales, coupled with the rapid changes in the song over time, provides evidence for vocal learning in these animals (K. B. Payne et al. 1983).

There is a striking lack of evidence for these kinds of vocal imitation among nonhuman terrestrial mammals. Since vocal learning is so important for human communication, the lack of evidence for vocal learning is particularly striking in nonhuman primates. This observation highlights the importance of investigations into the evolutionary origins of vocal learning in other mammals. The question can be addressed by studying the current utility of learned displays and then comparing the phylogenetic relationships of species with and without skills for vocal learning.

There is some evidence for a link between echolocation and vocal learning among some bats and dolphins. Several species of bats have hearing that is particularly sensitive in

a narrow frequency band. This frequency band is so narrow that the Doppler shift in frequency of their outgoing pulse, induced by the relative motion of bat and target, can shift the echo outside of the bat's best hearing band. These bats modify their outgoing signal to maintain the appropriate frequency of the Doppler-shifted echo, a process called Doppler compensation. This frequency shift is required for effective operation of their sonar system. While this frequency shift takes place in milliseconds, and involves changing one's outgoing pulse depending upon the echo characteristics of one's own earlier vocal production, it is otherwise similar to the frequency matching between mother and infant that is reported as evidence for vocal learning in the horseshoe bat. Beluga whales and bottlenose dolphins have been shown to imitate a variety of pulsed and whistle-like sounds. Both of these species are able to echolocate, and, as in the case of Doppler compensation in bats, vocal learning may play a role in the effective operation of their sonar. Both species have been shown to be able to shift the peak frequency of their echolocation clicks, either as a result of differing ambient noise (belugas: Au et al. 1985) or through training (bottlenose dolphins: Moore and Pawloski 1991). These findings suggest that the requirements of echolocation may have selected for a simple form of vocal learning in these species.

Bottlenose dolphins are skilled at imitating whistle-like sounds, and whistle matching appears to play a role in their natural communication system. Their use of whistles in individual recognition, coupled with the problems associated with voice cues for individual recognition in diving animals, suggests that vocal learning may play a critical role in individual recognition and in maintaining individual-specific social relationships in whistling odontocetes (Tyack 1991a; Janik and Slater 1997). The diving habit of cetaceans may create significant differences in how they perform vocal individual recognition compared with terrestrial mammals. Slight variations in the vocal tracts of terrestrial animals cause predictable differences in the voices of individuals. Many of the features that distinguish the calls of individual terrestrial animals appear to be subtle cues that result from these variations in the vocal tracts of different individuals. These involuntary characteristics of voice are not likely to be reliable cues for diving animals, however. The vocal tract is an air-filled cavity, and gases halve in volume for every doubling of pressure as an animal dives. Since different parts of the vocal tract are more or less elastic, changes in volume will lead to changes in shape. These depth-induced changes in the vocal tract are likely to outweigh the subtle developmental differences that lead to voice differences. For example, the whistles of a beluga

whale recorded at different depths show strong differences in their frequency spectra (Ridgway 1997). If diving animals rely upon individually distinctive calls, they may be unable to use voice cues and may need to create distinctive calls by learning to modify acoustic features under voluntary control, such as the frequency modulation of whistles.

Selective pressures for the evolution of complex advertisements appear to have played a role in the evolution of vocal learning in songbirds and baleen whales. As in the case of most oscine songbirds, vocal learning in humpback whales has been described only for their song, which is a reproductive advertisement display that has evolved by sexual selection. Indirect evidence also suggests that sexual selection was a significant factor in the evolution of vocal learning in some seals. Evidence for vocal learning among seals (Ralls et al. 1985) is particularly interesting from an evolutionary perspective, because the pinnipeds evolved from a different terrestrial ancestor than the cetaceans. This suggests that there were at least two independent origins of vocal learning among marine mammals. Vocal imitation in harbor seals has been reported only for adult males (Ralls et al. 1985), and adult male harbor seals have been reported to produce repetitive acoustic displays during the breeding season (Hanggi and Schusterman 1994). Many seals produce songlike advertisement displays during the breeding season (Ray et al. 1969; Sjare and Stirling 1993; Stirling 1973; Thomas et al. 1983). Further research is urgently needed on the potential role of vocal learning in these seal songs. Among the cetaceans, there appear to be a variety of current functions for vocal learning, including echolocation, individual identification, and producing advertisement displays. This variety makes it difficult to determine whether vocal learning has arisen several times independently in this taxon, and if not, which was the original function for which the skill evolved. Janik (in press) suggests that vocal learning initially evolved in cetaceans for individual recognition, and only later played a role in evolution of songs in baleen whales. Whatever its origin, cetaceans use vocal learning for developing a remarkable array of signals with different social and sonar functions.

