

FUNCTIONAL AND ORGANIZATIONAL ASPECTS OF
VOCAL REPERTOIRES IN BOTTLENOSE DOLPHINS
"TURSIOPS TRUNCATUS"

Vincent M. Janik

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**Functional and organizational aspects of vocal repertoires
in bottlenose dolphins (*Tursiops truncatus*)**

by
Vincent M. Janik

**Submitted in fulfilment of requirements for
the degree of Doctor of Philosophy
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Abstract

Bottlenose dolphins (*Tursiops truncatus*) produce a wide variety of sounds but little is known about the function and organization of their vocal repertoires. This thesis investigates several aspects of call usage and compares the biological validity of classification methods for dolphin whistles. Passive acoustic localisation methods were used to identify which animal produced a sound.

Observations of captive dolphins in the Zoo Duisburg, Germany, showed that signature whistles are almost only used when the group was split up, but not if all animals swam in together in the same pool. This finding supported the hypothesis that signature whistles are cohesion calls. Whistles from these observations were used to compare whistle classification conducted by eye with three computer methods using different similarity measures. Only the human observer classification was able to recognize whistle types that were used in a context-specific way by the animals confirming the power of this common classification method.

Copying of signature whistles and whistle matching between animals was rare in captivity. However, observations of whistle interactions in the Moray Firth, Scotland, showed that wild dolphins do not tend to interact vocally in general, but that whistle matching was more frequent than expected by chance. Whistle matching in captivity was rare. Sound pressure measurements of dolphin whistles in the wild showed that source levels can reach up to 169 dB re 1 μ Pa and that the active space of a dolphin whistle can range up to 38 km. Finally, observations of foraging in wild dolphins revealed that they produce low frequency braying sounds in this context. Other dolphins would rapidly approach the caller in response to a bray. However, it is not clear whether brays function to attract conspecifics or manipulate prey behaviour.

Chapter 1

General Introduction

The communication of dolphins has been studied since the first specimens were caught and held in captivity. McBride & Hebb (1948) first described the behaviour of captive bottlenose dolphins (*Tursiops truncatus*). Lilly & Miller (1961a, b) were the first to use a sonograph to investigate dolphin sounds and to look at the contexts of sound production. Both they and Dreher & Evans (1964) were the first to try to describe the species repertoire. Both teams thought that dolphin communication was very complex and comparable to human language. Dreher and Evans in particular compared its theoretical information content to that of human language and concluded that the two systems are similar. Also early on, Bastian (1967) trained two bottlenose dolphins successfully to cooperate in a task that required acoustic information transmission. Whether this transmission was a communicative act or was achieved by eaves-dropping on echolocation or gaining information from splashing sounds was not clear.

Other researchers focussed more on the biology of dolphin communication itself rather than trying to establish a link between humans and dolphins. Continuous research by Caldwell and Caldwell showed that bottlenose dolphins use individually specific signature whistles that could be used in individual recognition and group cohesion (Caldwell & Caldwell 1965, 1968; Caldwell et al. 1990). Later work by Sayigh et al. (1990) showed that these whistles remain stable for up to at least 12 years. However, at around the same time, Tyack (1986b) found that dolphins also copy each other's stereotyped whistles, which casts doubt on the idea that signature whistles could be used for individual recognition. Furthermore, he and Sayigh presented evidence that these whistles were learned (Tyack & Sayigh 1997). These findings have led some people to doubt the signature whistle hypothesis (McCowan & Reiss 1995a, 1997).

If we compare the number of scientific publications on dolphin communication with those on the communication of other animals it becomes evident that we are only at the beginning of this field despite the fact that it started in the 1940's. The main reason for the scarcity of papers is the difficulty one faces if dolphins are to be studied. They are very mobile and difficult to follow in the water and their sound production does not involve any visible motor behaviours that indicate who is calling. Sound production occurs internally and the resulting sounds are transmitted through the tissue of the animal. Techniques that can be used to identify a caller despite these difficulties are laborious and have hardly been applied to the study of dolphin communication.

The aim of this thesis is to further our understanding of dolphin communication by applying such techniques in captivity and in the wild. Each chapter is written so that it can be read without much reference to the others. Thus, each has its own separate introduction and discussion. Chapter 2 is a review of the relevant knowledge we have on dolphin communication. It explains some of the implications of the current theories on the evolution of vocal learning and individual recognition in dolphins. Thus, it provides the theoretical background for the following chapters. In Chapter 3 I investigated whether signature whistles are used in group cohesion and individual recognition. Even though this has long been suspected this is the first study that gives evidence for this possibility by investigating the context specificity of signature whistle use. Chapter 4 compares different methods of whistle classification. It shows that computer methods currently used on the sounds of dolphins and other animals were unable to reliably identify signature whistles. However, signature whistle types defined by humans were used in a context-specific way by the dolphins, confirming their biological importance. Chapter 5 investigates whether bottlenose dolphins use whistle matching in the wild more than expected by chance. This is an important point since matching could counteract individual recognition by signature whistles. In Chapter 6 I present source levels of bottlenose dolphin whistles in the wild. This gives information on the theoretical range over which dolphins could use whistles to communicate and also gives evidence that dolphins face more background noise in the frequency band used for their communication than most terrestrial

animals. Finally, in Chapter 7 I document the use of dolphin brays in feeding events and their effect on other individuals in the area. Researchers have largely concentrated on whistles, but dolphins produce a wide variety of sounds and these are also likely to be used in communication. But, even though braying attracted other dolphins, the acoustic features of brays suggest that they might be used to modify prey behaviour. Chapter 8 is a general discussion and conclusion in which I focus mainly on the further questions I consider most pressing in the study of dolphin communication and suggest ways of answering them.

Chapter 2

Origins and implications of vocal learning in bottlenose dolphins

Introduction

Before we can study functional aspects of social learning it must be established first that a behaviour pattern is learned and second that it is learned socially. The investigation of social learning in communication systems requires only the first step. If learning takes place it can only be social since communication can only occur between individuals. Social learning can affect animal communication in three different ways. The two more common ones are through changes in comprehension (i.e. learning to understand the contexts with which a particular call is associated), and changes in usage (i. e. learning when to use a call). These forms of learning have also been described as contextual learning (Janik & Slater 1997). A rarer form of social learning in animal communication is vocal learning. This term describes the process whereby an individual modifies its acoustic signals in form in relation to those of another individual. It can result either in matching signals or in distinct differences arising between individuals. Contextual learning that is related to communication has been found in many mammalian species (Salzinger & Waller 1962; Molliver 1963; Lilly 1965; Myers et al. 1965; Schusterman & Feinstein 1965; Burnstein & Wolff 1967; Lal 1967), but only a few studies have shown vocal learning.

In mammals, primates have been the main focus of research on vocal learning. This is partly because vocal learning is a prerequisite for language acquisition in humans, and comparative studies have tried to investigate the evolution of vocal learning by looking at non-human primates. However, despite extensive research efforts by primatologists, no convincing evidence for vocal learning in non-human primates could be found (Janik & Slater 1997). Given this, some authors assume that among mammals vocal learning is more or less unique to humans (Jürgens

1992; Meltzoff 1996). However, studies from as far back as 1972 have demonstrated clearly that some mammals are capable of vocal learning. Caldwell & Caldwell (1972) described vocal learning in a captive bottlenose dolphin (*Tursiops truncatus*), results confirmed later in a more detailed study by Richards et al. (1984). All individuals within a humpback whale (*Megaptera novaeangliae*) population change their song in synchrony in a way that can only be explained if vocal learning is involved (Guinee et al. 1983; Payne & Payne 1985). Harbour seals (*Phoca vitulina*) are capable of imitating human speech (Ralls et al. 1985) and infants of greater horseshoe bats (*Rhinolophus ferrumequinum*) adjust the main frequency of their echolocation calls to that of their mother by vocal learning (Jones & Ransome 1993).

Unfortunately we know very little about the adaptive significance of vocal learning in these cases. In the greater horseshoe bat vocal learning seems to be important for mother-infant recognition, but, it is not clear what other contexts might be affected by their vocal learning skills. Humpback whales and harbour seals show singing behaviour, in which males produce repetitive sequences of sounds over long time periods during the breeding season suggesting convergent evolution with the songs of songbirds. Of those mammals that show vocal learning dolphins are the most similar to primates in their social behaviour. They do not produce songs but use their sounds extensively in social interactions within complex social groups. Experimental studies have shown that their cognitive abilities rival those of the great apes and they may even exceed them in the processing of grammatical information (Herman et al. 1993). However, unlike non-human primates, they rely almost entirely on the acoustic channel for their communication and they are capable of vocal learning. In this chapter I will evaluate what role vocal learning played in the evolution of cetaceans and what implications it had once it evolved. But to consider hypotheses about the origins and implications of vocal learning for my study species we need first to look at current knowledge about the social structure and vocal communication of bottlenose dolphins.

The social structure of bottlenose dolphins

Bottlenose dolphins can be found in groups of one to several hundred animals. The average group size lies between 3 and 30 individuals (reviewed in Wells et al. 1980). In some areas group size is slightly larger in deep water (Würsig 1978), but average group size does not seem to vary significantly between coastal and pelagic areas. However, groups of several hundred individuals can only be found in the open ocean (Scott & Chivers 1990). The waters off southern Africa present a notable exception, as average group size there was 140.3 animals in coastal areas (Saayman et al. 1973). Differences in group size may be related to environmental factors that influence group structure. Dusky dolphins (*Lagenorhynchus obscurus*), for example, show different group sizes in different coastal habitats (Würsig et al. 1991). However, differences in average group sizes or individual association coefficients between studies can also be caused by different definitions of what a group is and one has to be careful comparing data from different studies.

Studies on bottlenose dolphin communities have revealed patterns of association between individuals that are characteristic of a fission-fusion society. Members of a community form groups of different sizes but the individual composition of these groups changes frequently. Detailed studies of bottlenose dolphin social structure at Sarasota, Florida, (Wells et al. 1987; Wells 1991) and Shark Bay, Australia (Smolker et al. 1992) have revealed some of the patterns underlying this organisation. Individual male dolphins can be found associating with different female groups on different days. However, in both areas males also tend to associate in dyads or triplets. These male alliances herd and consort with females for mating purposes (Connor et al. 1992a, 1996). Different alliances have been observed to fuse into a second-order alliance of four or more animals that took females from dyadic alliances (Connor et al. 1992a). Alliances between specific males can be extremely stable, resulting in association coefficients as high as those of mother and calf pairs. In some cases males have not been seen without their ally for over two years (Smolker et al. 1992).

Females, on the other hand, tend to associate in matrilineal groups. Here, group composition seems to be much more fluid, leading to the impression of a female network rather than an organisation of entirely separate groups. Females give birth to one calf after 12 months of gestation. In Sarasota mothers and calves were almost always seen together until a calf reached 3-4 years of age. Association coefficients between mothers and calves then decreased gradually in the following years (Wells et al. 1987). Once they have been weaned bottlenose dolphins associate in subadult groups that are composed of both sexes. This lasts from weaning to approximately 8-12 years of age in females and to 10-15 years in males (Wells 1991). After that time males and females show adult association patterns with females returning to their matrilineal group and males starting to form alliances with specific individuals.

The vocal repertoire of bottlenose dolphins

Bottlenose dolphins produce various different kinds of sounds. Among these clicks, burst-pulsed sounds and whistles have received the most attention so far. Clicks are very brief, broad-band signals used for echolocation. The communicative value of these sounds has not yet been identified. Certain dolphin species, like the Hector's dolphin (*Cephalorhynchus hectori*), do not produce whistles and use only click sounds to communicate (Dawson 1991). Bastian (1967) found that a bottlenose dolphin was capable of copying the lever pressing behaviour of a concealed conspecific that produced elaborate click trains during its performance. However, bottlenose dolphins are able to extract information from the echoes of clicks produced by conspecifics purely by eavesdropping on them (Xitco & Roitblat 1996). Thus, it will be a challenging task for researchers to distinguish between clicks used for echolocation and those emitted to communicate.

Burst-pulsed sounds consist of click trains with a very short interclick interval, so that they appear somewhat tonal to the human ear. We do not know how a dolphin perceives such a sound and whether the distinction between clicks and burst-pulsed sounds has any relevance to the animal itself. There are many cases in

which these sounds start with a slower click train which then accelerates to become a burst-pulsed sound. The reverse process can be found at the end of burst-pulsed sounds. However, they are usually composed of low frequency clicks and these are unusual in echolocation. It has been shown that they are a common vocalisation form in agonistic interactions (Overstrom 1983).

The best studied communication signals of bottlenose dolphins are their whistles. The repertoire of an individual bottlenose dolphin comprises several whistle types, one of which is highly stereotyped (Caldwell et al. 1990; Janik et al. 1994). Caldwell & Caldwell (1965) described this stereotyped whistle for the first time and found that it was consistent within individuals. They called these signals signature whistles and hypothesised that they facilitate individual recognition (Caldwell & Caldwell 1968). In all studies in which individuals were isolated for recording, the signature whistle was the primary whistle type, often accounting for almost 100% of all whistles (Caldwell & Caldwell 1965; Caldwell et al. 1990; Sayigh et al. 1990; Janik et al. 1994; Sayigh et al. 1995). However, in more varied contexts signature whistles can be less prevalent (Janik et al. 1994). Studies on repeatedly captured wild individuals have shown that the signature whistle of an individual can remain stable for at least 12 years (Sayigh et al. 1990). These results support the idea that signature whistles could be used for individual recognition and group cohesion, but so far no study has compared the vocal behaviour of the same individuals in separation and other contexts. Dolphins were either studied in isolation or in groups. In some studies bottlenose dolphins have been found to produce stereotyped whistles even if swimming together (Caldwell & Caldwell 1965; Tyack 1986b; Caldwell et al. 1990). However, these were individuals in unusual situations, mostly shortly after capture or medical procedures. If co-operating animals are exposed to novel situations, contact calls can be expected at higher rates since group cohesion becomes more important. McCowan & Reiss (1995a) could not find any signature whistles in animals that were undisturbed, but it is not clear whether this was an artefact of the methods used, since they chose to ignore differences in duration of whistles in their classification methods (McCowan 1995). Thus, a demonstration that signature whistles are only used in contexts that require a group cohesion mechanism but not in close proximity is still needed.

Infants develop their own signature whistle in the first few months of their lives (Caldwell & Caldwell 1979). There is accumulating evidence that signature whistle development is strongly influenced by vocal learning, with the calf using stimuli from its acoustic environment in its own signature whistle (Tyack & Sayigh 1997). Vocal learning in bottlenose dolphins has been reported from experimental studies for clicks (Moore & Pawloski 1990), burst-pulsed sounds (Caldwell & Caldwell 1972), and whistles (Caldwell & Caldwell 1972; Richards et al. 1984). Dolphins are extremely versatile in copying new sounds and have been shown capable of producing copies of novel sounds at the first attempt (Richards et al. 1984). However, we do not know yet how genetical parameters limit the flexibility of call ontogeny in cetaceans.

At the end of this section it is important to note that there are several other calls that do not fit into the three categories mentioned so far. A few examples are brays (dos Santos et al. 1990; dos Santos et al. 1995), low-frequency, narrow-band (LFN) sounds (Schultz et al. 1995), and pops (Connor & Smolker 1996). Like LFN sounds brays are low frequency and narrow band but much longer in duration and with many harmonics, while pops are very short, low frequency, broad-band signals. We know very little about the functional significance of these call types and further research on them is badly needed.

Origins of vocal learning in dolphins

Several hypotheses have been brought forward to explain the evolution of vocal learning. Janik & Slater (1997) argued that many of these seem not very likely in cetaceans because of the marine environment they live in. Three hypotheses for the evolution of vocal learning in birds relate to features of the environment. The population identity idea assumes vocal learning to be important to maintain local adaptations to specific habitats (Nottebohm 1972). In comparison to most terrestrial environments the sea is a vast, very homogeneous habitat. Therefore specific local adaptations are less likely to be of importance. The habitat matching hypothesis suggests that vocal learning is important in matching the acoustic

transmission characteristics of different habitats (Hansen 1979). However, differences in sound transmission characteristics between marine environments are a lot smaller than between terrestrial ones. Finally, the intense speciation hypothesis suggests that vocal learning helps to maintain species recognition in a habitat where species density is high (Nottebohm 1972). This hypothesis was put forward for a tropical rainforest situation with hundreds of different bird species. It is unlikely that coastal areas could have supported a large number of different cetacean species like that at any time. Those species that were not restricted to coastal areas, on the other hand, did not face any spatial limits to dispersal. Thus, all these three hypotheses seem unlikely for cetaceans.

The most plausible hypotheses for the evolution of vocal learning in cetaceans refer to sexual selection and individual recognition. If the complexity of the call repertoire of an individual relates to its fitness this can be used to assess quality in mate choice or intrasexual competition. Here, sexual selection would greatly favour the evolution of vocal learning to enlarge an animal's repertoire and therefore increase its reproductive success. Many birds, for example, use song in mate attraction and territory defence (review in Catchpole & Slater 1995). In cetaceans both toothed whales and baleen whales show vocal learning. Singing behaviour can be found in baleen whales, and sexual selection could have favoured the evolution of vocal learning in this group. However, toothed whales such as dolphins do not produce song but seem to use vocal learning in other contexts.

Vocal learning can also facilitate individual recognition (Janik & Slater 1997). In most animals individual recognition is made possible by individual differences in voice characteristics. These are caused by differences in vocal tract morphology or in the neural control of sound production. Thus, they affect the production of all calls emitted by an individual. In some mammals individuals produce isolation calls. These are usually better suited for long distance communication than other calls but identity is encoded in voice characteristics (e.g. Liebllich et al. 1980) and not in the call type that is used. Such voice characteristics tend to have a higher variability in species that live in noisy environments than in those living in quieter ones (Beecher 1991; Loesche et al. 1991). An individual recognition system

becomes more effective as the ratio between inter-individual variability and intra-individual variability in the recognition parameter gets larger (Beecher 1991). However, at a certain background noise level it becomes difficult to maintain individual recognition with variants of the same call type even if the intra-individual variability is very small. Noise can mask significant differences between calls. Masking of recognition signals could either be caused by non-specific noise in the same frequency band or by conspecifics calling at the same time. Another problem for a voice based recognition system arises if voice characteristics are not individually specific. Vocal learning would allow an individual to solve such problems by incorporating a new call type specifically for individual recognition.

The fission-fusion structure of dolphin societies is similar to those of several primate species in which communication is needed to maintain bonds and alliances. Additionally, dolphins need an effective communication system simply to stay in touch with members of their current group. This becomes most obvious in the case of mothers and calves. In Shark Bay, Australia, non-weaned calves spend a considerable amount of time away from their mother, either socialising or on their own, and separation distances of more than 100 meters have been found (Smolker et al. 1993). Similar observations have been made in the Moray Firth, Scotland (Janik, unpub. data). Separations that leave the calf on its own are most likely related to the mother's feeding strategies. Adult dolphins can reach swimming speeds of up to 10 meters per second (Lang & Pryor 1966) and dispersal is possible in all three dimensions. Infants can probably not keep up with their mothers when they are hunting and will also save energy by staying behind. But calves are also vulnerable to predation and need the mother for nursing. Dolphins obviously cannot carry their infant or deposit it at some sort of den. Therefore an effective communication system to keep track of each other is the only way to maintain mother-infant contact.

Only certain communication channels have the required properties to ensure long distance contact. Dolphins have a good sense of vision, but underwater visibility is very limited, especially in turbid, nutrient rich waters. Olfaction is a very important communication channel for mother-infant recognition in mammals

(reviewed in Halpin 1991). Dolphins can detect different solutions of chemicals by taste, but it seems that they have no sense of smell (Nachtigall 1986). Furthermore, communication by chemical substances is relatively slow at long distances especially in water. Thus, only the acoustic channel is suited to individual recognition and group maintenance at longer distances for a marine mammal.

There are three different ways in which dolphins could keep track of each other acoustically. First, dolphins might be able to locate group members by using their elaborate echolocation system. However, there are several reasons why this is an unlikely solution. Echolocation is very directional, so that the animal would have to scan all possible directions to locate a group member. Furthermore, the blubber and skin of bottlenose dolphins have anechoic properties (Au 1996). The acoustic target strength of a dolphin is much lower than that of a fish, especially at the high sound frequencies that could give enough detail to distinguish between individuals. This makes it likely that individual recognition by echolocation is rather limited. Additionally, the air-filled cavities of dolphins that reflect sound best change shape under different water pressures. In a diving mammal these would not be good features for use in individual recognition.

The second possibility is simple eaves-dropping on the echolocation sounds produced by other group members. If these clicks are individually distinctive they could be used to keep track of group members. However, similar problems apply. Echolocation clicks are very directional. The eavesdropping animal would have to be in line with the echolocation target of the relevant group member. Furthermore dolphins do not produce clicks continuously, and this would make position monitoring more difficult. High frequencies also get attenuated quickly, so that this system would not have a very wide range.

Finally, individuals could make their position and identity known by emitting individually specific recognition signals. Currently we do not know how large the active space of a dolphin whistle is but it is likely that it exceeds the range of dolphin echolocation since it is of much lower frequency. But why do dolphins not simply recognise each other by their voices without the need to learn a special

signal? We have already seen that background noise can be a problem. The sea is a high background noise environment (Spiesberger & Fristrup 1990) that can mask individual differences especially over the long separation distances that can be found between communicating dolphins. But there is another potential problem that is related to diving. Individual voice characteristics are influenced by head morphology. Dolphins have several air sacs that are used to recycle air for sound production. It is likely that the shape of these air filled cavities in the dolphin's forehead influence its voice characteristics. Such cavities change shape if an animal is diving because of the increasing water pressure outside. Thus, not only the shape of these cavities but also voice characteristics might change with swimming depth (Tyack 1991). Indeed, Ridgway et al. (1997) showed that the power spectra of beluga (*Delphinapterus leucas*) sounds are very different depending on the depth at which the sound is produced. Therefore, dolphin voice characteristics do not seem to provide reliable information on the identity of a caller. Instead bottlenose dolphins seem to ensure individual recognition over long distances by encoding identity in a specific whistle type. The modulation of such a whistle is resistant to pressure changes. Vocal learning gives them the opportunity to develop new whistle types that can be used in this context.

This leaves us with two possible reasons for the evolution of vocal learning in all cetaceans if we assume that it is still used in its original context. Baleen whales seem to use it in the context of mate attraction and/or intra-sexual competition (Tyack 1986a). Toothed whales on the other hand most probably use it in individual recognition. It is difficult to decide which of these was the original context in which vocal learning evolved or whether it evolved twice within the cetaceans. One argument can be made to support the primacy of individual recognition. Baleen whales only branched off from the older toothed whales around 10-40 million years ago (Milinkovitch et al. 1993). Thus, since none of the toothed whales has been found to show singing behaviour it could be argued that individual recognition was the significant factor in the evolution of vocal learning. However, further studies on individual recognition, especially in baleen whales, are needed to come to a conclusion about its role in the evolution of vocal learning in cetaceans.

Implications of vocal learning

One of the main problems for a recognition system that is based on learned signals is the fact that others can copy the recognition signal. Even though one bottlenose dolphin produces its specific signature whistle consistently if it is isolated from its group members, other individuals are capable of producing the same whistle. This can introduce a serious problem if learned signals are crucial for individual recognition. How does the receiver know which individual produced a call if it cannot use voice characteristics? Birds, for example, find it more difficult to distinguish between individuals that sing the same song type than individuals that sing different song types (McGregor & Avery 1986; Beecher et al. 1994a). However, bottlenose dolphins nevertheless seem to use learned signals in individual recognition.

Two questions are critical to the impact of whistle copying: Do bottlenose dolphins copy the signature whistles of others, and why would they do so? Tyack (1986b) was the first to investigate signature whistle copying. To identify which of the two individuals in a pool was producing a call he employed so-called vocalights. Vocalights consist of a microphone and amplitude sensitive light emitting diodes (LED's). These devices were attached to a dolphin's head so that whenever an individual produced a call its LED's lit up. With this setup Tyack found that each individual produced mainly one of the two stereotyped signature whistles he recorded, but that approximately 25% of its whistles were copies of the other animal's signature whistle. Thus, strictly speaking signature whistles are not individually specific. However, apart from this study on two captive individuals we know nothing about how this ability is used in dolphin communication.

There are several possible reasons why dolphins copy signature whistles. Feekes (1977) hypothesised that shared, learned calls can act as a password to exclude non-members from a group. This hypothesis depends on the fact that an individual cannot produce an exact copy of a call on first exposure to it. In dolphins Richards et al. (1984) have shown that an individual was able to produce high fidelity

copies of novel calls immediately. It is, of course, difficult to assess whether another dolphin could recognise that a copy was emitted by an animal with no practice in producing that call. However, the cues present for such recognition could only lie in small parameter variations. In the previous section on the origins of vocal learning I discussed problems imposed on the communication system by background noise and changing water pressure. That discussion showed that it seems unlikely that an individual could discriminate between genuine and copied calls of the same type at a distance by listening to slight parameter differences.

This would make whistle copying a useful tool to deceive others. Floater male song sparrows (*Melospiza melodia*) for example learn to sing the shared songs of a neighbourhood and then insert their territory between territories of these neighbours. Beecher et al. (1994b) argue that the established birds are deceived in that they do not recognise the floater as an intruder and, thus, show less aggression than towards a stranger singing different songs. In dolphins there are several situations in which copying could be used for deception. A mother could be lured away from a food patch by copying her infant's whistle and in agonistic or territorial encounters a dolphin could pretend to be more than one individual by producing calls of several animals as in the Beau Geste hypothesis proposed for birds (Krebs 1977). Deception is likely to occur if the costs involved in being detected are lower than the benefits that can be achieved by the performance or if detection is highly unlikely. Considering the cognitive abilities of dolphins even tactical deception (Whiten & Byrne 1988) seems possible. However, false signals can only be advantageous if they are relatively rare (Wiley 1994). If not, specific adaptations to counteract deception would be expected, since signature whistles still seem to be important in individual recognition and group cohesion. These issues have so far received no research attention in dolphins.

The ability to copy signature whistles may also have advantages for the maintenance of group cohesion. Tyack (1986b) suggested that copying another individual's whistle is used to address a particular animal. In the highly fluid social system of bottlenose dolphins this interpretation is particularly convincing. Since individuals often swim within acoustic range of each other, the ability to address specific individuals could be used to maintain group cohesion even in

large feeding aggregations. Also if individuals are trying to coordinate their movements at a distance such a system would be useful. Bottlenose dolphins have been found to hunt cooperatively (Hoese 1971) and adult males sometimes synchronise their swimming in the context of mating (Connor et al. 1992a). Tyack (1993) described an instance in which a female reacted selectively to the copying of her whistle by another female while other animals did not. Gwinner & Kneutgen (1962) observed similar cases in which ravens (*Corvus corax*) and white-rumped shamas (*Copsychus malabaricus*) used specific calls of their mates, which caused the partner to return to the caller. Matching another animal's calls can also occur in agonistic contexts and can elicit an aggressive response without cooperation being involved. Many song birds use song matching in such contexts (reviewed in Catchpole & Slater 1995). Bottlenose dolphins do not seem to use whistles much in aggressive interactions at close range (Overstrom 1983), but they could be important over longer distances.

Richards et al. (1984) trained a bottlenose dolphin to imitate specific computer sounds in response to different objects. They called this behaviour vocal labelling and suggested that dolphins use signature whistles as labels for other dolphins. While copying is a descriptive term, labelling suggests that the individual has a learned, internal representation that connects the label and the corresponding object independent of the context. In observational studies it is often difficult to recognize whether the animal has made such a connection or whether it only formed a context-specific association, i.e. that the production of a specific call leads to a specific result. Context-specific associative learning is very common in animals. Gwinner & Kneutgen (1962) in their study on call copying in birds, for example, argued that the female bird had learned to associate her copying with a return response of the male. This does not require the internal connection between the male and its call that is required for labelling. In human language, on the other hand, new labels are created spontaneously and are used to communicate about the environment. Terrace (1985) and Wilkins & Wakefield (1995) have suggested that labelling behaviour may have been a first step in the evolution of human language. They pointed out that several animal species can be taught to use new labels for objects, but none shows that behaviour in its own communication system or uses new labels without being rewarded. Humans, on the other hand,

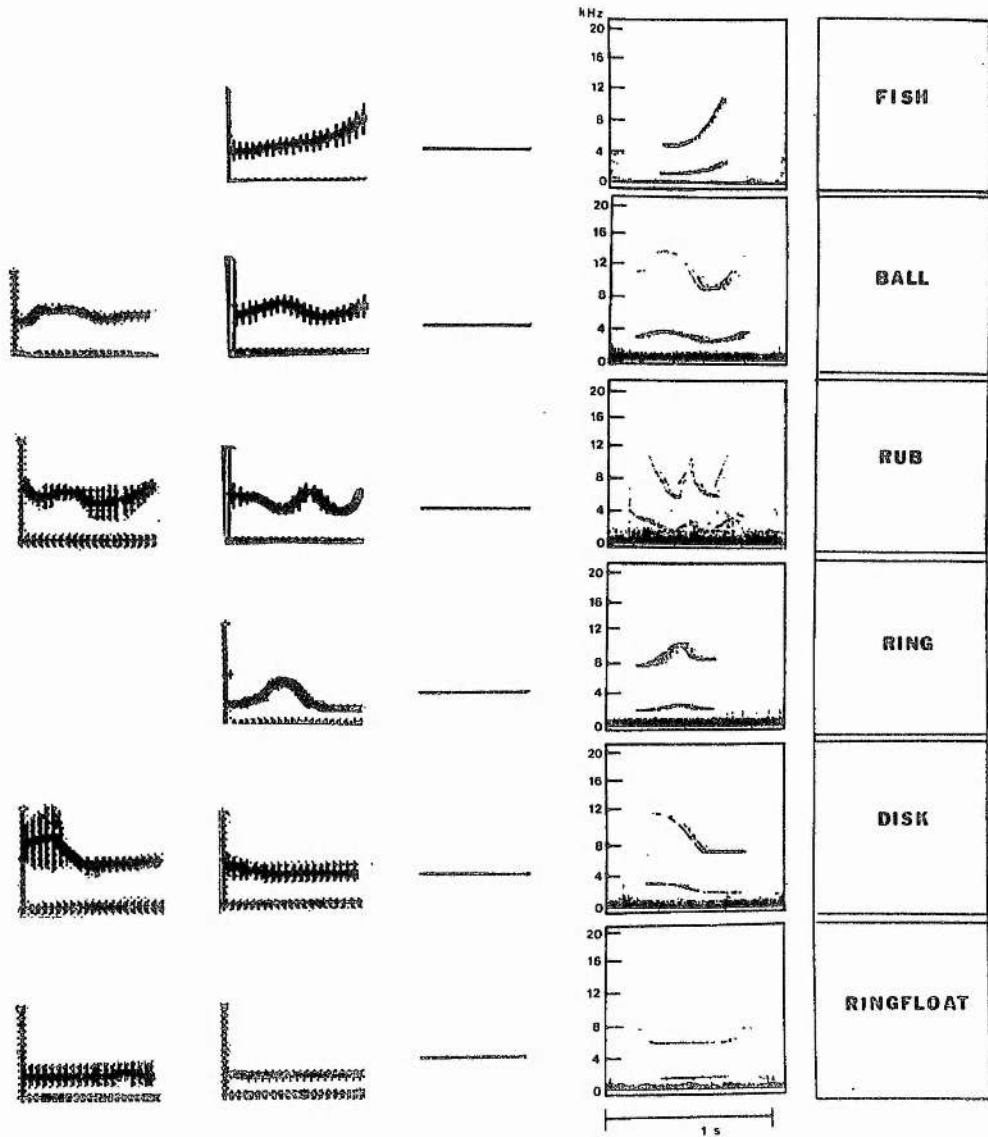


Figure 2.1: Selected whistle types of bottlenose dolphin subjects previous to the start of the Reiss & McCowan (1993) vocal mimicry study (left two columns) and spectrograms of model whistles used in that study (right column). The dark lines in the left two columns represent the mean frequency contours of each whistle type, and vertical lines represent the standard deviations (from McCowan & Reiss 1995b). Contours on the left are normalized for differences in duration (x-axis) and the y-axis represents frequency from 0 to 20 kHz. The visual comparison between whistles on the left and on the right suggests that the whistles used as models in the vocal mimicry study were present in the repertoires of the animals before the onset of the study. Thus, it is questionable whether vocal learning was demonstrated in Reiss & McCowan's (1993) study.

develop or copy novel sounds spontaneously to label objects often without any reward being involved.

Very little is known about the mechanisms of whistle copying or possible labelling in dolphins. Reiss & McCowan (1993) investigated labelling behaviour in dolphins experimentally. They reported that bottlenose dolphins spontaneously produced whistles that have been presented to them during presentations of different objects. These whistles were later also heard when the animals were allowed to manipulate these objects in their tank without any further reward being given by the experimenters. However, in studies such as this it can be difficult to determine whether a call is newly learned or was in an animal's repertoire before. Reiss & McCowan (1993) reported that the whistles used were novel to the animals. However, the spontaneous whistles produced by their study animals while manipulating objects were remarkably similar to contours in their baseline data from the same individuals before onset of their vocal mimicry study (Fig. 2.1). Bottlenose dolphins can shift the frequency band which a whistle contour lies in (Richards et al. 1984), so that differences in the absolute frequency of contours seems less important. Therefore it is still not clear whether bottlenose dolphins use novel sounds spontaneously to label objects. The social system of bottlenose dolphins and the large number of individuals each interacts with would make a complex labelling system advantageous. However, further studies on the contexts of call copying are needed to decide what mechanisms might be involved.

Conclusions

We have seen that individual recognition was a likely selection pressure for the evolution of vocal learning in dolphins. Since they are limited to acoustic signals for communication due to the properties of their environment and their high mobility, this puts special selection pressures on their communication system. It may have led not only to the development of learned recognition calls, but possibly also to the usage of copies of these calls to address specific individuals.

The evolution of vocal learning seems to be a crucial event in the phylogeny of odontocetes and probably greatly facilitated their development into the social, highly mobile, aquatic predators they are today. Inevitable separations of mothers and infants while feeding on fast fish are not a problem if identity and position information can be transmitted reliably between them. This allows for a prolonged nursing phase and frees the mother from providing a massive amount of resources to her offspring in a very short time as is the case in other marine mammals such as many phocid seals (reviewed in Trillmich 1996).

A long nursing phase also gives the infant time to acquire many of its abilities by learning. In societies where cooperation and/or social learning occur, it is possible to invade new habitats rapidly by exploiting food sources that otherwise would not be available (e.g. Byrne 1995; Terkel 1996). Bottlenose dolphins seem to have made extensive use of this possibility. They can be found world-wide in almost all marine habitats and have adopted a generalist feeding strategy displaying a wide variety of feeding methods, e.g. using a sponge as a tool to chase fish from the bottom (Smolker et al. 1997), herding fish on to a beach and then feeding on them by beaching themselves (Hoese 1971), digging for fish in the bottom by burying themselves (Roszbach & Herzog 1997) and, possibly in association with false killer whales (*Pseudorca crassidens*), causing sperm whales (*Physeter macrocephalus*) to defecate or regurgitate and then feeding on half digested food items (Palacios & Mate 1996). These techniques usually occur in only one population or group of dolphins and are apparently not part of the whole species' repertoire. There also is some evidence for teaching of feeding strategies in the largest dolphin species, the killer whale (*Orcinus orca*) (Guinet & Bouvier 1995). A long nursing phase allows the young to gather information on feeding techniques as well as about the social structure of the community.

We still know very little about how dolphins use sounds socially. It is likely that vocal learning affects many other aspects of communication in addition to the individual recognition system. Maintaining complex social relationships requires complex communication. Any form of cooperation or coordinated behaviour would require extensive transmission of information. Again, due to the lack of visual contact position information is probably one of the most important, but

other referential information is required as well if a specific behaviour has to be performed in synchrony. A good example is in cooperative hunting strategies. Lions (*Panthera leo*) (Stander 1992) and chimpanzees (*Pan troglodytes*) (Boesch 1994) rely heavily on visual information to coordinate their behaviour during cooperative hunts. In dolphins all this information would have to be transmitted acoustically. They show coordinated behaviours in feeding contexts (Hoese 1971) and between males in alliances (Connor et al. 1992b). However, we know little about how such coordination is achieved. To understand the role that vocal learning might have played in the evolution of sociality we need to investigate, first, the extent to which non-communicative sounds like swimming noises or sounds produced for echolocation are used to acquire information that is not available through vision and, second, how communication sounds are used to transmit information that is needed to cooperate in a particular behaviour.

Chapter 3

Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls*

Introduction

All mobile species in which associating with particular conspecifics is advantageous need a mechanism for maintaining group cohesion. This is particularly obvious in animals where mothers and their dependent offspring frequently separate (e.g. during foraging trips). But even among adults it can be at a premium. Group living animals in which social bonds exist need to be able to locate specific partners or must simply stay in their social group. There are two possible ways to locate an individual after separation. Firstly, spatial cues can be used to find the location where the last interaction occurred. However, this method becomes less and less reliable as mobility or local population density increases. The second possibility is the development of a recognition system, based on cues given out by one individual that another can home in on. Like many other signals recognition signals give not only information on the identity but also the location of an individual. Both of these are important for the maintenance of group cohesion.

Individual recognition of vocal signals is often possible from general voice characteristics that affect any of the calls produced by an animal (Cheney & Seyfarth 1980, 1988; Lind et al. 1996; Rendall et al. 1996). Individual variation in such characteristics is higher in species that live in noisy environments than in those living in quieter ones (Beecher 1991). Cliff swallow (*Hirundo pyrrhonota*) chicks, for example, show higher inter-individual variability in their begging calls than barn swallow (*Hirundo rustica*) chicks (Loesche et al. 1991). Unlike barn

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swallows, cliff swallows nest in dense colonies where a lot of background noise is created by conspecifics. However, if animals live in high background noise and are very mobile genetic differences in vocal tract morphology that cause differences in voice characteristics could become insufficient to assure individual recognition, and specialised signals may be necessary.

Research on captive and temporarily captured wild bottlenose dolphins (*Tursiops truncatus*) has shown that each individual uses its own distinct, stereotyped signature whistle if it is isolated from conspecifics (Caldwell & Caldwell 1965; Caldwell et al. 1990; Sayigh et al. 1990; Janik et al. 1994). Researchers have distinguished between signature whistles by looking at their frequency contours which is the unique modulation pattern of the fundamental frequency of the whistle. With this method it has been shown that signature whistles remain stable for up to at least 12 years (Sayigh et al. 1990). Caldwell et al. (1972) also showed that a bottlenose dolphin can be trained to distinguish between different signature whistles. Caldwell & Caldwell (1968) were the first to hypothesize that these whistles could be important for individual recognition and group cohesion. Recognition or isolation calls of other animal species often show a remarkable similarity in their overall contour in all individuals if compared to the variability of contours found in just one individual's call repertoire (e.g. Lieblisch et al. 1980; Beecher et al. 1981; Stoddard & Beecher 1983). In contrast, dolphin signature whistles are unique frequency contours that are as dissimilar between individuals as are different non-signature whistles in an individual's repertoire. Unlike recognition calls of other animals they look like completely different whistle types to the human eye. Such increased variability in whistles used for recognition by different individuals increases their resistance against interference tremendously (Beecher 1991). In contrast to the recognition calls of most other mammals, the development of signature whistles is influenced by vocal learning (Tyack & Sayigh 1997). Vocal learning is a relatively rare ability among mammals and it has been hypothesized that its evolution in dolphins was closely connected to the constraints imposed on signature whistles by the marine environment (Janik & Slater 1997). In a marine environment, not only high background noise levels but also changing water pressure on the sound production apparatus can conceal differences in voice characteristics that would otherwise identify the caller (Tyack

1997). Vocal learning most likely evolved at the time when cetaceans re-entered this environment and enabled each individual dolphin to develop its own unambiguous signature whistle type.

However, even though individual recognition and group cohesion are considered the most likely functions of signature whistles today, there are some problems with this idea. Vocal learning, for example, influences more than just signature whistle development in infants. The ability is present throughout the dolphin's life and adult bottlenose dolphins can produce copies of novel sounds at the first attempt (Richards et al. 1984; Sigurdson 1993). Tyack (1986b) studied whistle usage in two captive bottlenose dolphins and found that they frequently produced each other's stereotyped whistles. He hypothesized that these whistles represented the subjects' signature whistles and that whistle copying could be used to address a specific individual in a group. But this copying ability could also work against individual recognition. If several animals produce the same signature whistle, then individual recognition could not work assuming that voice characteristics are not reliable indicators of identity. If signature whistles are identification signals it still remains to be shown how confusion with copying individuals is avoided. Thus, to be able to assess the functional significance of signature whistles it is important first of all to investigate the contexts in which they are used.

Even though signature whistles have been studied since 1965 we still know astonishingly little about the contexts in which they are used. This is partly because dolphins rarely provide any visible signs of sound production. Sounds are produced in the head and travel directly through the tissue into the surrounding water (Dorner 1979). No opening of the mouth or the blowhole is required. For this reason, many studies have focused on isolated individuals so that caller identification was unproblematic. But isolation is just one very specific context and gives little information on whistle usage in other situations. Studies on whole groups of dolphins on the other hand have mostly not been able to identify the caller and so have given little information on the contextual usage of whistles. Therefore the hypothesis that signature whistles are used for individual recognition or group cohesion still remains to be tested.

Only two studies to date have been able to identify the caller and have looked at individual whistle usage in groups of dolphins at the same time. Tyack (1986b) developed a telemetry device, called a vocalight, attached to a dolphin's head with a suction cup. Light emitting diodes which lit up whenever the animal was calling allowed him to identify a caller. With this device Tyack showed that each of two captive individuals primarily produced one stereotyped whistle type, but each also produced the other's stereotyped whistles frequently. In the other study, McCowan & Reiss (1995b) looked at whistle usage in captive groups by using bubble streams out of the blowhole to identify the caller. Dolphins sometimes produce such bubble streams while vocalizing. McCowan & Reiss (1995b) could not find any stereotyped whistle contours likely to have been signature whistles in their sample. It is somewhat puzzling that these two studies had different results. There are three possible explanations for this discrepancy, two of which are concerned with the different methods used. First, it could be that bubble streams are associated with specific whistle types. McCowan (1995) argued that they are not, but, in her comparison of whistle type production with and without bubble streams in a captive group, the sample sizes were very small (20 and 50 whistles, respectively). Second, McCowan & Reiss (1995b) used a very different method to categorize whistles. In their method, they condensed or stretched all whistles to the same length and used only 20 frequency measurements to describe each contour, while Tyack (1986b) categorized the original whistle spectrograms by eye. Thus, it is difficult to compare the results of the two studies. The third possible reason for the discrepancy is the difference in recording context. While Tyack's group consisted only of the two animals that were wearing vocalights, McCowan & Reiss' groups were larger and undisturbed. Without further study it is impossible to decide which reason is responsible for the difference found.