### Comparison of Social Signals with Social Organization

This volume has described a great diversity of social systems, life histories, and mobility among cetaceans. Data on acoustic communication and social behavior also suggest diverse patterns of variation in communicative signals, from individually distinctive signals, to group-specific vocal repertoires, to signals shared among groups over broad geo-

graphic areas, to vocal dialects in different areas. Socioecological comparisons between species suggest diverse functions for these signals among cetaceans.

There is a clear correlation between the types of social bonds and the types of communication signals seen in different cetacean groups (Tyack 1986a). Individual-specific signals have been reported for species, such as the bottlenose dolphin, with strong individual social bonds; group-specific vocal repertoires have been reported for species, such as killer whales, with stable groups; and population-specific advertisement displays have been reported among species, such as humpback whales, in which adults appear to have neither stable bonds nor stable groups. Vocal learning appears to be involved in the development of many of these signals. It is possible that vocal learning evolved *de novo* in these different taxa as independent solutions to the different problems posed by their differing social organizations. However, once a flexible system of vocal development evolved to solve one problem, it may have allowed the flexibility to solve different problems. As the descendants of animals that had evolved abilities of vocal learning branched into other niches, they may have used vocal learning to other ends.

The rarity with which vocal learning has evolved in animals suggests that the evolution of a system of vocal development with this kind of flexibility may be a slow and unlikely process. If a system for vocal communication cannot be modified through learning, but changes via the evolution of genetic predispositions, then modification of the system may take evolutionary time scales. Yet animal populations may face new socioecological opportunities on ecological time scales that are shorter than the evolutionary scales. For example, bottlenose dolphins that reside in in-shore local habitats may benefit from different group sizes and structures for feeding and predator avoidance than migratory offshore populations. The recognition systems required to maintain these different societies are also likely to be quite different. While I separated the functional problems of parent-offspring recognition from those of group

and individual recognition, it appears that dolphins may use whistles, and sperm whales may use clicks, for all of these recognition problems. We cannot assume that cetaceans have evolved specific signals independently for each of these functions. It is also possible that cetaceans have evolved an open system of vocal development in which individual animals develop vocal repertoires through learning that match their locally adapted social groupings. Suppose that cetaceans develop a signal distinctive enough for parent-offspring recognition and then imitate common signals in their environment. Even if they followed the same system of vocal development, animals living in stable social groups might then develop group-distinctive repertoires, while animals living in fluid societies might develop repertoires characterized by more individual-distinctive signals and a diverse set of other calls. Further research will be required to test whether these kinds of patterns reflect an adaptive system in which vocal learning allows fine-tuning of a communication system to local demands, or whether vocal learning may create variation in signals with little adaptive significance, as has been suggested for some songbird dialects (Andrew 1962; Bitterbaum and Baptista 1979; Wiens 1982).

One of the most promising areas for future research on communication among cetaceans involves detailed behavioral studies of how individuals of different age and sex classes in a variety of different species use communication signals. New techniques for identifying which individual is vocalizing in the wild, and for following details of social interaction, will better integrate studies of cetacean communication with social interaction. Longitudinal studies of individuals will be important for studying vocal development. The current status of knowledge of communication in cetaceans highlights the importance of cetaceans for studying relationships between social signals and social structure, interactions between echolocation and communication, social influences on vocal development, and the evolutionary origins of vocal learning.