In fact, such differences in the findings of studies on dolphin whistles have led some authors to question the claims of signature whistle studies (Herman & Tavolga 1980; McCowan & Reiss 1995a). Studies that have found signature whistles reported them to be the most common whistle type in all contexts investigated. But since their usage was not context-dependent, no biological confirmation of their existence in the natural repertoire of the animals was achieved. If the recognition/group cohesion hypothesis is right, signature whistles

would mainly occur when animals were separated and out of sight of each other. We would also expect them to occur in novel and possibly threatening situations when group cohesion is of major importance for a cooperating animal like the bottlenose dolphin. Studies on groups of dolphins that have been recently captured (Caldwell & Caldwell 1968) or were exposed to novel situations like lowering of the water level in the pool (Caldwell et al. 1990) have, in fact, already demonstrated that stereotyped whistling can occur while animals are together. However, to date no study has compared whistle production of the same individuals (after they have been well habituated to captivity) both while they were in isolation and in a group without any human intervention.

To investigate the hypothesis that signature whistles are used to maintain group cohesion and are not just induced by stressful situations, this study compared whistle usage in a group of four bottlenose dolphins while together and in isolation. Additionally, I investigated the occurrence of whistle copying when animals were in separate pools to address the question of individual specificity.

Methods

Subjects and Facility

The study was conducted at the dolphinarium of the Zoo Duisburg in Germany. The subjects were four North Atlantic bottlenose dolphins. This group consisted of one adult male (Playboy, 23 years old) and one adult female (Pepina, 14 years old), both collected in the Gulf of Mexico on different occasions several years previously, and one subadult male (Duphi, 7 years old) and one juvenile female (Delphi, 3.5 years old) both born at the facility. They had different mothers but the adult male was possibly father to both of them. The adult female present in the pool was not the mother of either of the captive born individuals, but was pregnant at the time of this study. Her calf was born 7 months after this study was completed. Two connected indoor pools were used by the animals. The larger main pool was oval, 25 m long and 15 m wide; the smaller pool was a square with

side lengths of 10 m and 9 m. Both pools were 5 m deep, and were connected by a gap 1.79 m deep and 1.23 m wide at the surface of the shared wall. Throughout the study all animals could use both pools at any time.

Data Collection

Data were collected over 10 days in January 1996. Each pool was equipped with a Dowty SSQ 904 sonobuoy hydrophone with custom built preamplifiers. Both hydrophones were placed at 1 m depth and output from them recorded on two separate channels of a Marantz CP 430 tape recorder. Both channels were set at the same recording level. The recording system had a frequency response from 1 to 20 kHz \pm 3 dB (calibrated by Neptune Sonar Ltd., UK). This corresponds to the frequency range of whistle contours in bottlenose dolphins. I continuously noted the location (large or small pool) of each dolphin. Recordings were made either while all animals were swimming together in the main pool or whenever one animal swam separately from the others in one of the pools. These separations were not induced but occurred spontaneously in the daily behaviour of the animals. No recordings were made during feeding or training sessions. Each session was started after the animals had been undisturbed for at least 10 min. Aggressive behaviours were sampled continuously to investigate whether separations were induced by aggressive interactions. Behaviours sampled corresponded to those investigated by Samuels & Gifford (1997). Observations were made from an elevated point 15 m from the pool.

Data Analysis

Frequency spectrograms of all recorded whistles were calculated using SIGNAL software (Engineering Design, Belmont); (FFT size: 1024, time resolution: 20.5 ms, frequency resolution: 48.8 Hz, number of FFT steps: 200, weighting function: Hanning window). In the first step, I inspected spectrograms by eye and classified them into separate whistle types without knowing the context in which they were

produced or the identity of the dolphin. Sayigh et al. (1995) demonstrated the validity of this method by showing that human observers agree on what whistles look similar to each other on a frequency spectrogram. Furthermore, computer methods that have been used to classify dolphin whistles are still not able to detect some of the gestalt features of signature whistles and are therefore not suited to investigate signature whistle usage (see Chapter 4). Spectrograms were inspected twice. In the first run only very stereotyped whistle types were identified; in the second run all remaining whistles were categorized into more variable types which were defined by the shape of the frequency contour of a whistle (see results). However, to test for inter-observer reliability a subset of 104 randomly chosen whistle contours was classified by five additional observers (see Chapter 4). No observer had any information on contexts of whistles or caller identity. The inter-observer reliability of all six observers in the classification of what they considered stereotyped whistles was extremely high (Kappa statistic (Siegel & Castellan Jr. 1988): $K = 0.92$, $z = 22.16$, $P < 0.0001$) and corresponded closely to the initial classification.

Next I used a comparison of the amplitude of each whistle on the left and the right channel of the tape recorder to determine which pool a whistle came from (Janik et al. 1994). Whistles are omnidirectional since a dolphin's head does not focus low frequency sounds like whistles (Evans et al. 1964). Thus, the orientation of the animal has no influence on the amplitude comparison. Whistle type production was analysed for each individual when it was swimming on its own, for the whole group swimming together, and for the remaining group if one animal was separate. Data on aggression were analysed for each 1-min period before a separation occurred.

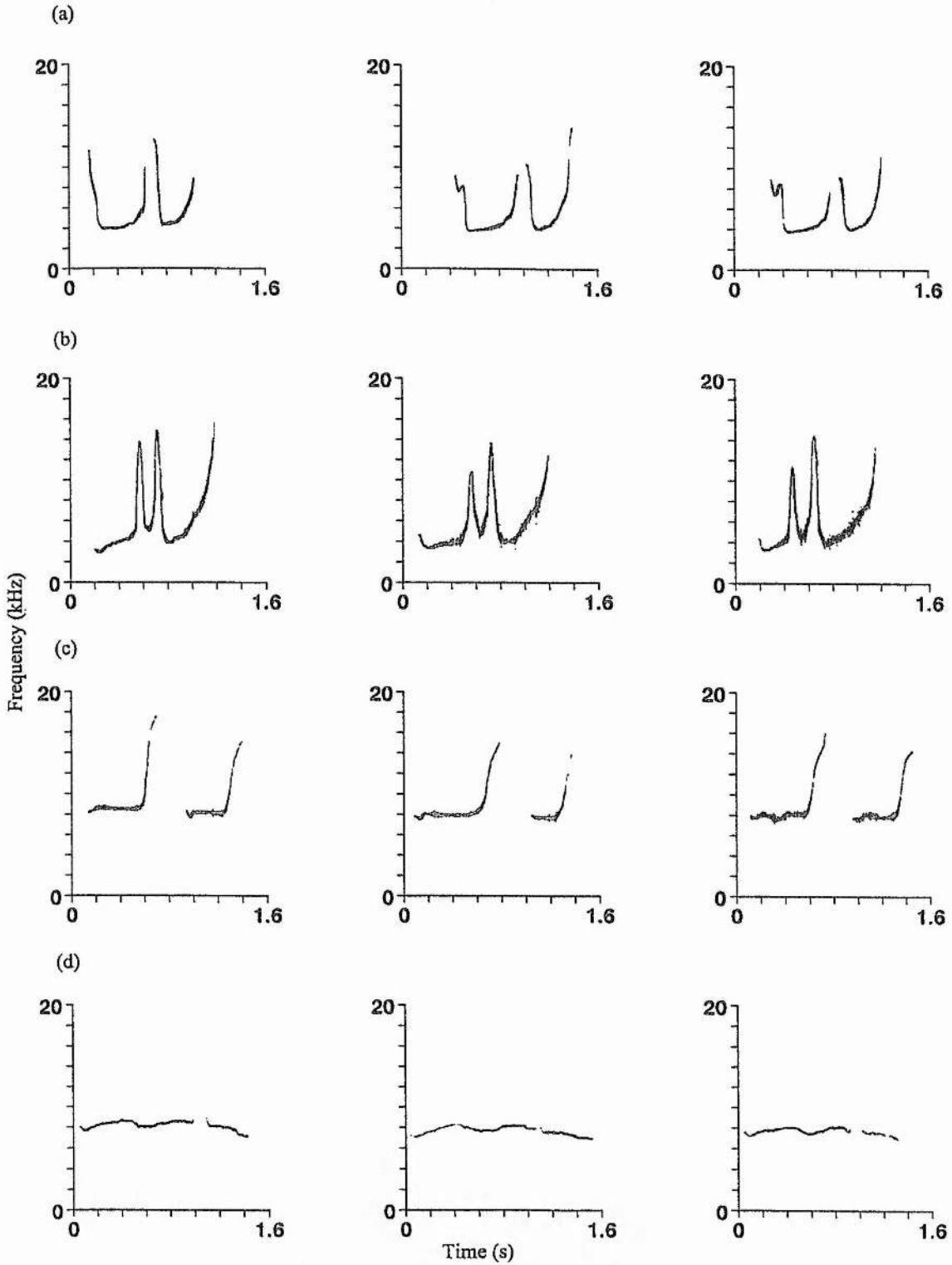


Figure 3.1: Three randomly chosen spectrograms of each of the stereotyped whistle types: (a) whistle type A, signature whistle of the adult male; (b) whistle type B, signature whistle of the adult female; (c) whistle type C, signature whistle of the subadult male; (d) whistle types D_{1&2}. Contours D_{1&2} almost always followed each other and made up the signature whistle of the juvenile female. Background noise and harmonics have been removed on all spectrograms since the frequency response of the recording system was not sufficient to record complete harmonics.

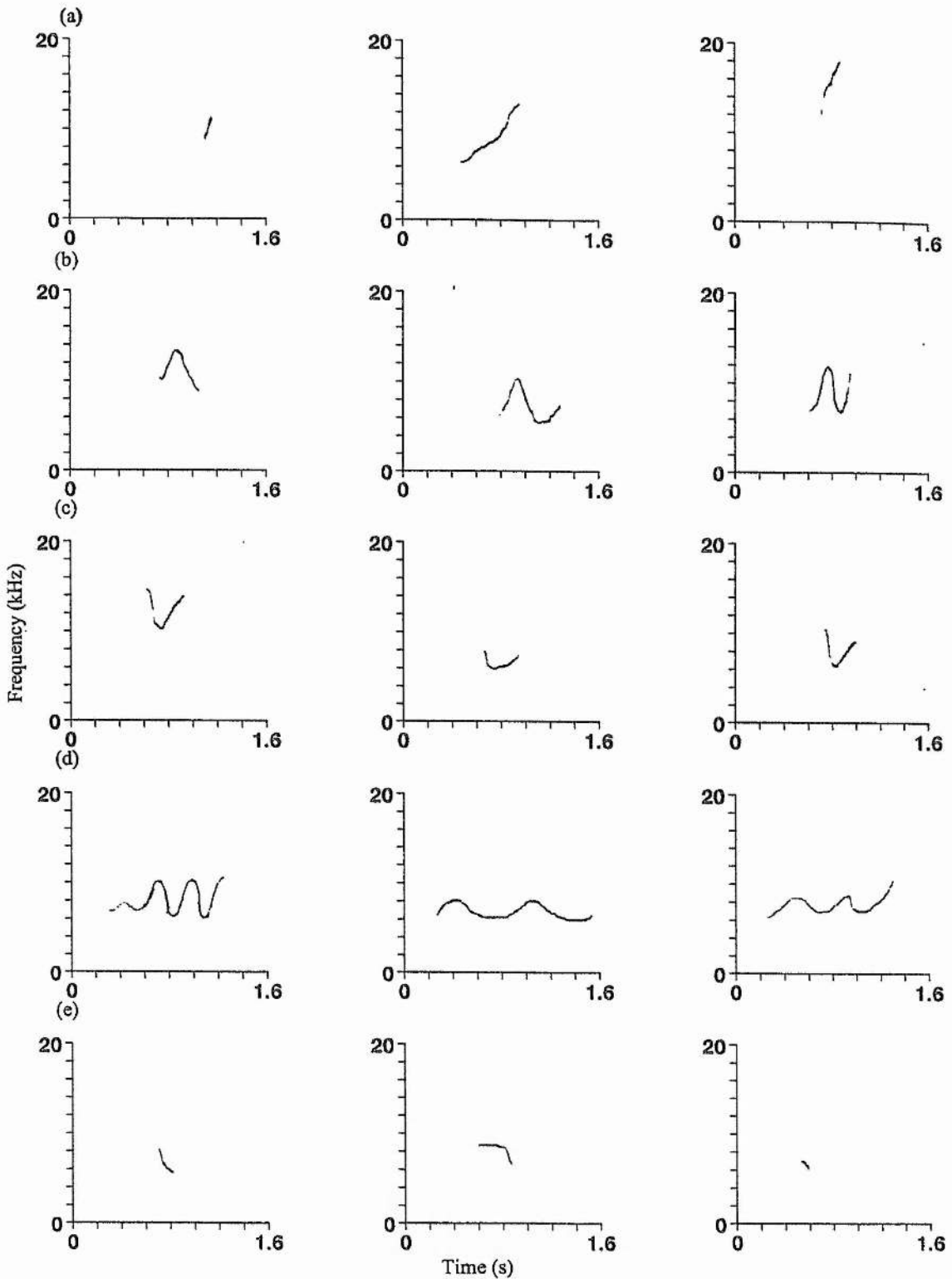


Figure 3.2: Three randomly chosen spectrograms of each of the more variable whistle types: (a) whistle type RISE; (b) whistle type WAVE; (c) whistle type U-SHAPE; (d) whistle type SINE; (e) whistle type FALL. Background noise and harmonics have been removed on all spectrograms (see Fig. 3.1).

Results

Whistle Classification

All 2472 whistles were categorized into whistle types A, B, C, D₁, D₂, RISE, WAVE, SINE, U-SHAPE, FALL and RESIDUAL (Figs. 3.1 and 3.2). Types A, B, C, D₁, and D₂ were the stereotyped whistle types identified in the first scan of the spectrograms. Figure 3.1 shows example spectrograms for each of these stereotyped whistle types. The classification of non-stereotyped whistles followed that of Tyack (1986b) and Janik et al. (1994).

For further analysis all types that occurred at least 80% of the time in close sequence (less than 500 ms apart) were considered one whistle. Such multi-loop whistles have been described before and seem to represent one unit in the repertoire of a dolphin (Caldwell et al. 1990; Sayigh et al. 1990, 1995). The multi-loop whistles found were types A, C, and D (Fig. 3.1). In types A and C two very similar contours followed each other, while in type D the two contours were different (D₁ followed by D₂). Only 40 out of the 394 contours that made up type A in the total whistle sample of 2472 whistles recorded for this study occurred on their own. In type C it was 53 out of 391 contours, and in type D the first contour occurred 54 times on its own, the second one did so three times, and the two occurred together on 261 occasions. None of the less stereotyped whistle types formed multi-looped whistles.

Whistle Usage

Whistle rates per individual did not differ significantly between isolation and group swimming (Table 3.1; Kruskal-Wallis test: $H_4=6.335$, NS). However, the distribution of whistle rates was different between contexts (Table 3.1). While the median whistle rate is lower in the group swimming context, whistle rates of nil were rare. Conversely, in separations animals often did not whistle at all, except in a few separations when high whistle rates were apparent.

Table 3.1: Sample sizes and whistle rates for each individual in isolation and for the group swimming together.

Individuals	Number of sessions	Total recording time (min : s)	Total number of whistles*	Percentiles of whistles per individual per session per min †		
				25	50	75
Adult male	38	60:55	128	0	1.73	3.67
Adult female	33	37:43	110	0	2.73	5.43
Subadult male	10	31:58	133	0	0	6.31
Juvenile female	21	47:40	238	0	2.05	9.28
Group swimming	37	219:00	714	0.13	0.79	1.54

* A further 1149 whistles were recorded from the rest of the group at times when one individual was separate. These have been analysed separately since they are not independent from the data of the isolated individual.

† Note that percentiles describe the distribution of whistle rates from each separation or group swimming event. Thus, the median here is not equal to the overall whistle rate (total number of whistles/total recording time).

Figure 3.3 shows how whistle types were distributed between the different contexts. Each individual used a different stereotyped whistle type when it was separated from its group. The signature whistle was the most frequent whistle type for each individual when it was in isolation. Thus, I termed these whistles the signature whistles of these individuals. Type A was the signature whistle of the adult male (68.5% of his whistles in isolation), type B belonged to the adult female (31.8% of her whistles in isolation), type C to the subadult male (91.7% of his whistles in isolation), and type D to the juvenile female (72.7% of her whistles in isolation). Signature whistles were the most common whistles in the isolation context. However, signature whistles did not occur during every separation. Short separations often did not involve any whistling or only non-signature whistle types. The animals also used RISE, WAVE, SINE, U-SHAPE, FALL and RESIDUAL whistles when in isolation, but almost never any of the other individuals' signature whistles. The only two such cases were when the sub-adult

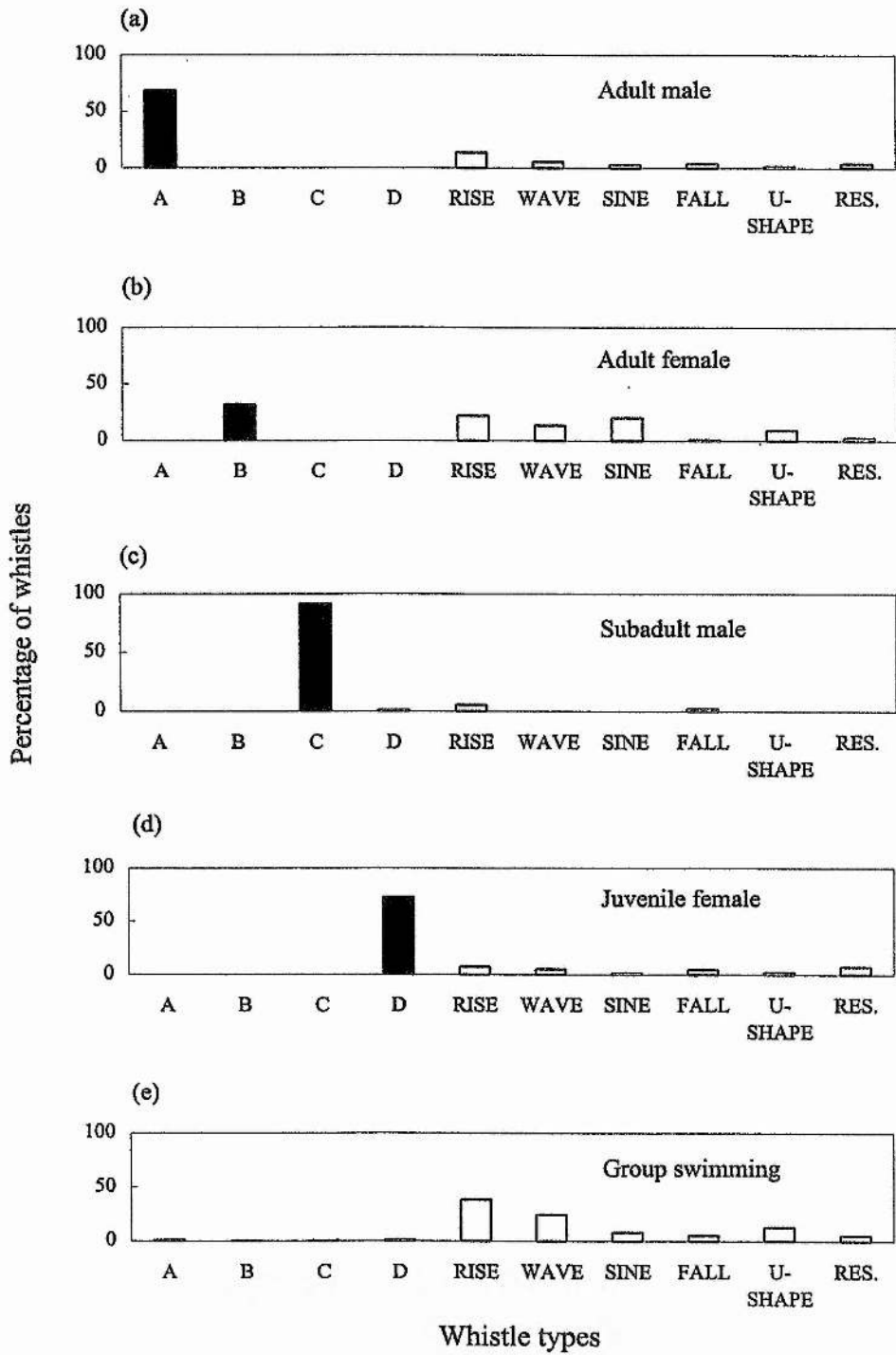


Figure 3.3: Whistle type usage in different contexts: (a) adult male in a separate pool; (b) adult female in a separate pool; (c) subadult male in a separate pool; (d) juvenile female in a separate pool; (e) all animals together in one pool. Black bars indicate signature whistle types, white bars are non-signature whistle types. RES. = RESIDUAL class.

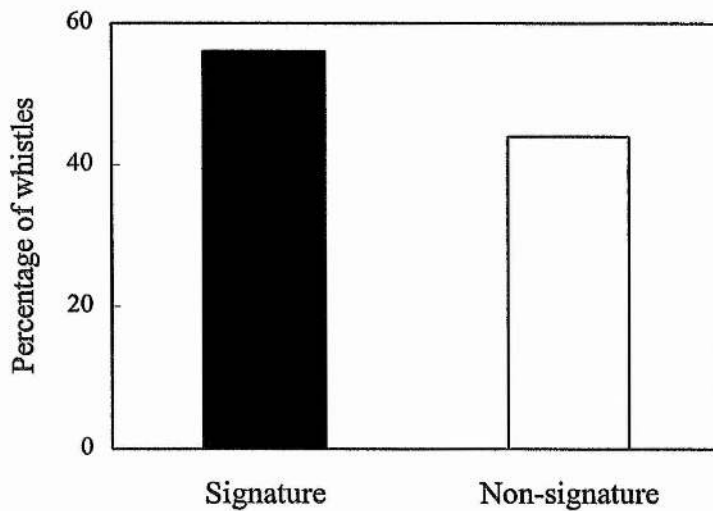


Figure 3.4: Histogram showing the percentage of signature and non-signature whistles produced by the three animals that remained together while a fourth animal was in a separate pool.

male produced parts of the juvenile female's signature whistle while he was in the separate pool (see below). The three animals that remained in the other pool together also used primarily their signature whistles if one animal was separated from them (Fig. 3.4). Of the 1149 whistles recorded from these remaining individuals 56% were signature whistles. Given the total lack of signature whistles when all four animals were in the same pool, this is a particularly striking result.

Almost all signature whistles used occurred when the whistling animal was separate from the rest of the group. Only 17 signature whistles were recorded during group swimming, representing 2.4 % of all whistles recorded in that context, and 10 of these occurred in two bouts of five signature whistles each. When all four were together in a group the animals used almost entirely non-signature whistles. However, this is only true for undisturbed animals. I observed one incident in which all individuals produced almost entirely signature whistles while together in one pool. This happened when a feeding session was delayed. During this whistling bout the animals were often facing underwater windows where keepers were visible. This event was not part of the sample analysed in this

study since the animals were not undisturbed at the time (several humans were present at the pool). However, it suggests that signature whistles are sometimes used in other contexts than separation.

The analysis of aggressive behaviours revealed that separations were not induced by aggression. Aggression in this group was rare and I observed only one case in which an aggressive act (a chase) preceded a 22 s separation.

Signature Whistle Copying and Whistle Matching

Signature whistle copying could only be investigated during separations since this was the only context in which one caller was known. If the signature whistle of the animal in isolation was heard from the pool where the rest of the group was swimming it must have been copied by an animal in that pool. In the total recording time of 397 min and 16 seconds that one animal was separated from the rest of the group, only five cases of signature whistle copying were found (Fig. 3.5). Signature whistle copying did not initiate the end of a separation and there was no consistent vocal response to copying. However, signature whistle copying only occurred after the copied whistle had been produced at least once within the preceding minute by the other individual. In all cases the copied whistle was also heard at least once in the minute after the copying from the other pool. For non-signature whistles only direct matching of whistles could be analysed since all individuals used all non-signature whistle types. A matching interaction was defined as an individual producing the same whistle type as another one within 3 seconds after the end of the first caller's whistle. Using the same strict criteria as for signature whistles I found no whistle matching involving non-signature whistles. However, it could be that the animals shared rarely used stereotyped non-signature whistles but simply did not use them in matching interactions.

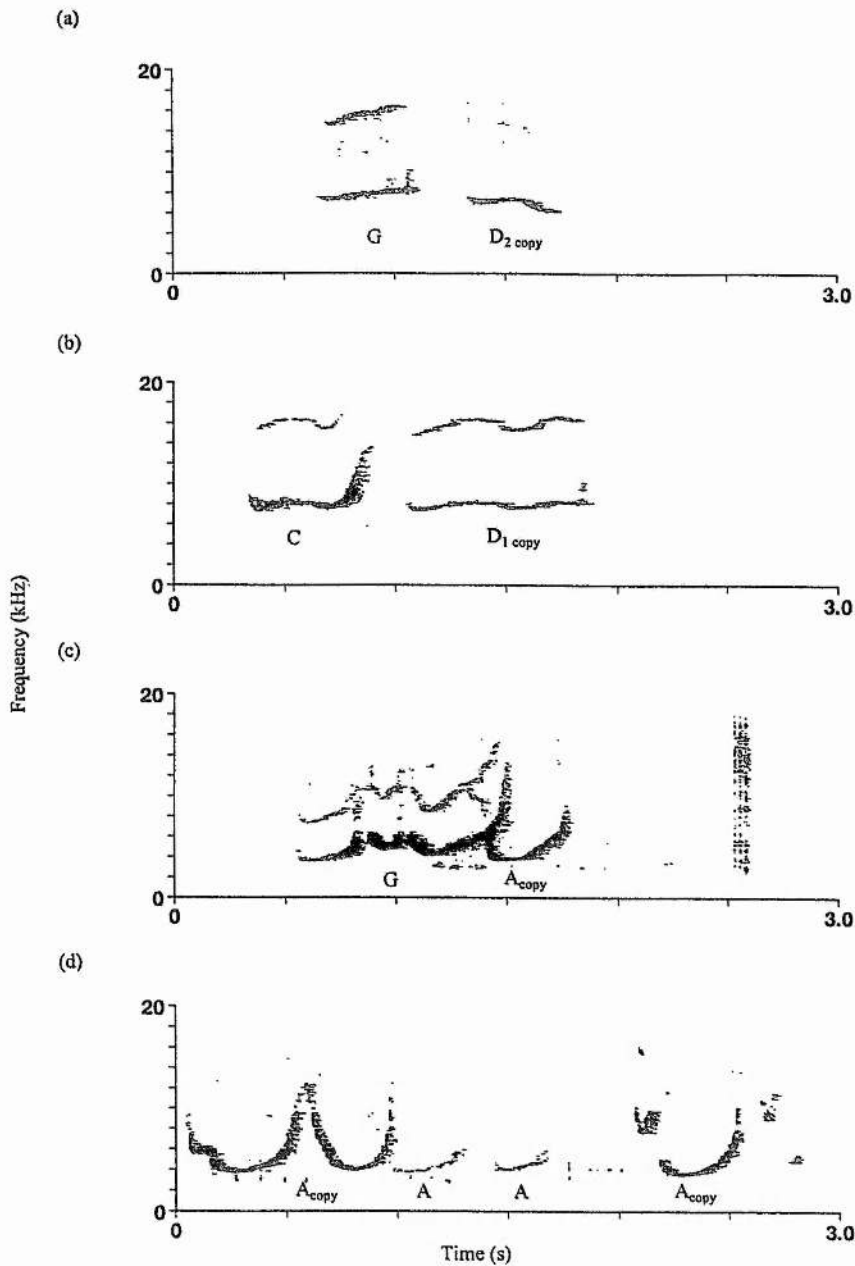


Figure 3.5: Spectrograms of all cases of signature whistle copying found in this study. (a) Subadult male copies second loop of the juvenile's signature whistle. (b) Subadult male copies first loop of juvenile's signature whistle. (c) Animal in remaining group copies one loop of adult male's signature whistle. (d) Animal in the remaining group copies adult male's signature whistle twice. The first and the last contour were produced by animals in the remaining group, the faint contours in the middle were produced by the adult male. Note that these spectrograms have been produced from only one channel of the recording system. Whistles that are faint or seem interrupted are in fact complete and continuous versions of signature whistles from the other pool. Signature whistle produced by adult male (A), remaining group copies whistle of adult male (A_{copy}), whistle of subadult male (C), subadult male copies signature whistle of juvenile female (D_{1&2 copy}), whistles of the remaining group of three(G).

Discussion

Previous studies on dolphin whistles did not find such clear differences in whistle type usage between contexts as those presented here. Studies on signature whistles found them to be the most common whistle type in all investigated contexts (Caldwell et al. 1990; Janik et al. 1994), while some other studies could not find any highly stereotyped whistling at all (Dreher & Evans 1964; McCowan & Reiss 1995a). This suggests the possibility that differences between studies were simply due to different methods (Herman & Tavolga 1980; McCowan & Reiss 1995a). But which methodology is appropriate to investigate whistle types? Any classification method for animal signals involves decisions by humans on the parameters to be used. Further validation is needed to find out which method represents the best approximation to how dolphins themselves classify whistles. Without any data from perception experiments one of the best methods to confirm the existence of a particular category found in one's data set is a test on an external variable (Aldenderfer & Blashfield 1984). This involves carrying out tests to compare the whistle types on variables that have not been used to define them (= external variables). In this study I followed this procedure by classifying whistles by eye and then looking at who used which whistle type in what context. Here, usage of whistles is the external variable. The results, showing that signature whistles occurred almost exclusively in the separation context but not in the group context and that they were very individually specific, confirmed that these whistle types are important units in the dolphin's repertoire. However, no such confirmation has been found for non-signature whistles in this or any other study. To draw conclusions on what represents a non-signature whistle type, we will need specific classification experiments, such as those that have been done with birds (Horn & Falls 1996).

The results of this study also imply that differences between previous studies have been caused by differences in the contexts that were investigated. Studies that have looked at isolated individuals (Caldwell & Caldwell 1965; Caldwell et al. 1990; Sayigh et al. 1990; Janik et al. 1994), animals shortly after capture (Caldwell & Caldwell 1968; Caldwell et al. 1990), or in unusual situations like during a lowering of the water level in the pool (Caldwell et al. 1990), while many

people were around the tank or while the animals were wearing telemetry devices (Tyack 1986b), revealed that bottlenose dolphins almost only use signature whistles in such contexts. On the other hand, no stereotyped whistle types were found in studies in which animals well habituated to captivity and not exposed to any human intervention were recorded without being separated (Dreher & Evans 1964; McCowan & Reiss 1995a, b). This study applied the same whistle classification method to the investigation of whistle usage in both context types, and suggests that the difference is not based on methodological differences, but that signature whistles are used only in the separation context. Thus, all results together show that signature whistles are primarily emitted in situations when behaviour helping to maintain group cohesion is likely to occur.

Researchers have used various different terms to describe calls given in isolation. Infant calls that elicit an approach by the care giver for example have been described as isolation or distress calls (reviewed in Maestriperi & Call 1996). Cohesion or monitoring calls on the other hand are used by isolated animals but do not elicit an approach and seem to help an animal to stay in touch with its group (Petter & Charles-Dominique 1979; Caine & Stevens 1990). The term contact call has been used for both of these categories (e.g. Pola & Snowdon 1975), and there is no clear cut distinction between these two classes. Signature whistles could also be used by infants to elicit an approach by the mother, but this is not known. The results presented here, and the fact that bottlenose dolphins can easily distinguish between different signature whistles (Caldwell et al. 1972), strongly support the hypothesis that these signals are used to communicate identity and maintain group cohesion. Further studies are needed to investigate their role in other contexts.

The findings on whistle copying in this study suggest that it is a relatively rare event. Similarly low rates of signature whistle copying in captive animals have been reported by Burdin et al. (1975). But, even though the results reported here are similar to those of some other studies, they differ markedly from what Tyack (1986b) found in his group of two individuals. In his study stereotyped whistling was high while both individuals were in the same pool, independent of whether they were wearing vocalights or not, and whistle copying was common. His

subjects were also well habituated to captivity so recent capture could not have caused these differences. However, all his recordings were made in one day. The increased activity around the pool and the wearing of the vocalights could have influenced the vocal behaviour of his subjects. Captive dolphins can be very sensitive to changes in their daily routines. Bottlenose dolphins produce higher rates of whistles in response to novel situations (McBride & Hebb 1948; Defran & Pryor 1980) and this could have been a factor influencing Tyack's results. Novel situations might not only lead to an increase in overall whistle rates but maybe also to an over-representation of particular whistle types in the expressed repertoire. Another possible explanation could be a delay in the normal feeding schedule. In the present study all individuals produced almost entirely signature whistles while together in one pool on one occasion when a feeding session was delayed. Thus, while Tyack's study was the first to draw attention to the occurrence of signature whistle copying, it was probably not representative of undisturbed vocal behaviour in bottlenose dolphins.

We still know very little about how whistles are used in wild bottlenose dolphins. One has to be careful in extrapolating results from studies on captive dolphins to wild ones. Data from captive individuals can give us some information on functions of whistles, but the pattern of occurrence of signature whistles and signature whistle copying may be very different in the wild. This is mainly because certain contexts do not appear in captivity. The main differences relevant to this study are that there were no other dolphins within hearing distance and that the animals did not need to search for food. The visual range under water is low compared to the acoustic range. In the wild, groups spread out to feed or to socialize with other individuals, situations in which we would expect signature whistles to occur. However, even in a group, wild dolphins might still be in contact with other dolphins that are out of sight. The situation in the wild seems to resemble that of a communication network (McGregor & Dabelsteen 1996) in which individuals constantly move into and out of acoustic range of each other. Thus, one could expect a much higher rate of signature whistling. However, it is difficult to make predictions about signature whistle occurrence in the wild since both announcing and concealing one's presence could be of advantage according to the particular context (see Chapter 2). Smolker et al. (1993) showed that

stereotyped whistling was common during separations and reunions of wild mother-calf pairs and that whistling usually stopped after infants returned to their mothers. This also supports the individual recognition/group cohesion hypothesis. Among mothers and their infants the advantage of giving information on identity and position is clear. Among adults it is more difficult to make predictions. There is a similar lack of data on the occurrence of signature whistle copying. The high rate of whistle copying in Tyack's (1986b) study could have been stimulated by the method he used for caller identification. In the present study whistle copying was very rare. However, if Tyack's hypothesis that copying can be used to address specific individuals is right, we would expect it to occur more in the wild where many animals are within hearing range and the ability to address just one particular individual would be advantageous to cooperating animals. This will be investigated in Chapter 5. To assess other possible functions of signature whistles one of the next steps must be to look at how these learned cohesion signals are used in the wild.

Chapter 4

Pitfalls in the categorisation of animal behaviour: a comparison of dolphin whistle classification methods

Introduction

A crucial step in any study of animal behaviour is division of the observed behaviour into separate categories. If those chosen have any relevance to the animal itself, a selective usage of these patterns according to some external variable should be observable. Examples for such a variable are a particular context or individual. Thus, if a category is only used in one particular context or by only one individual, it confirms the biological significance of this category. This is one of the most basic principles in animal behaviour research.

All classification methods include decisions by the investigator as to what parameters should be considered and how they should be weighted. The most common approach is the classification by human observers using their pattern recognition abilities. There are two main problems with this method. One is the issue of observer bias. If a researcher wants to confirm a chosen category by an external variable as described above it is important to ensure that the initial categorization was carried out without any knowledge of when or by whom a behaviour pattern was produced. Martin & Bateson (1986) and Milinski (1997) have provided excellent reviews of this problem and how to avoid it. The other problem is the reproducibility of a categorisation method. Two human observers might weigh parameters differently in their pattern recognition and so come up with different categories. This problem can be avoided by using several observers to obtain a measure of observer agreement. If agreement is high one can assume that the method is reproducible by others.

One disadvantage of classifications by human observers is that threshold values for categorising the behaviour patterns are not clearly defined. Furthermore, certain small parameter differences that might be relevant to the animal could be missed by the human. With recent developments in computer technology an increasing number of studies have started to use computers to obtain threshold values and look at possible subclasses of behaviour that are characterised by small parameter differences. This approach is very powerful if behaviour patterns can be separated by looking at one or more crucial parameters that are sufficient to describe the different behaviour types.

But is visual observation always a less adequate method? One way of using computers for pattern recognition is by the development of a similarity measure. Examples of such measures are cross-correlation coefficients or differences in average values like the mean sound frequency of a call. Another approach is the application of computer-based neural network systems. However, these methods often do not perform as well in pattern recognition as humans do (see Khanna et al. 1997; Lippmann 1997). Furthermore, the threshold values used to define a particular category are often difficult to retrieve from the program (e.g. Lehky & Sejnowski 1988). Thus, a researcher has to think carefully about what method to use in a study. This is particularly important with complex patterns. To date, only a few studies have compared different classification methods (Nowicki & Nelson 1990; Terhune et al. 1993; Lippmann 1997). However, such studies are important to assess how useful a particular method is and to aid in choosing the most appropriate one.

In this chapter I investigate the advantages and disadvantages of three different methods for the classification of bottlenose dolphin (*Tursiops truncatus*) whistles. To assess how useful different methods are a baseline is needed that defines which behaviour types are the "right" ones, i.e. which types correspond closest to natural categories formed by the animal. One way of obtaining such an external validation of behaviour types defined by a researcher is by looking at their usage by the animal. If a behaviour type turns out to be used very selectively in only one context, it must closely resemble a natural behaviour category of the animal. In bottlenose dolphins such a selective usage has been found for signature whistles.

In Chapter 3 I have shown that each signature whistle was used almost exclusively by only one individual and only if it was isolated from other members of its group. Like most other studies on dolphin communication the authors used visual classification to define whistle types before looking at when they were used by the animals in their study. Thus, they were able to show that visual inspection of frequency spectrograms is a valid method for recognizing at least one natural category in a dolphin's whistle repertoire. In this study I take a subset of the whistles recorded for Chapter 3 and compare the results of three computer-based methods with those obtained through visual classification by human observers. The computer based methods are a) a method developed by McCowan (1995) that normalises whistles in duration and uses principal component analysis and k-means cluster analysis, b) a comparison of cross correlation coefficients using hierarchical cluster analysis, and c) a comparison of average differences in absolute frequency that also uses hierarchical cluster analysis. The aim was to compare how well these computer methods could identify the signature whistle types already known to be used almost exclusively when an individual was isolated, and thus validated as natural categories of behaviour.

Methods

The Whistle Sample

The sample of dolphin whistles used for this study was a subset of 104 randomly chosen whistles from a total of 1323 whistles recorded from four bottlenose dolphins in January 1996 at the Zoo Duisburg, Germany. The entire sample used in this study is shown in Fig. 4.1 and 4.2. The dolphin group consisted of an adult male, an adult female, a subadult male and a juvenile female. Recordings were made while either all animals swam together in the same pool or while one animal had moved into a separate pool. Recording conditions have been described in Chapter 3. To classify whistles into types spectrograms were calculated (FFT size: 1024; time resolution: 20.5 ms; frequency resolution: 48.8 Hz; weighting function: Hanning window) and a line spectrogram of the fundamental frequency was extracted with the SIGNAL (Version 3.0) sound analysis software as

described in Janik et al. (1994). This method provides a line that represents the contour of the fundamental frequency of the whistle. Bottlenose dolphins often produce multi-loop whistles in which separate whistles follow each other closely and occur together most of the time. For the analysis here each separate whistle from such multi-loop whistles was considered on its own.

Human Observer Classification

All 104 line spectrograms were printed on separate sheets and five observers were asked to classify calls independently by their shape. All observers had extensive experience in classifying bird sounds but no experience with dolphin sounds. No information on recording context or caller identity was given to them. However, observers were asked to pay particular attention to the possible occurrence of very stereotyped signals. Each observer was allowed to categorise the contours into as many classes as he or she thought appropriate. These types were then scanned for common types that could be found in the classification of all observers.

The McCowan Method

McCowan (1995) presented her own method to classify whistles. To replicate her method 20 frequency measurements had to be taken from each whistle contour. These measurements were equally distributed over the contour by dividing the duration of each whistle by 19 and then taking frequency measurements at every $1/19^{\text{th}}$ point of the total duration including the start and the end of the whistle. The resulting 20 frequency measurements were then taken as 20 variables for further calculations. The effect of this method is an elimination of any differences in the duration of whistles. All whistles are represented by the same number of frequency measurements and are, therefore, only compared by the shape of their contour.

In the next step these 20 frequency measurements were used to compute a Pearson product-moment correlation matrix. A principal component analysis on the

correlation matrix was carried out to reduce the number of collinear variables. Only factors with an eigenvalue of greater than 1.0 were used for subsequent analysis. In the final step factor scores from each data set of whistles were used in K-means cluster analyses using BMDP (Version 1988) statistical software, the package used by McCowan (1995). Solutions for six to 50 clusters were calculated. McCowan (1995) used the cluster solution that produced the maximum number of non-overlapping clusters as indicated by BMDP. However, BMDP only indicates overlap in a two-dimensional representation of a k-dimensional space (Dixon et al. 1990). Thus, clusters can overlap without BMDP indicating an overlap, or they can overlap in the two dimensions but be clearly separate in a dimension not displayed. The overlap indication was therefore not considered a satisfactory criterion to decide which cluster solution was appropriate. Instead I inspected all cluster solutions for possible agreement in whistle classification with the other methods. All analyses were conducted using BMDP default settings (maximum iterations: 30) (Dixon et al. 1990).

Cross-Correlations and Cluster Analyses

Finally two different similarity measures and two different cluster analysis methods were compared in their usefulness for whistle classification. The first similarity measure was calculated by cross-correlating every contour with all other contours in the sample. All cross-correlation analyses were conducted using SIGNAL software. The XCS command in SIGNAL was used in order to perform cross-correlations that used a time-varying normalization. The shorter of two whistles had to have at least 75% of the duration of the longer whistle. This threshold was set arbitrarily. Otherwise the cross-correlation coefficient was set to nil, the value for two very different contours.

The second similarity technique also involved cross-correlating contours. The two contours were aligned so that the cross-correlation yielded its maximum value like described above, but instead of using the correlation coefficient the absolute difference in frequency between the two contours was calculated every 5 ms. All differences were added up and then divided by the number of differences

calculated. If one whistle was longer than the other the values were added only over the duration of the shorter whistle. Again the shorter whistle had to have at least 75% of the duration of the longer one. If the difference in duration was larger the similarity value was set to 20000, the value for two very different contours in this comparison.

These two methods resulted in two matrices, one with a measure of similarity (the cross correlation coefficients) and the other one with a measure of dissimilarity (the average frequency difference between all pairs of whistles). Each matrix was used for hierarchical cluster analyses employing the SPSS (Version 6.1) statistical software package using the between groups average linkage method and the complete linkage method. The average linkage method is one of the most commonly used clustering methods in biological sciences. It requires that a whistle has to be within a certain level of similarity to the average of the cluster to be included in that cluster. It was compared to the complete linkage method, which requires that a whistle has to be within a certain level of similarity to all members of that cluster. This latter method should favour the formation of very stereotyped whistle types (Aldenderfer & Blashfield 1984). All cluster trees were drawn using rescaled distance measures for the branch lengths. The results were compared between all methods used.

Results

Signature Whistle Classification

The visual inspection method revealed that observers agreed on the classification of signature whistles. Five very stereotyped whistle types could be found in the classification of all observers (types A, B, C, D₁, and D₂) (Fig. 4.1, Tab 4.1). Each of these types was used almost exclusively by only one individual dolphin if it swam isolated from its group members in a previous study in which visual classification by one observer was used (Chapter 3). Thus, they represent the signature whistles in the sample. None of the whistles identified as signature whistles in this study was given by any other individual or outside the separation

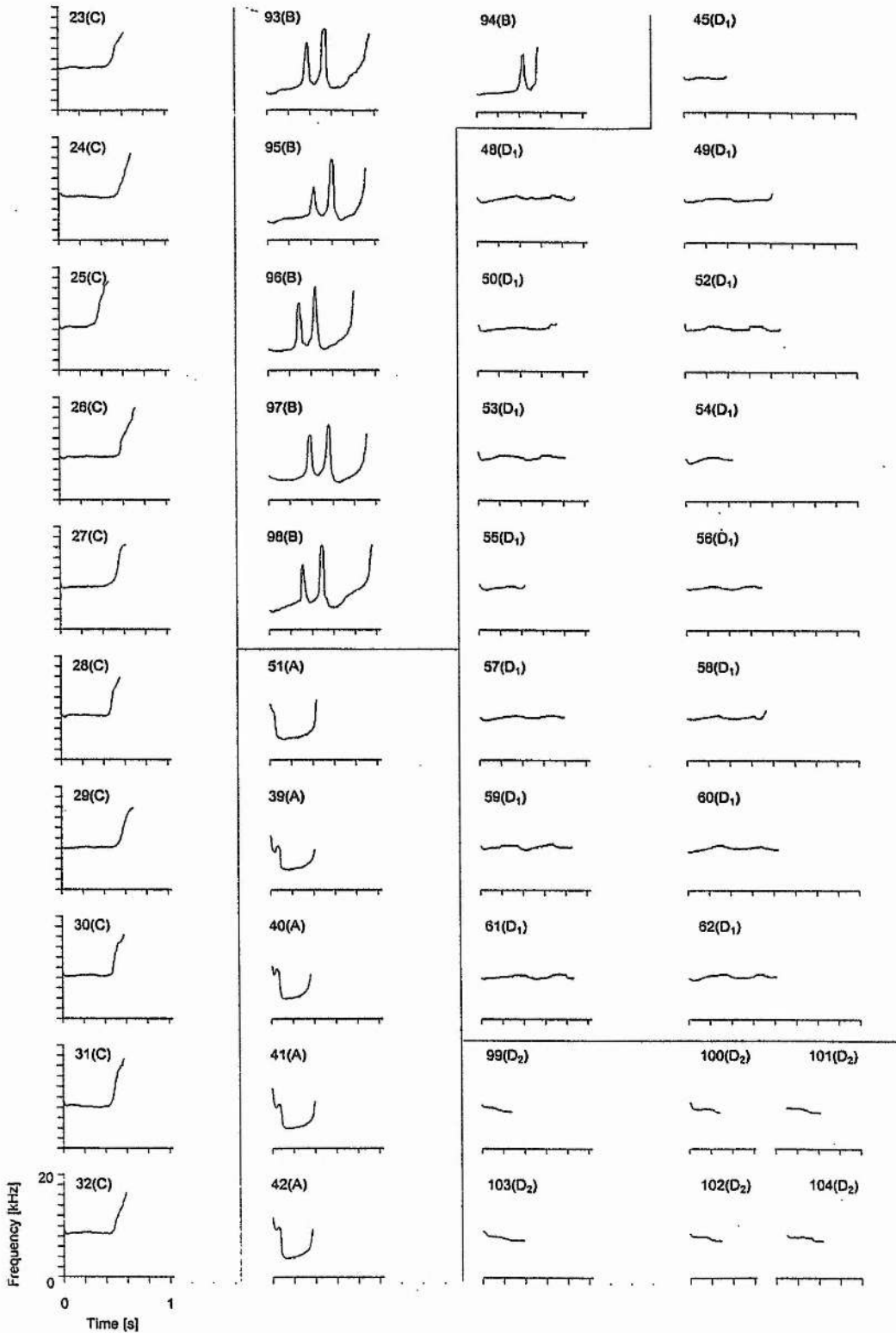


Figure 4.1: Line spectrograms of all signature whistles that were considered in this study. The number on each spectrogram is its identification number followed by a letter indicating which whistle type it belonged to in Chapter 3.

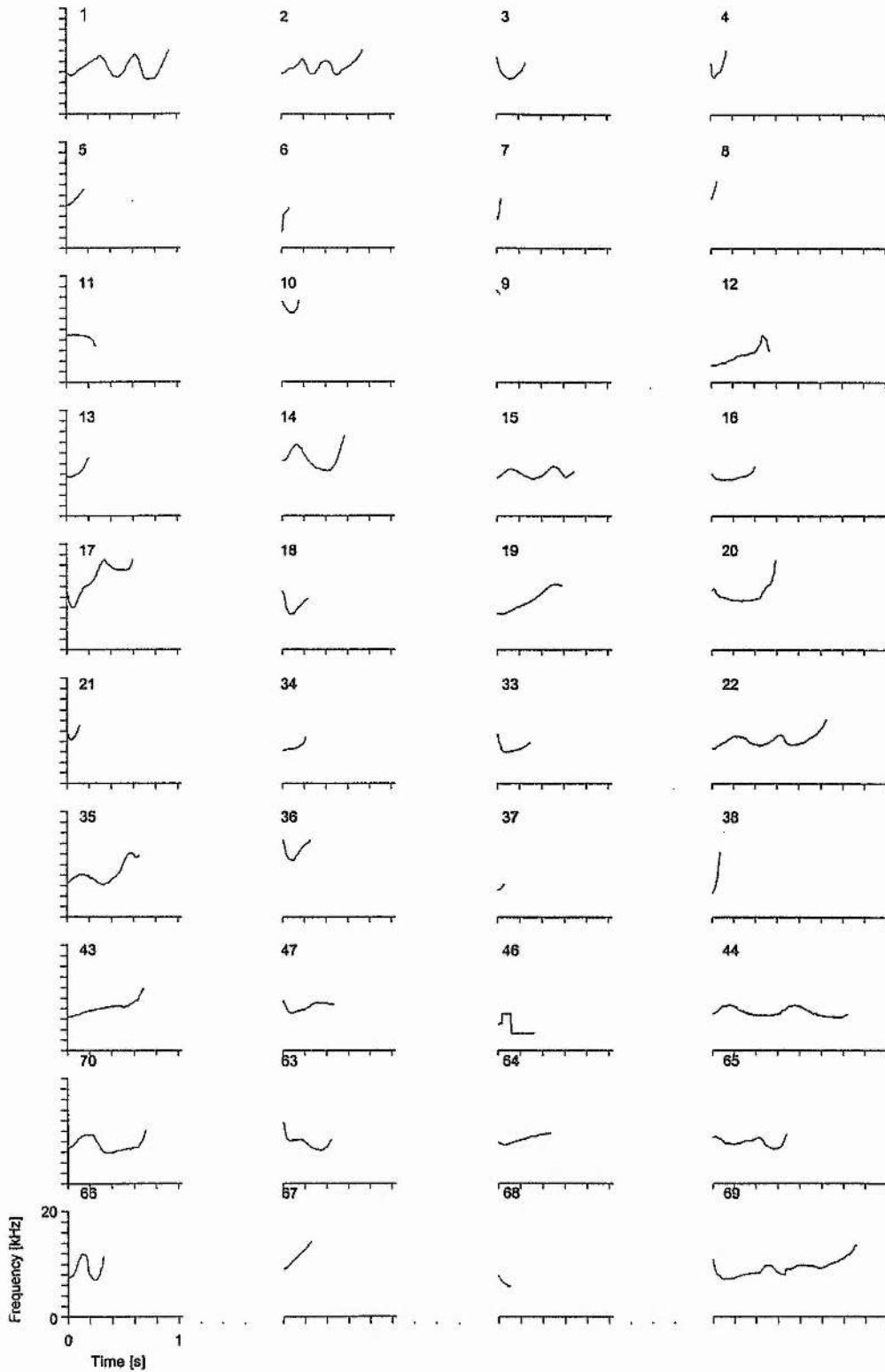


Figure 4.2: Line spectrograms of all non-signature whistles that were considered in this study. The number on each spectrogram is an identification number (continued on next page).

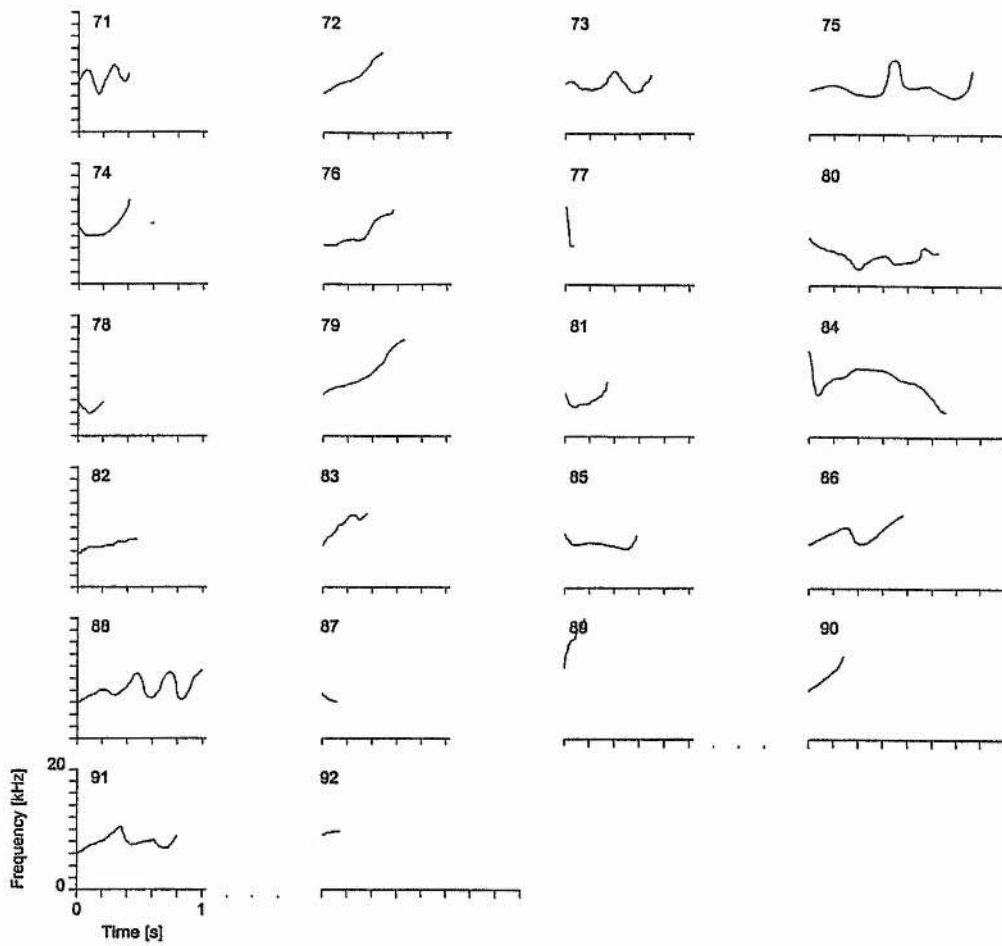


Figure 4.2: (cotinued)

Table 4.1: Human whistle classification. Bold numbers represent the ID numbers of each whistle from Figs. 4.1 and 4.2. Numbers in brackets indicate how many observers put the corresponding whistle into a type. No brackets indicate that all five observers agreed on the classification of a whistle. Whistles that were produced by only one dolphin are boxed in.

Whistle type	Type A	Type B	Type C	Type D1	Type D2
Whistle ID numbers	39	93	23	45 (4)	68 (2)
	40	94	24	48	87 (2)
	41	95	25	49 (4)	99
	42	96	26	50 (4)	100 (4)
	51 (3)	97	27	52	101
	81 (1)	98	28	53	102
			29	54 (4)	103
			30	55 (4)	104
			31	56	
			32	57	
			20 (1)	58 (4)	
				59	
				60	
				61	
				62	
				64 (1)	
				82 (1)	

context. Whistle types D₁ and D₂ were two parts of a multi-loop signature whistle used by one of the animals. They occurred together most of the time in the study presented in Chapter 3. In Fig. 4.1 all signature whistles from the random sample used in this study are shown. If only signature whistle types were considered, and all others were considered as a single residual class, observer agreement was extremely high (Kappa statistic (Siegel & Castellan Jr. 1988): $K = 0.92$, $z = 22.37$, $P < 0.0001$). The observer classification turned out to be identical with the one used in Chapter 3. However, Table 4.1 shows that up to two observers in this study sometimes also included one or two other whistles in a signature whistle type. Type D₁ was split up into two types by one observer, but no additional whistles included with the resulting types. To be conservative only the type that had more whistles in it was considered in Tab. 4.1. Thus, there are a few whistles that only four observers agreed on in type D₁.

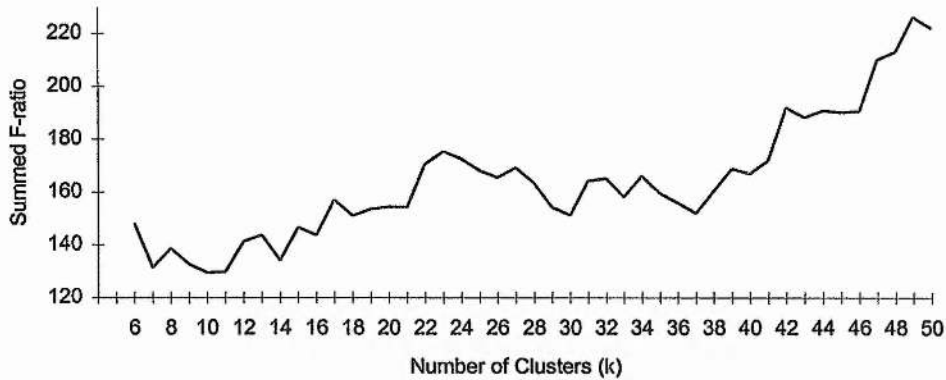


Fig. 4.3: Distribution of summed F-ratios from the McCowan method. A local peak can be found at $k = 23$. The cluster solution of that point is shown in Tab. 4.2.

The principal component analysis on the 20 frequency measures taken from each whistle to reproduce McCowan's method resulted in three principal components with eigenvalues greater than 1.0. K-means cluster analyses on the factor loadings of these components revealed that this method could not identify signature whistles as reliably as the human observers. Only one signature whistle type (type A) was reliably recognised in solutions where $9 < k < 43$, where k is the number of clusters in the k -means cluster analysis. All whistles of type C were grouped together in all solutions where $6 < k < 26$. However, in all cases between two and 13 other whistles were included in the same cluster. A similar situation was found for types D_1 (found in all solutions where $12 < k < 39$, but number of other whistles in the same cluster varied from six to 11) and D_2 (found in solutions where $12 < k < 42$, number of other whistles in the cluster from three to eight). Type B whistles were never all together in one cluster. The additional whistles found in clusters containing signature whistles were never classified as belonging to that cluster by human observers. They also were not produced by the respective individual in isolation in the study presented in Chapter 3. One method to select the best solution in k -means cluster analysis is a comparison of the sums of F-ratios (between cluster sum-of squares / within cluster sum-of-squares). The

Table 4.2: McCowan whistle classification ($k = 23$). The numbers are whistle identification numbers (see Figs. 4.1 and 4.2). Signature whistles are printed in bold. Signature whistles belonging to one type have a box around them and, if split, are connected by a curved line.

Whistle type	A	B	C	D1	D2	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t	u	v	
Whistle ID	39	95	23	1	11	2	7	63	8	19	33	34	5	3	10	66	14	9	17	46	77	84	89	
numbers	40	96	24	15	44	4	12	68	67	72	78	37	43	18	36	91	20							
	41	97	25	47	65	13	38	70	83	76	80	45	64	71										
	42	98	26	48	99	16	93	85	90	79	81	82	88											
	51	6	27	49	100	21	94	87																
			28	50	101	22																		
			29	52	102	69																		
			30	53	103	86																		
			31	54	104																			
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				61																				
				62																				
				73																				
				75																				
				92																				

solution that maximises the sum of the F-ratios is then selected (Nowicki & Nelson 1990). Fig. 4.3 shows the distribution of summed F-ratios for the McCowan method. As the cluster number increases towards 50 clusters the summed F-ratio increases. However, at $k = 23$ a local maximum is reached. Table 4.2 shows the classification at that point. Only two of the signature whistles (types A and C) that were found by the human observers were identified equally well by the McCowan method.

Fig. 4.4 shows the cluster tree that resulted from the analysis of the cross correlation coefficients with average linkage cluster analysis. It becomes clear that this method can only pick out one signature whistle type reliably if cut at the right point (type B). Other signature whistle types were either grouped together with many other whistles or split up into different clusters. Trees created with the two different cluster analysis methods were almost identical. The analysis of the

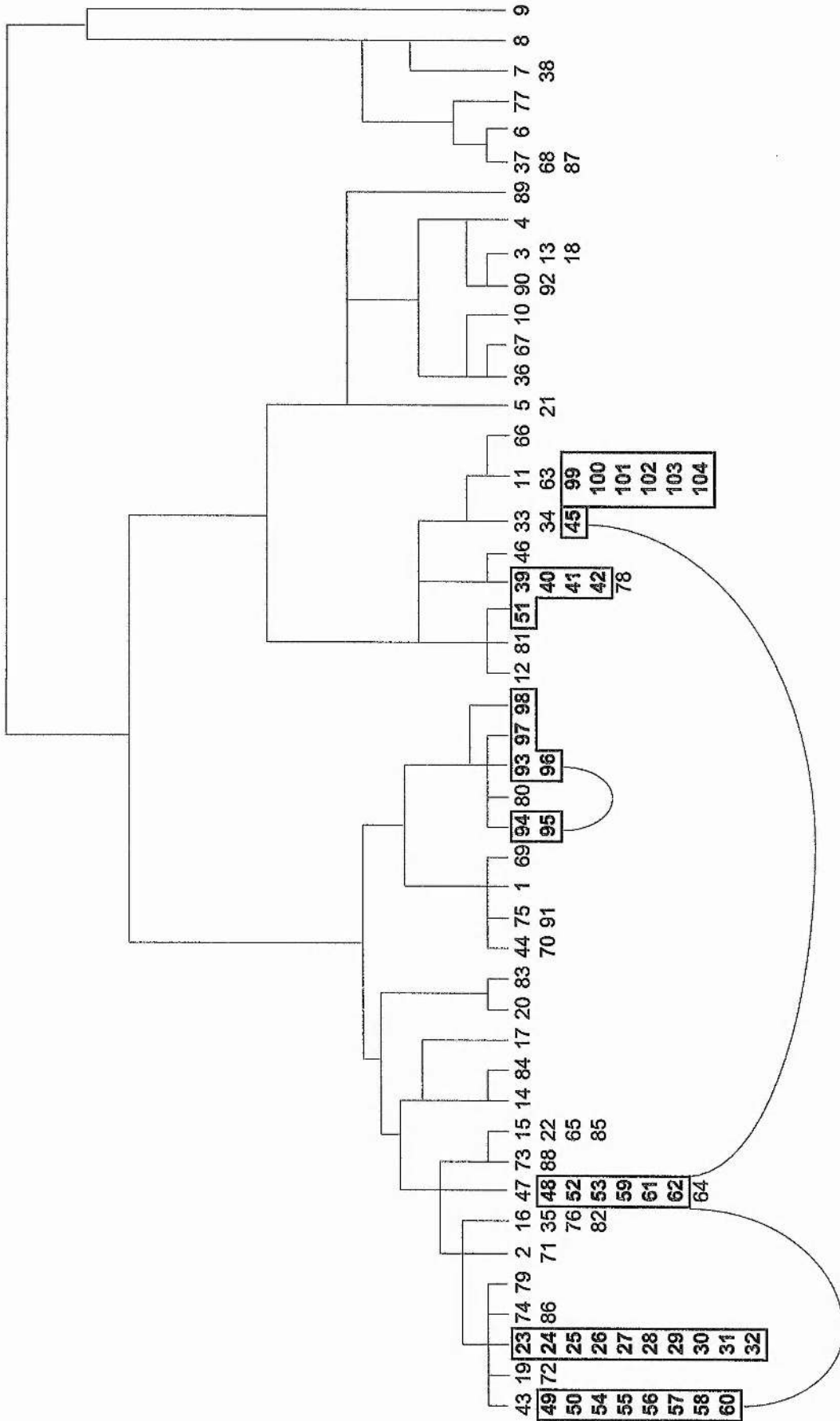


Figure 4.5: Cluster tree of the matrix of average frequency differences. Cluster method: between group average linkage. Numbers are ID numbers of whistles (see Fig. 4.1 and 4.2). Signature whistles are printed in bold. Those belonging to one type have a box around them and, if split, are connected by a curved line.

average frequency differences between whistle contours was more successful in identifying signature whistles (Fig. 4.5). Here four out of five signature whistles could be identified. However, it depended again at what distance level in the tree would be used to define whistle types. The appropriate level was different for different signature whistle types. This frequency difference method is like the McCowan method not suitable to identify signature whistles in a sample. Again, using the two different cluster analysis methods resulted in almost identical trees.

Classification of Non-Signature Whistles

Additional whistle types similar to those described in Tyack (1986b) and Janik et al. (1994) could be found in the classifications of the five observers, but observer agreement was low. Certain whistles were always grouped together in each observer's classification. The following triplets of whistles were always found together in each observer's classification: 8-38-89, 5-72-79, 18-33-36, 22-44-88 (Fig. 4.2). However, the number of different whistles they were grouped with was large and varied between observers. In each case the whistles observers agreed on formed less than 60% of that type in each observer's category.

Of the non-signature whistles that showed the highest observer agreement in the human observer classification only two (number 72 and 79) were grouped together by the McCowan method. The method using cross correlation coefficients, however, only disagreed on one of the triplets defined by the human observers (8-38-89) and did not group whistle number 5 with 72 and 79. Finally, the frequency difference method grouped some pairs of these whistles together, but found none of the triplets.

A comparison of the classification of non-signature whistles between the computer methods revealed that they also showed very little agreement between them. But while the McCowan method resulted in very different whistle clusters, some of the differences between the cross correlation coefficients and the frequency difference tree seemed to result from the finer resolution of the latter tree.

Discussion

The results showed clearly that methods only agreed to a very limited extent. Signature whistles were identified best by human observers. This might not come as such a surprise since these whistle types had been defined by a human observer in the original study presented in Chapter 3. However, only after the whistle types had been defined in Chapter 3 was it found that these whistle types were used almost exclusively by one animal and only if it was isolated from its group. Even though it is unlikely that the perception of a whistle by a human observer maps exactly onto that of a dolphin such an exclusive use of a behaviour type is rare. It shows that the human classification has recognised a class of behaviour that is significant for the animal. Such an external validation justifies the usage of a particular method if data on how the animal perceives and classifies whistles are not available.

It is still possible that other methods could have discovered significant classes that were missed by the humans. It could be that dolphins use very different criteria for the classification of signature and non-signature whistles. With the exception of the signature whistles identified none of the classes defined by the computer methods that included at least three whistles, were used exclusively by one animal in isolation. But classes could be important in other contexts that were not considered in this study. However, the McCowan method on the one hand and the hierarchical cluster analysis techniques on the other did not agree on the classification of non-signature whistles either. Furthermore, the signature whistles they split up into several clusters were different ones. This disagreement between the computer methods showed that they concentrated on very different features of whistles. Studies on bottlenose dolphins in which McCowan's method has been used did not find such clear differences in the usage of whistle categories (McCowan & Reiss 1995a, b, 1997). It is difficult to assess what role the whistle types described in those studies play in the animals' repertoires because there is no external validation for them. As we have seen above such an external validation has so far only been achieved for signature whistles (Chapter 3), but these whistle types could not be identified reliably by the McCowan method in this study.

It becomes clear that what is needed are good perceptual studies on dolphin whistles. The strength of classification by human observers certainly lies in their pattern recognition ability. Perception experiments should start by concentrating on gestalt perception, but also try to assess the stability of whistle recognition if parameters like duration start to vary. The McCowan method assumes that duration is irrelevant to the classification of whistles. To date, there is no evidence that this is the case. It has been shown that bottlenose dolphins vary the duration of given whistle types according to the context (Janik et al. 1994). A certain stability towards parameter changes can be assumed, but it is likely that there is a point at which whistle type identification starts to break down. Perception experiments should tell us, for example, whether a very short whistle is an interrupted version of a longer type or simply a complete short version of yet another whistle.

Similar problems exist in the frequency domain. The fact that the McCowan method and that based on average differences in frequency, both of which concentrated on absolute frequency values, had problems identifying signature whistles reliably showed that these might be less important than the overall gestalt of the whistle. The failure of the cross-correlation coefficients to find signature whistles can probably be ascribed to the weakness of this method to detect small differences in the gestalt of whistle contours (Khanna et al. 1997). Bottlenose dolphins also vary frequency parameters in relation to context (Janik et al. 1994). But again it is likely that there are limits within which parameters have to be found for a whistle to be ascribed to a certain type. It has been suggested by Richards et al. (1984), for example, that bottlenose dolphins are not sensitive to the frequency band a signal lies in but only to its general shape. This is based on their finding that the experimental animal imitated an artificial low frequency model sound but transferred it up one octave. This is an intriguing result and asks for further investigation. However, it is premature to assume that absolute frequency is unimportant in the classification of dolphin whistles. Ralston & Herman (1995) showed that dolphins are able to learn to generalise between frequency contours that lay in different frequency bands. However, their study animal concentrated on absolute parameter differences in its classification in the

initial stages of the training. Again, further studies are needed to investigate the role that absolute parameter values play in the classification of sounds by the animal.

The results presented here demonstrate that if data from perception experiments are not available it is of great importance to find another way of externally validating the behaviour types defined. This is true for human observers as well as for computer methods. A very selective usage by the animal of a behaviour type that was defined by a researcher represents such a validation, but only if the type was defined before the usage was investigated. In dolphins such a validation has been found for signature whistles. But observers and computer methods disagreed strongly on the classification of non-signature whistles. Previous studies have used general design features of whistles for the classification of non-signature whistles, such as generally rising frequency, sinusoidal modulation or falling frequency contour (Tyack 1986b; Janik et al. 1994). Such types could also be found in the classification by the observers used in this study, but the boundaries of these types were diffuse and observers disagreed on borderline cases. It is obvious that to date we know very little about any whistle types other than the signature whistle and that more studies are badly needed.

It is important to note that the issues discussed here using the example of whistle classification in dolphins, are relevant to all observations of animal behaviour. Computer methods are widely used to classify behaviour patterns. They can be used in two ways. One is a description of parameter differences in different contexts. This approach is very powerful and gives interesting results that concern single parameters (e.g. May et al. 1988; Elowson & Snowdon 1994; Janik et al. 1994; Slabbekoorn & ten Cate 1997). The other one is to arrive at some sort of a similarity measure as with the computer methods used here. Since a combination of parameters is used to define categories in these methods the results are more difficult to interpret. In this study the chosen computer methods could not identify signature whistles reliably. As long as there is no other external validation for the categories formed by these methods we know little about their biological relevance. Such methods can of course be successful (e.g. Nowicki & Nelson 1990) but a careful examination of the classification obtained is needed. In many

cases it will be useful to use categories defined by visual inspection that are used selectively in certain contexts by the animals and then investigate how parameters within such types change. Such studies can lead to the discovery of a distinction between types that were previously pooled together. The study of categorical perception is one example in which small parameter differences can lead to a different classification by the animal. To be able to find biologically relevant methods for comparisons between behaviour types, studies on differential usage of behaviour types, and perceptual studies on call classification by the animal should be carried out. Only then will we be able to assess how the animals themselves classify behaviour patterns.

Chapter 5

Whistle matching in wild bottlenose dolphins

Introduction

The bottlenose dolphin is one of the few mammalian species in which vocal learning has been demonstrated (Janik & Slater 1997). Experimental studies looking at vocal learning in adult individuals have shown that they can imitate new whistle sounds accurately even at the first attempt as judged by human observers (Richards et al. 1984; Sigurdson 1993). Bottlenose dolphins are probably therefore capable of incorporating new calls into their repertoire throughout their lives. This ability makes it difficult to determine their whistle repertoire and raises the question of the code that their communication is based on. But even though early attempts to describe a species' repertoire have failed because of this difficulty, there is a remarkably stable component in each individual whistle repertoire. Each bottlenose dolphin develops its own signature whistle (Tyack & Sayigh 1997) which is highly stereotyped and remains stable for at least 12 years (Sayigh et al. 1990). These signature whistles are thought to help maintain individual recognition and group cohesion in the marine environment (Caldwell & Caldwell 1968; Caldwell et al. 1990). However, in a species in which individuals copy each other's calls individual recognition can be difficult. Tyack (1986b) showed that two captive individuals frequently produced each other's signature whistles while swimming together in the same pool. Since there are no visible correlates to vocalising (e.g. beak movements) he used telemetry devices to identify the caller. Tyack hypothesised that this production of the signature whistle of another individual is used to address a specific group member and so to facilitate group cohesion in large aggregations of dolphins. However, such events seem to be rare among undisturbed, captive dolphins (see Chapter 2, Burdin et al. 1975) and only seem to occur in matching interactions that involve signature

whistles (see Chapter 3). We know little about whether and how this is used in the wild. In this study I employed a passive acoustic localisation method to investigate whistle interactions between wild individuals and so determine whether animals match each other's whistles in the wild. I also give information on how often these interactions occur and at what separation distances.

Methods

This study was carried out in the Kessock Channel of the Moray Firth in Scotland, UK (Fig. 5.1). Water depth increases from 6 to 38 m from East to West in the middle of the channel. Maximum tidal differences in water depth are approximately 5 meters. The sea floor consists of mud and pebbles. The resident population of bottlenose dolphins in the Moray Firth contains around 130 individuals of which several spend large amounts of time in narrow passages like the Kessock Channel during the summer months (Wilson 1995). To localise calling dolphins I used a passive acoustic localisation technique. Three HTI – SSQ94 hydrophones were installed in a triangle to form a two-dimensional array. Two hydrophones were placed on the North shore of the channel and one on the Southern shore. Inter-hydrophone distances were 208, 513, and 560 meters. Each hydrophone was about 50 m from the shore at a depth of 1 to 5 m depending on the state of the tide. They were fitted with radio transmitters (Micron TX100), so that all signals could be recorded together at an observation point on the North shore 30 m above water level. Each transmitter was connected to a simple whip aerial. The receiving and recording station consisted of a Yaegi directional aerial, 3 Yaesu FRG-9600 receivers and a Fostex 380S multitrack tape recorder. The frequency response of the whole system was 50 Hz to 18 kHz \pm 3 dB re 20 μ Pa. From the observation point the total number of animals present was estimated every 5 minutes. I only analysed periods in which animals were dispersed, so that at least two animals were at least 50 m apart during all periods.

All data were analysed with the SIGNAL software localisation module (Engineering Design, Belmont, USA). The localisation of a sound source by this system is based on the time difference with which a signal arrives at each pair of

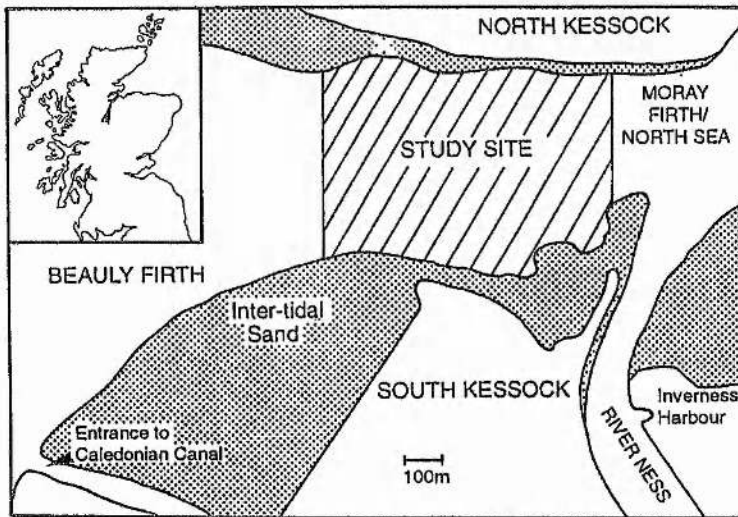


Fig. 5.1: A map of the study area in the Moray Firth, Scotland. North is at the top of the map.

hydrophones. These delays are preserved on the simultaneous multitrack recording of all hydrophones. If the speed of sound in the medium and the transducer positions are known, the difference in time of arrival of the same sound at a given pair of hydrophones holds information on the possible sound source locations (Spiesberger & Fristrup 1990). Each time delay corresponds to a specific hyperbola of possible source locations. The hyperbolas of all three pairs of hydrophones (1-2, 1-3, 2-3) have a common point of intersection that represents the actual position of the calling individual (Fig. 5.2c). The speed of sound was determined as 1567 m/s by measurement with an artificial source over known distances. The hydrophone locations were determined by using two Magellan GPS ProMark X units with Magellan Mstar software (Version 1.05) in a differential global positioning system setup. To determine the time delay between two hydrophones I used a cross-correlation of frequency spectrograms (Fig. 5.2b). Sounds were digitised at a sampling rate of 50000 Hz. Spectrograms were calculated with a 75% overlap between different FFT's (Fast Fourier Transforms, dt: 10 ms, df: 98 Hz, FFT size: 512) resulting in an effective time resolution of 2.5 ms. Even though the cross-correlation of frequency spectra instead of waveforms results in a slightly larger error due to the averaging over small time slices of the original signal, frequency spectrograms allow the detection of a signal in high

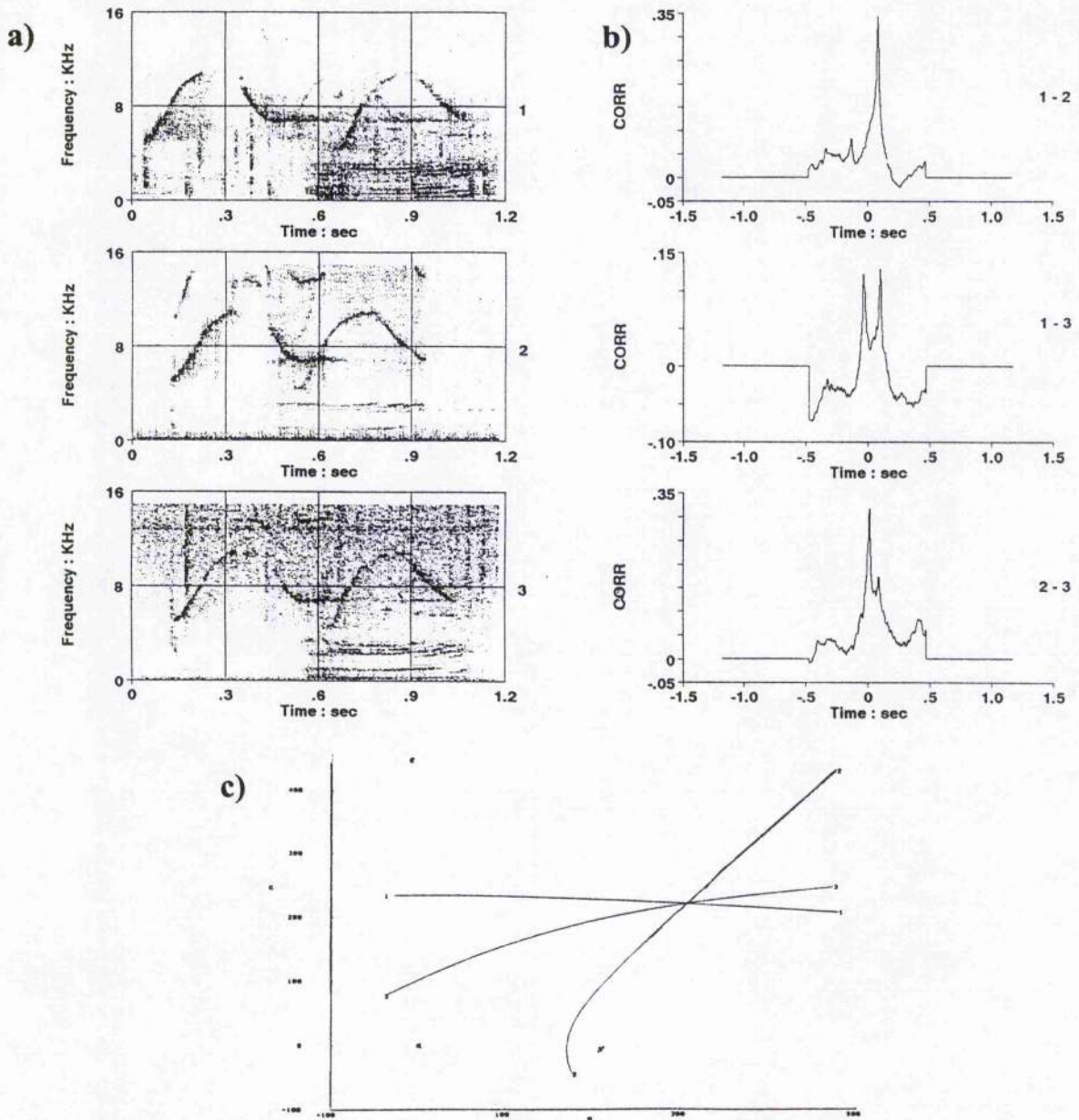


Fig. 5.2: Illustration of steps in the localisation procedure. (a) Three spectrograms of the same signals received at the three different hydrophones. Note that the same signal starts at slightly different times in each spectrogram. (b) Cross-correlation functions of the spectrograms shown in a). Numbers on the left indicate which spectrograms have been cross-correlated. The peak of each correlation function corresponds to the time difference in the time of arrival of a sound at the compared hydrophones. In this figure several peaks can be found because there are three signals in the spectrograms in a). For the actual localisation spectrograms were cut or digitally filtered before the cross-correlation to minimise background noise and to ensure that only one signal was in the spectrogram. In all cases the results of the cross-correlation procedure were checked manually with on-screen cursors to confirm that the correlation peaks corresponded to the signal of interest. (c) An overhead view of the study area with the resulting hyperbolas from the correlation peaks in b). Asterisks indicate the position of the hydrophones. The point of intersection of the hyperbolas indicates the position of the sound source.

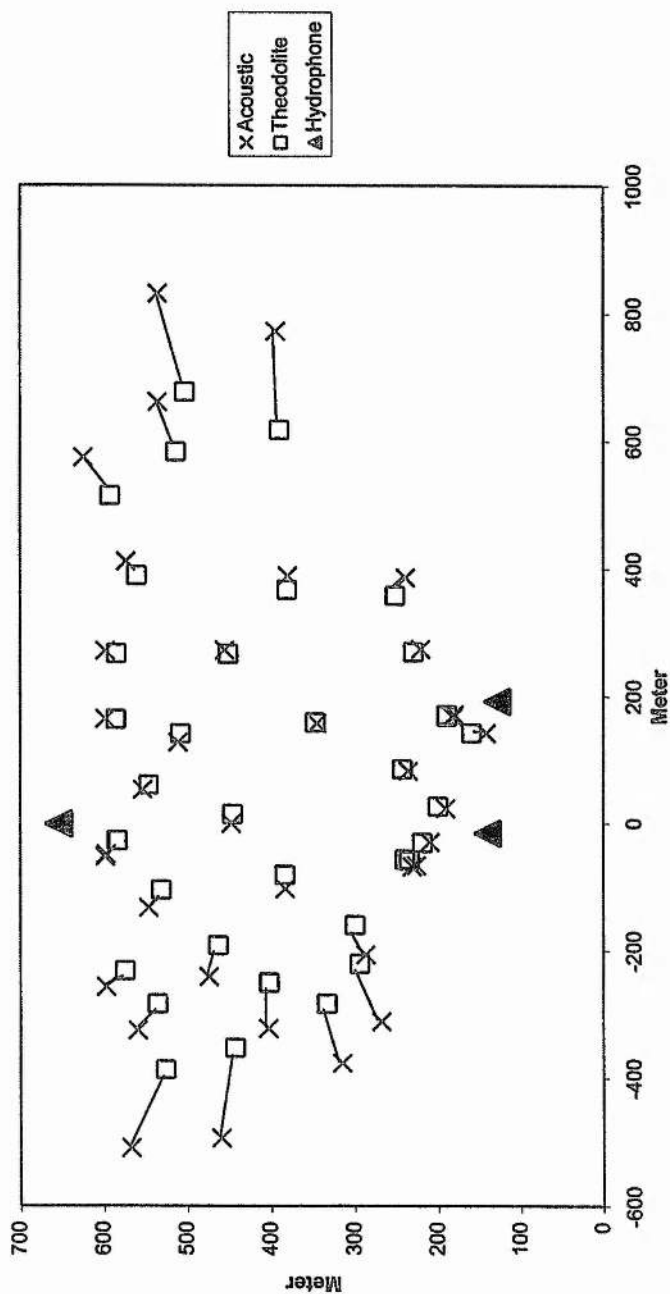


Figure 5.3: An overhead view of the study area with a plot of the localisation errors. The triangles indicate the position of the hydrophones. The squares indicate the position of the sound source as determined by the theodolite. The crosses show the results of the acoustic localisation. If the cross lies outside the corresponding square they are connected by a straight line. Note that the direction of each sound source from the centre of the hydrophone array is very accurate at all distances, but that the distance is overestimated by the acoustic localisation procedure if the sound source is far from the array. The error of the sound localisation was smaller than 15 meters inside the array and in its immediate vicinity. In the area outside the array the error grew larger with distance, systematically overestimating the distance of the caller from the array centre.

background noise and enable the researcher to check the validity of the calculated time delay visually. If the hyperbolas did not intersect at one point but formed a triangle the corner points of the triangle were saved. For the analysis the point of the triangle that was closest to the other caller was assumed as the actual caller position.

A test of the localisation accuracy was conducted with an artificial sound source (two pieces of metal banged together) employed from a small zodiac dinghy. The position of the boat was determined with a Sokkisha digital theodolite and then compared to the acoustic localisation. The test showed that the localisation error inside and in the immediate vicinity of the hydrophone array ranged from 2.4 to 14.9 meters (Fig. 5.3). Most interactions that were analysed occurred in this area. On either side of the array the error increased with distance from the centre of the array. Interactions in those areas were only considered if the first caller position was nearer the hydrophone array than the second one. In such cases the error would have led to an underestimation of the actual distance one animal would have had to swim to produce both sounds. Thus, the same criteria as for the inner array area could be applied to identify interactions in those areas (see below).

Whistle interactions were defined as any two whistles produced by two different dolphins that were separated in time by less than 3 seconds. Two whistles were considered as coming from different animals if one dolphin could not have covered the distance between the two sound source locations within the silent inter-whistle interval. For this the highest swimming speed that had been reliably measured in this area (7.5 m/s) (Lütkebohle 1995) was assumed. To allow for the localisation error 30 meters were subtracted from the calculated distance between the two sound source locations, 15 meters for each location. In addition I report all overlapping whistles that come from the same location as determined by these criteria as possible interactions. However, it has been found that some dolphins can produce two whistles at the same time (Caldwell & Caldwell 1969; Markov & Ostrovskaya 1990) and therefore some of the overlapping whistles might not represent interactions. For this reason data on overlapping whistles are presented separately. Spectrograms of whistles were inspected by eye to determine whether an interaction contained matching whistles. To improve the frequency resolution

for this analysis spectrograms were recalculated with a FFT size of 1024. Spectrograms shown in Figures 5.4 and 5.5 were calculated this way. Whistles were only considered as matching if the contours matched closely and were in the same frequency band and of similar length. These criteria were the same as those usually used for the recognition of highly stereotyped signature whistles of only one individual. Thus, the number of matching interactions presented here is conservative.

Results

A total of 4 hours, 18 minutes, and 43 seconds of recordings from 7 different days in July and August 1994 and 1995 were analysed. Four to 15 animals (average 10) were present during these. A total of 1719 whistles was recorded in that time. Fifty-eight % of all whistles ($n = 991$) were recorded with a sufficient signal to noise ratio on all hydrophones for the localisation procedure to be employed. Among these 188 whistle interactions were found. Of these 43 consisted of overlapping whistles from the same group. In the whole sample 45 cases of whistle matching were found. Of the matching interactions only 8 consisted of overlapping whistles from the same group of animals. Matching interactions in which whistles overlapped also occurred between individuals of different groups ($n = 7$). Fig. 5.4 shows six examples of matching and non-matching whistle interactions. In one case a matching interaction between three different animals from three different locations was found (Fig.5.5). The average distance between the positions of individuals that took part in a matching interaction was 167 (SE: 23.97) meters. Matching whistle interactions were found on every day for which recordings were analysed.

If there are several animals in different groups in an area it can be expected that some whistles follow each other within 3 seconds simply by chance. This would not represent a vocal interaction. To test for this possibility an exact randomisation test was used (Sokal & Rohlf 1995). For the test 999 sets of random data with 991 whistles in 15523 seconds observation time were generated. The total time and number of whistles were taken from the actual data. The

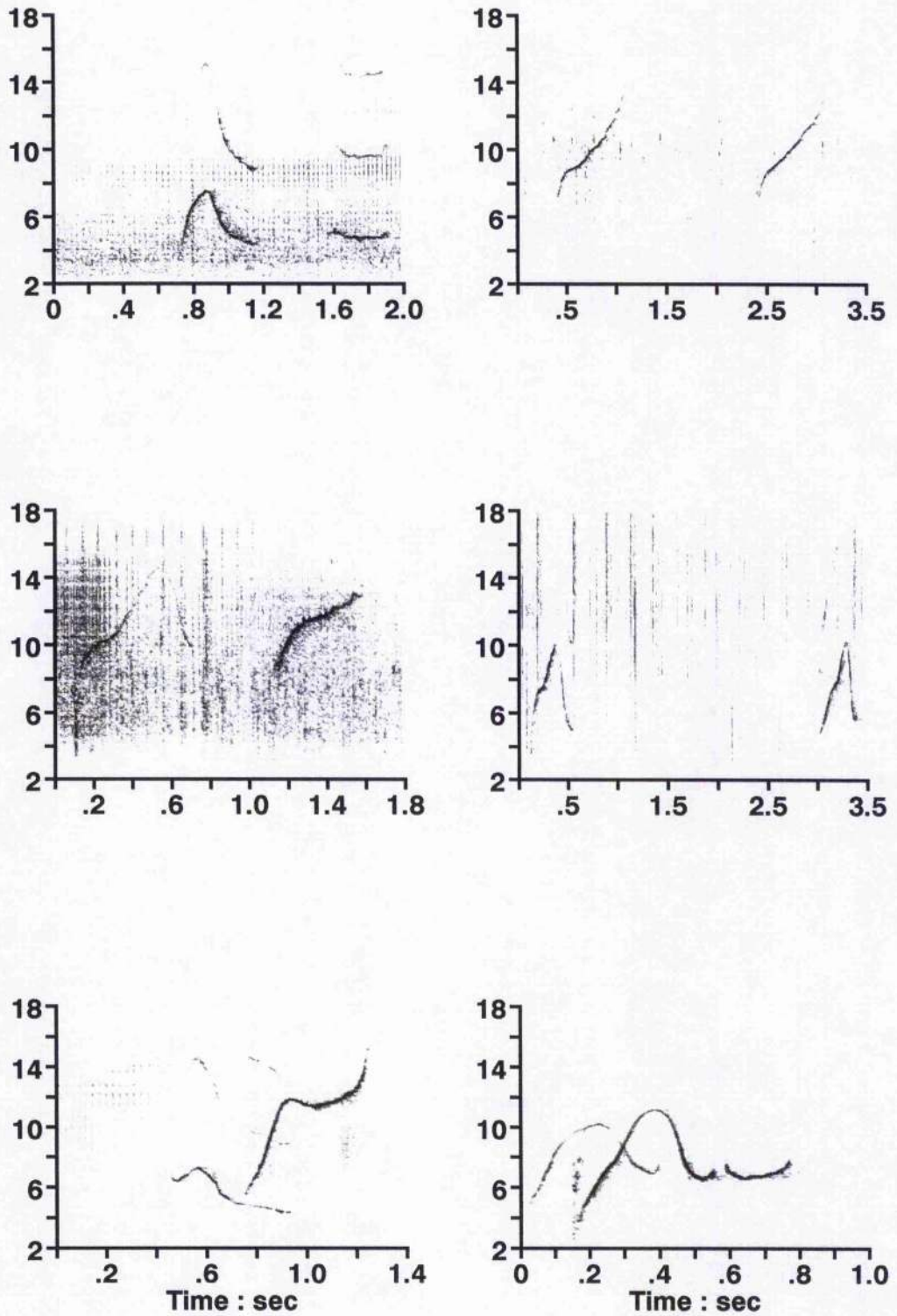


Fig. 5.4: Examples of non-matching (left column) and matching (right column) whistle interactions.

number of whistle interactions occurring in each of these sets was counted. To test the null hypothesis that the number of whistle interactions observed corresponded to what would be expected by chance the number of sets (n) that yielded a proportion of whistle interactions at least as large as that observed in the real data set was counted. The p -value for this test is $n/1000$ if the observed proportion is added as the 1000th data point. The number of whistle interactions expected by chance increases with the number of animals and decreases if animals whistle with different rates. In reality the animals usually swam in two to five groups in the study area, but single animals would split off temporarily. To be as

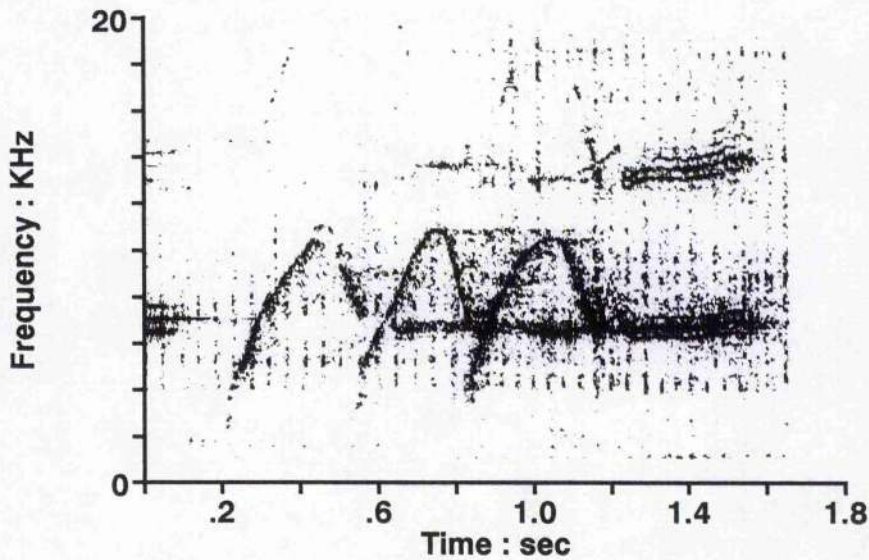


Fig. 5.5: The only case of whistle matching that involved three different animals. The whistles in this spectrogram were counted as two matching interactions. However, while in such cases usually the two outer whistles came from the same location, here all three whistles came from different locations. The caller positions formed a triangle with side lengths of 88, 97, and 183 meters.

conservative as possible in the test the average number of dolphins (10) in the area was used as the number of individuals at different locations and all animals were assumed to whistle at equal rates.

The exact randomisation test using these assumptions showed that the observed number of whistle interactions was not significantly different from what would be expected by chance (observed proportion: 0.012, chance proportion: 0.011, n.s.) for 10 animals swimming separately in the area. Since the assumptions for this test were very conservative, we cannot conclude for certain that dolphins did not interacted vocally. However, it can be concluded that dolphins definitely did not avoid vocal interactions. To determine whether the amount of whistle matching is what could be expected by chance, we have to calculate the probability for each whistle type to occur. This is a difficult task since there is some debate as to how many whistle types are in a dolphin's repertoire. If we again choose a conservative approach we can assume that there were at least as many whistle types as there were animals present since each animal has a stereotyped signature whistle. For the exact randomisation test 10 animals with a shared repertoire of 10 whistles were assumed. The test also assumed that each individual was swimming at a different location. Again these are very conservative assumptions. The test showed that the observed proportion of whistle matching was significantly larger than expected by chance even if the 8 matching interactions that were detected by overlap only were discarded from the data set (observed proportion: 0.0024, chance proportion: 0.0011, $p=0.001$).

Discussion

The results showed that the number of whistle interactions that could be found in wild dolphins is what could be expected by chance. Since the assumptions of the test were very conservative we can only conclude that dolphins did not avoid vocal interactions. If the assumptions were wrong the proportion of whistle interactions expected by chance would decrease, which could result in a significant difference indicating that dolphins tended to interact vocally. The number of matching interactions, on the other hand, was significantly larger than the chance level even with the conservative assumptions. This shows that whistle matching is a significant part of the communication system of these animals. The observed amount of whistle matching, at 4.5 % of all whistles, was slightly higher than the amount of matching (see Chapter 3) or signature whistle copying reported

in other studies (Burdin et al. 1975). The term copying is used here as a description of an event when animal A is producing the signature whistle of animal B. This can happen in a matching interaction but also at other times. Since the temporal patterns of whistle production were not reported in other studies, we do not know whether copying of signature whistles in these studies occurred in matching interactions. Note that even though the term copying is used here we do not yet know whether a copied signature whistle was actually learned from the animal that produces it primarily. However, this is the most likely explanation given the use of signature whistles in captivity (see Chapter 3). Tyack (1986b) found a high rate of signature whistle copying, but copying rates in his study were probably increased because of the methods used (see Chapter 2).

But do the matching interactions observed in this study involve signature or non-signature whistles? Sayigh (1992) showed that wild bottlenose dolphins use few non-signature whistles. Most whistles she recorded were the signature whistles of the individuals present. Furthermore, matching of non-signature whistles did not occur in the captive group investigated in Chapter 3. Thus, it is likely that whistle matching in this study consisted primarily of signature whistles. Furthermore, signature whistle copying seems to occur only in matching interactions that involve the signature whistle owner (Chapter 3). Burdin et al. (1975) did not study the temporal pattern of whistling between individuals, but showed that signature whistle copying almost only occurred when animals were in acoustic contact. This finding has interesting implications. It sheds some light on the apparent contradiction between the high flexibility of vocal learning in dolphins on the one hand and the amazing stability of signature whistles over the years on the other. It seems that bottlenose dolphins use their abilities to copy signature whistles of others primarily when interacting with these individuals vocally. Thus, most recorded signature whistles would still come from the actual owner of the whistle. Furthermore, the immediate reply of an individual to a copy of its own signature whistle would prevent the usage of whistle copying for deception.

Most hypotheses that have been put forward to explain why vocal matching occurs are based on the assumption that matching can be used to address a specific individual. Tyack (1986b) hypothesised that dolphins could address a

particular group member by simply copying its call. Thus, the caller could either produce a copy of a signature whistle to find the corresponding group member or reply to a caller with a copy to indicate that it has been received. In such interactions the initial caller and the responding animal exchange information about their positions. Thus, it could also be used to elicit an approach. This pattern of copy usage has been found by Gwinner & Kneutgen (1962) in ravens (*Corvus corax*) and white-rumped shamas (*Copsychus malabaricus*), where the female could elicit an approach by the male if it copied its vocalizations. The mechanisms involved in such an interaction can be fairly simple (see Chapter 2). In the shamas the male often attacked the female if it copied his song, like the reaction towards an intruder. In dolphins such approaches were not observed (Chapter 3). Thus, it seems likely that the mechanism involved in dolphins is different.

Another idea that has been suggested for dolphins is the password hypothesis (Janik & Slater 1997) that was originally put forward by Feekes (1977) for birds. It suggests that sharing of calls can be used to label the membership of a group or to keep non-members out of a group. This is based on the assumption that it takes time to learn a new call. Dolphins can copy sounds at first exposure. However, call sharing could still be used to announce or reinforce a bond between animals. Non-members of a group could be kept outside by receiving increased levels of aggression if they produced the call. Especially in male dolphins that form relatively stable alliances (Connor et al. 1992a) this could be a function of call sharing. The interaction shown in Fig. 5.5 shows that more than two individuals can be involved in a matching interaction. Smolker (1994) also found that three male bottlenose dolphins that formed an alliance produced the same whistle type as their most common whistle. Again we have to ask whether these are signature whistles or not. Signature whistle convergence would contradict drastically the finding by Sayigh et al. (1990) that signature whistles are stable for at least 12 years. However, the whistles used for reinforcing bonds could be non-signature whistles. Smolker recorded males in larger groups while they were interacting with humans in very shallow water. This is not a situation in which signature whistle production would be expected. Thus, even though the shared whistle in Smolker's study was also the most common one for each of the alliance members we have no evidence as to whether this whistle also represented the actual

signature whistle of each animal. Further studies are needed to investigate the potential existence and use of stereotyped whistles in alliances.

In the case of male alliances it is possible that whistle matching is used in pair bonding. But it could also be used in the opposite way. In birds, playbacks that simulate matched countersinging often elicit aggressive responses (Krebs et al. 1981; McGregor et al. 1992) or retreat (Todt 1981). In such aggressive encounters matching can again be used to address a specific individual. In dolphins, matching could be used in a similar way. Furthermore, some of the overlapping interactions that were found in this study are very similar to those found in birds. It is important to note that in this study most overlapping interactions occurred between members of the same group. This pattern is similar to that found in robins (*Erithacus rubecula*), where overlapping also occurs mainly in close proximity interactions (Brindley 1991). Furthermore, overlapping seems to be a strong threat in robins (Dabelsteen et al. 1997) and great tits (*Parus major*) (Dabelsteen et al. 1996). Thus, from the data so far it is possible that dolphins use matching and overlapping in aggressive interactions, but also that whistle matching is used in maintaining group cohesion. It would be interesting to look at how different sexes and age classes use matching to elucidate in what ways addressing is most commonly used between dolphins.

Chapter 6

Source levels of bottlenose dolphin whistles in the wild

Introduction

Research on the acoustic properties of bottlenose dolphin (*Tursiops truncatus*) signals has mainly concentrated on echolocation clicks. Most of these studies have been conducted in captivity and investigated frequency, temporal patterning and amplitude of clicks (review in Au 1993). First studies on trained animals that were held in pens in the open sea showed that the source levels measured from captive animals were a lot lower than those used in open water conditions (Au et al. 1974). This result was hardly surprising since the acoustic characteristics of a concrete pool, especially its limited size and reverberation, differ drastically from those of the open ocean. Through careful comparisons of studies in dolphinarium and in the open sea we now have a lot of information on the range and resolution of dolphin echolocation in the ultrasonic range.

In contrast to echolocation clicks we know almost nothing about the source levels of dolphin whistles. This is somewhat surprising since only with this information would we be able to predict the acoustic range of whistles. We know that dolphins use whistles to maintain group cohesion and communicate over long distances (see chapters 3 & 5). The source levels that an animal can produce limit the range over which it can communicate with its conspecifics. Psychophysical studies have revealed both the hearing abilities (Johnson 1967) and the critical ratios for masking of sounds (Johnson 1968) in bottlenose dolphins. Together with information on the ambient noise, source level measurements would therefore enable us to predict the minimum distance over which dolphins could stay in acoustic contact. This knowledge is also crucial for the assessment of effects that human activities like boat traffic have on the animals.

In echolocation studies animals can be trained to perform an echolocation task and will automatically adjust their source levels to the task at hand (Au 1993). Even if a trained animal is taken to sea the transducer can be placed close to the dolphin and the animal can be held stationary during its performance. In the study of dolphin whistles we could train an individual to increase the amplitude of its whistles to find out maximum levels. This would give us a conservative estimate of what animals are capable of. But since these are social signals the animal might not produce its maximum levels even if rewarded with fish. To investigate what source levels are used in the wild we are limited to purely observational studies. Since it is often not possible to get within one meter of a wild animal (the distance required to measure source levels directly), sound pressure levels at greater distances must be used to calculate source levels. But since ambient noise limits the sensitivity of a transducer to distant sounds, even this approach requires one to get close to moving animals without producing noise that would compromise the measurement. Furthermore, to calculate source levels from measured sound pressure levels exact information on the distance between dolphin and transducer is needed. These obstacles in the study of wild dolphins explain why we know so little about this topic.

In this study I measured sound pressure levels of dolphin whistles in the wild using an area in which animals occurred at predictable times of the day and where a hydrophone array allowed me to localize the sound source position. With this information the source levels as well as the acoustic range of such signals can be calculated.

Methods

Recordings were conducted in the Kessock Channel of the Moray Firth, Scotland, (see Chapter 5) when bottlenose dolphins were present. Dolphins were recorded over three weeks in July 1996. All recordings were carried out in sea state zero. Water depth in the study area ranges from 4 to 20 m and the bottom consists primarily of mud.

The measuring equipment consisted of a Brüel & Kjaer 8103 hydrophone connected to a Brüel & Kjaer 2635 preamplifier. Sounds were recorded on a Nagra IV-S tape recorder. The frequency response of this system was 30-20000 Hz \pm 1 dB re 1 μ Pa at a tape speed of 38.1 cm/s. Recordings were conducted from a small inflatable dinghy anchored in the channel (Fig. 6.1). To measure distances from the recording point to the vocalizing animal, sounds were also recorded with the three hydrophone array described in Chapter 5. Only sounds from close to the array were used, so that the localization error was small (up to 14 m). The position of animals was calculated as described in Chapter 5. The position of the dinghy was also determined by passive acoustic localization. Two hammers were banged together underwater as a localization signal for the hydrophone array. All distances between the measuring hydrophone and the calling dolphin given in this chapter were calculated by subtracting the error twice from the originally calculated distance, since both locations were determined by acoustic localization. Ambient noise levels were measured 22 times at various times of day over a period of one week and then averaged to present an overall background noise level.

To calculate source pressure levels the recorded signals were analysed with the SIGNAL software package (Engineering Design, Belmont). The factor that a recorded waveform has to be multiplied by to result in the actual pressure of the sound is given by the following formula:

$$\text{multiplication factor} = \frac{\text{input signal [V]}}{\text{microphone sensitivity [V/Pa]} * \text{measured output [V]}}$$

To use this formula an input signal of known voltage had to be recorded at the start of each tape. This was done by using the internal reference oscillator of the preamplifier, which gave a reference signal of 1V. Sound pressure levels were determined by using the ANSI sound level meter incorporated in the SIGNAL software. Before measurements were taken signals were put through a high-pass

filter to exclude low frequency background noise. All dB values given are referenced to 1 μ Pa.

Transmission loss (TL) from the source to the receiver was calculated using the formula presented by Richardson et al. (1995), which was derived from the Marsh & Schulkin (1962) model for shallow water transmission:

$$TL = 15 \log r + \alpha r + a_T \left(\frac{r}{H} - 1 \right) + 5 \log H + 60 - k_L$$

where r is the range, α is the absorption coefficient of seawater, a_T is the shallow-water attenuation coefficient, H is water depth, and k_L represents a near-field anomaly. The values for k_L and a_T can be taken from tables in Marsh & Schulkin (1962), and $\alpha = 0.036f^{1.5}$ (dB/km) where f is the frequency. Water depth was taken from the admiralty chart of the area. This formula works well for sloping bottom conditions if the value for H is the average of the depth at the source and the receiver (Richardson et al. 1995). The error of this formula at a frequency of 2.8 kHz is about 4 dB at a range of 2.7 km (Marsh & Schulkin 1962). Errors for higher frequencies at shorter ranges were not measured in Marsh and Schulkin's study.

Results

To calculate sound pressure levels a signal had to have a peak signal to noise ratio of at least 3 dB at the Brüel & Kjaer hydrophone and it had to be received by all four hydrophones, so that the source location could be determined. Due to the sensitivity of the Brüel & Kjaer hydrophone this criterion was fulfilled for only 104 whistles in the total recording time of 21 h 38 min. The locations of the animals involved are shown in Fig. 6.1. The distribution of root mean square (rms) SPL's measured from the animals is presented in Fig. 6.2a. The maximum SPL measured was 129.91 dB and the average (\pm SE) was 114.05 (\pm 0.57) dB.

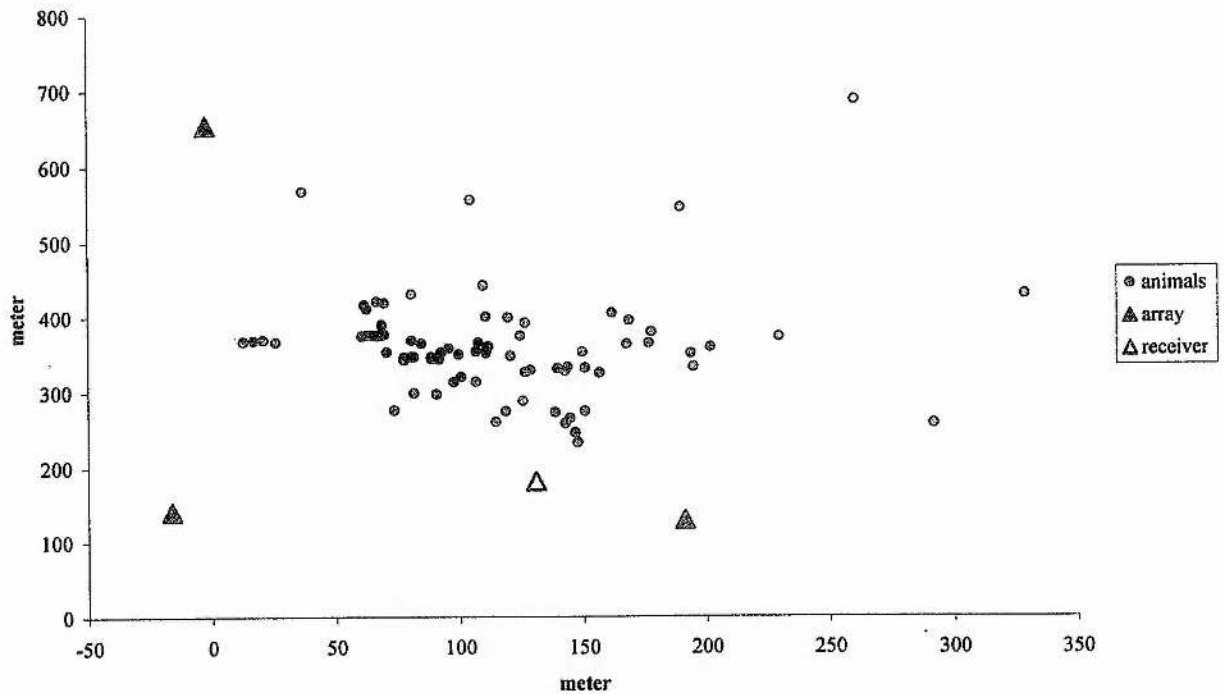


Fig. 6.1: Sound source locations for measured whistles. Triangles indicate the positions of the hydrophones. The open triangle indicates the position of the calibrated recording system.

Figure 6.2b shows the distribution of source levels calculated from measured SPL's using the source-receiver distances as determined by the passive acoustic localisation. Transmission loss was calculated for a frequency of 10 kHz, which corresponds to the average frequency of dolphin whistles. The maximum source level was 168.92 dB and the average (\pm SE) was 157.41 (\pm 0.63) dB. The animal that emitted the loudest sound was 77 m away from the measurement hydrophone. To determine whether only whistles from very loud animals could be analysed or whether the average source levels actually represented the average levels used by animals I also localized the source of 23 quieter whistles that occurred before or after a whistle of which the SPL was measured. In 13 cases the quieter whistles were from the same position as the whistles that were measured, and in 8 cases they were from further away. Only in one case was the quieter animal closer to the hydrophone. Thus, it can be concluded that the sample was biased towards loud animals, and that the resulting average source levels are for animals that produce whistles at above average source levels.

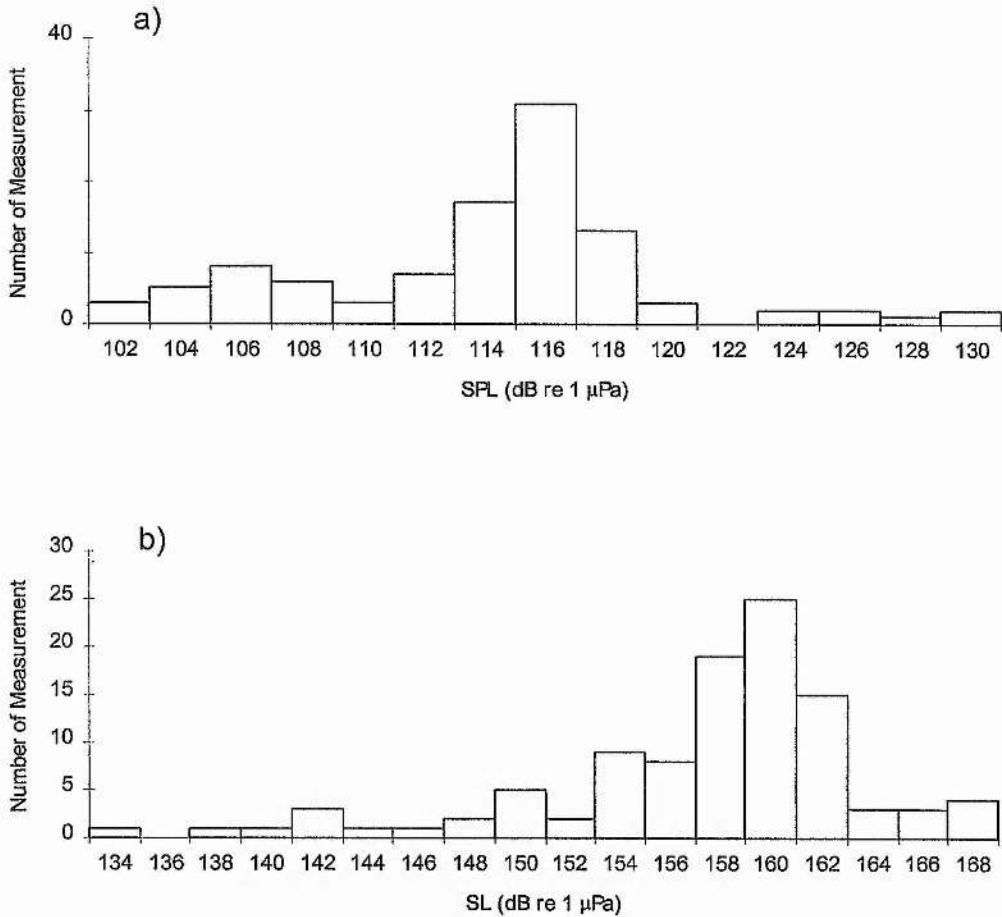


Fig. 6.2: Amplitude of whistles ($n = 104$) before and after correction for distance. (a) Sound pressure levels (SPL) received at the calibrated system. (b) Source levels (SL) calculated from a) by using distance information from the passive acoustic localisation.

To calculate the acoustic range of dolphin whistles we also need information on the ambient masking noise for whistles. Twenty-two measurements were taken over the entire recording period with at least one measurement each day. Ambient noise levels were measured at 1 Hz intervals (Figs. 6.3 and 6.4). To determine the effective acoustic range of dolphin whistles in this area we furthermore need to know the acoustic sensitivity and the critical ratio of the animals. This information was taken from studies carried out by Johnson (1967, 1968). I calculated the acoustic range of whistles (frequency range 3 – 20 kHz) at the frequency of

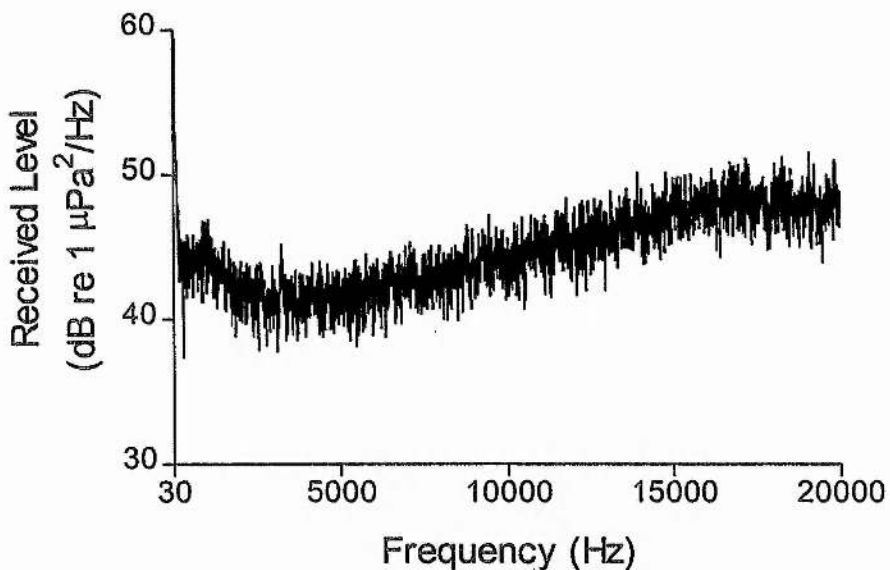


Fig. 6.3: Average sound pressure density spectrum levels for 22 ambient noise measurements. Analysis bandwidth: 3.05 s, FFT size 32768

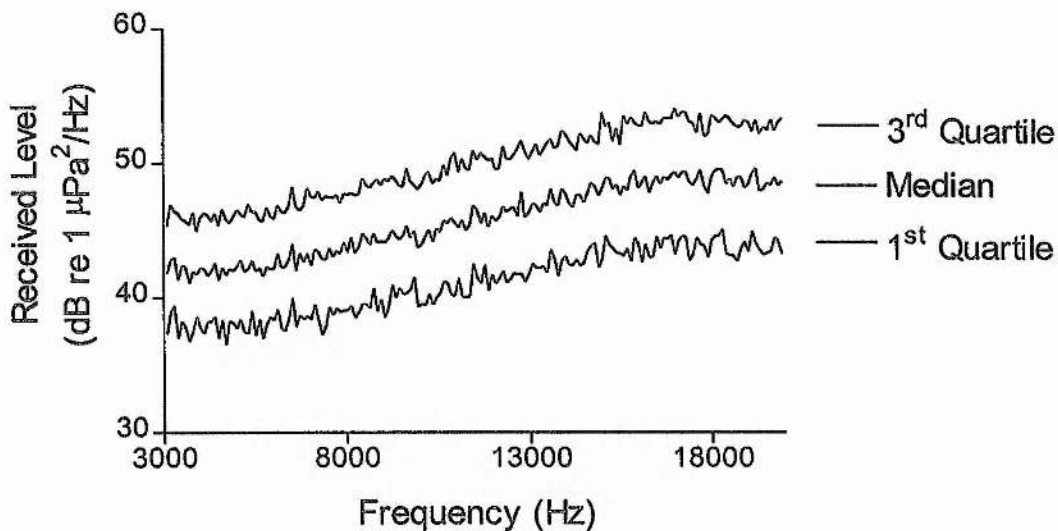


Fig. 6.4: Variation in underwater ambient noise. The curves show selected percentiles in the whistle bandwidth. Analysis bandwidth: 3.05 s, averaged over 100 Hz bands, FFT size 32768

highest sensitivity and at that with the lowest critical ratio. The highest sensitivity found for a bottlenose dolphin in the frequency range of 3 to 20 kHz was 38.6 dB at 14 kHz (Johnson 1967). The lowest critical ratio was 22 dB for a 6 kHz tone (Johnson 1968). In other words, the signal had to be 22 dB above background noise to be detected by a bottlenose dolphin. The average background noise (corrected for analyzer bandwidth) at 6 kHz in this study was 47.26 dB, at 14 kHz it was 51.08 dB. The sensitivity of a bottlenose dolphin at 6 kHz was 70.4 dB (Johnson 1967), and the critical ratio at 14 kHz was 32 dB (Johnson 1968). Thus, a 6 kHz whistle emitted at the average source level of 157.41 dB should be detectable up to 21.78 km from the caller. If the whistle was emitted with the maximum source level it could be detected up to 37.84 km from the caller. If we assume an error of four dB in the measurement of the transmission loss (see methods) the range would lie between 17 and 27 km for the average source level and between 32 and 44 km for the maximum level. This distance is limited by the sensitivity of the dolphin's hearing.

If we consider a frequency of 14 kHz, where the sensitivity of the dolphin is highest, the range is limited by the masking effect of the background noise. Values for a_T and k_L in this calculation were found by extrapolating linearly from the tables provided by Marsh and Schulkin (1962). A 14 kHz whistle emitted at maximum level would be audible to a dolphin at up to 14.57 (± 3) km and at average level it would range up to 7.03 (± 2) km.

Discussion

This study is the first to measure source levels in wild bottlenose dolphins and to estimate the acoustic range of these signals. The acoustic range is of great relevance to the question of group cohesion in dolphins. The results show that whistles have a range that covers the separation distances of up to 300 m reported for mothers and their infants (Smolker et al. 1993). The only other study that has measured source levels of wild dolphins reported whistle levels of 109-125 dB for spinner dolphins, *Stenella longirostris* (Watkins & Schevill 1974). Bottlenose dolphins in this study produced source levels well above these values. However,

the sampling period of Watkins and Schevill's study was very short and only looked at animals while they were resting during the day. Whistle source levels that have been measured from captive bottlenose dolphins ranged from 110 to above 140 dB (Tyack 1985). An upper limit could not be given since source levels were measured with a vocalight which is attached to the dolphin's head and did not indicate any increase beyond 140 dB. Tyack also cites values up to 171 dB for wild bottlenose dolphins from an unpublished report by Fish & Turl (1976), and these correspond closely to the value found here.

Considering the sound propagation characteristics of water it is not surprising that the acoustic space of dolphin whistles is larger than that of terrestrial animals. The largest range in air estimated for terrestrial animals was about 10 km for African elephants (*Loxodonta africana*) (Larom et al. 1997), which can only be achieved with very low frequencies. The data here have shown that the range decreases when the frequency of a call increases. This was to be expected since attenuation is higher for higher frequencies. Baleen whales that use low frequencies similar to those used by elephants achieve acoustic ranges of several hundred km underwater simply because sound travels better in water than in air (review in Richardson et al. 1995).

Apart from the implications for the distances over which animals can stay in touch acoustically, this large range is also likely to affect the design of a communication system. A large acoustic space means that a dolphin is exposed to calls of all animals present within that area. Thus, a large acoustic space results in a high masking noise for whistles simply because other dolphins use the same frequency range for their whistles. It would be interesting to combine information on animal density, acoustic space and calling rates for different species to test whether an increased noise level in the frequency band used for communication affects the design of a group cohesion mechanism in social animals. The large acoustic space for dolphins described here certainly supports the idea that they are exposed to increased background noise levels and that this could have contributed to the evolution of learned signature whistles to maintain acoustic contact between particular individuals.

However, there are two main problems with the acoustic range derived from measurements as presented here. One problem lies with the calculation of the transmission loss in shallow-water habitat. Underwater transmission loss is a complex phenomenon and the approximation that can be achieved by using empirically derived formulae is related to the acoustic topography of the area. Acoustic transmission characteristics of different shallow water areas do not vary as much as those of terrestrial habitats, but it is still important to consider regional variations. Strong currents, varying water depths or obstacles in the sound path can limit the range of an underwater signal drastically. The second problem concerns the transmission of information in a whistle. Animal signals carry different sorts of information. If we assume that identity is the most important one for dolphins, we need to know which parameters encode identity and how well they are transmitted. Even though whistles without much frequency modulation can be found in dolphins, this is not usually the case. The methods comparison in Chapter 4 showed that the identification of signature whistles was strongly affected if certain parameters were excluded. Caldwell et al. (1990) have shown that a bottlenose dolphin was able to identify a whistle if only part of it was heard. If identity is encoded in the overall pattern of the modulation of the fundamental frequency, further behavioural studies are needed to show at what distance different whistles can still be told apart by a dolphin. Only then will we be able to give more detailed estimates of the acoustic space of a dolphin whistle.

Chapter 7

Food-related calling in wild bottlenose dolphins

Introduction

Food-related signaling has been described in many animals. Bees (*Apis mellifera*) (von Frisch 1967) and naked mole rats (*Heterocephalus glaber*) (Judd & Sherman 1996) inform other members of their colonies about the location of food patches, and various birds (Elgar 1986; Marler et al. 1986; Brown et al. 1991; Heinrich & Marzluff 1991) and primates (Dittus 1984; Chapman & Lefebvre 1990; Elowson et al. 1991; Benz et al. 1992; Clark & Wrangham 1993; Hauser & Marler 1993) produce calls if they encounter divisible food items. Various different possible benefits for the caller have been proposed for this seemingly altruistic behaviour. Food calls could inform closely related kin of food sources and thus increase the caller's inclusive fitness (von Frisch 1967; Judd & Sherman 1996). The presence of other animals at the feeding site could increase the caller's food in-take (Brown et al. 1991) or decrease predation pressure (Elgar 1986). In social groups food calling could increase an individual's social status (Clark 1993) or help to avoid increased levels of aggression if others discover the same food source (Hauser 1992). Finally, food calls could be effective in attracting potential mating partners (Smith 1991).

In animals that use sound for echolocation or to manipulate prey behaviour the distinction between food-related signaling to conspecifics and food-associated calling that attracts conspecifics as a by-product is less clear. Many odontocetes produce sounds while they are foraging because they use echolocation clicks to detect and pursue prey. These echolocation signals are highly directional and therefore less likely to attract conspecifics. However, this has not been investigated systematically. In bats echolocation signals can attract conspecifics to

a feeding site (Barclay 1982). This attraction could be disadvantageous but unavoidable if other means of detecting prey are not available. Norris & Møhl (1983) have argued that dolphins might be able to debilitate prey with sound. Such calls could also attract conspecifics to a feeding site. Loud, low frequency calls like bangs have been recorded from feeding odontocetes (Marten et al. 1988), but we do not know whether they stun prey and/or attract other dolphins.

Information on food-related signaling to conspecifics in cetaceans is sparse. To date there is no report about such food calls in captivity. However, captive animals are usually fed with dead fish which could prevent the animals from giving food calls. In the wild it is difficult to identify from the surface when an animal is feeding or has found food. Würsig & Würsig (1980) noted that the surface behaviour of dusky dolphins (*Lagenorhynchus obscurus*) suggested that they produce food-related calls that attract conspecifics, but sounds were not recorded in their study. Some authors have argued that calls that were recorded during more obvious feeding behaviours like bubble-net feeding in humpback whales (*Megaptera novaeangliae*) (D'Vincent et al. 1985) and feeding on seals in killer whales (*Orcinus orca*) (Guinet 1992) function to recruit conspecifics. However, these studies could not show any correlations between calling and approaching behaviour of non-calling animals to the caller since the position of the caller was not known.

Bottlenose dolphins (*Tursiops truncatus*) produce a variety of low-frequency calls that have hardly been studied. One such call is the bray described by dos Santos et al. (1990, 1995). They concluded that this call is related to socializing and feeding. In this chapter I investigate the functional significance of braying in the behaviour of wild bottlenose dolphins in the Moray Firth, Scotland, by using a passive acoustic localization method. With this method it was possible to identify a caller and study the quality and direction of reactions of other animals if a bray was given.

Methods

The study was conducted in the Kessock Channel of the Moray Firth, Scotland. The Moray Firth contains a resident population of around 130 bottlenose dolphins (Wilson 1995). Sound recordings and localizations were conducted as described in Chapter 5. Data were only taken from an area where the localization error was smaller than 30 m. Only braying will be considered in this chapter. To investigate the response of other animals towards braying their surface behaviours in relation to the position where a bray was localized was recorded. Since brays often occur in bouts I only used the first bray in a series. Only cases in which no brays occurred for 1 min before such a braying event were considered. Throughout the chapter I use the term caller for the animal that emitted the first bray, and the term non-caller for all other animals. However, it is important to note that other animals could have brayed or produced other calls in response to a bray, but this was not investigated.

Observations of surface behaviour were carried out from a point on the North side of the channel 30 m above water level and 145 m from the nearest microphone. From this point the whole area could easily be monitored for the surface behaviour of all animals present. Data on the position, direction, and behaviour of each surfacing animal were recorded on a separate channel of the multi-track tape recorder and on the audio track of a Sony camcorder that monitored parts of the study area. The analysis was conducted by using these audio recordings together with the video recordings from the camera. By combining human observations with data from the video camera the whole study area could be monitored continuously. The following behaviour patterns were noted continuously using an event sampling method:

Fast swimming: A dolphin surfaces creating white caps around it due to its speed. **Porpoising** (i.e. shallow forward leaps of not more than one body width above the surface that sometimes occur when a fast swimming animal surfaces) were also counted as fast swimming. The direction of fast swimming was always noted.

Leaping: The whole animal leaves the water in any other way than during porpoising. Porpoising was not counted as leaping. Cases in which only the fluke stayed in the water were also counted as leaps.

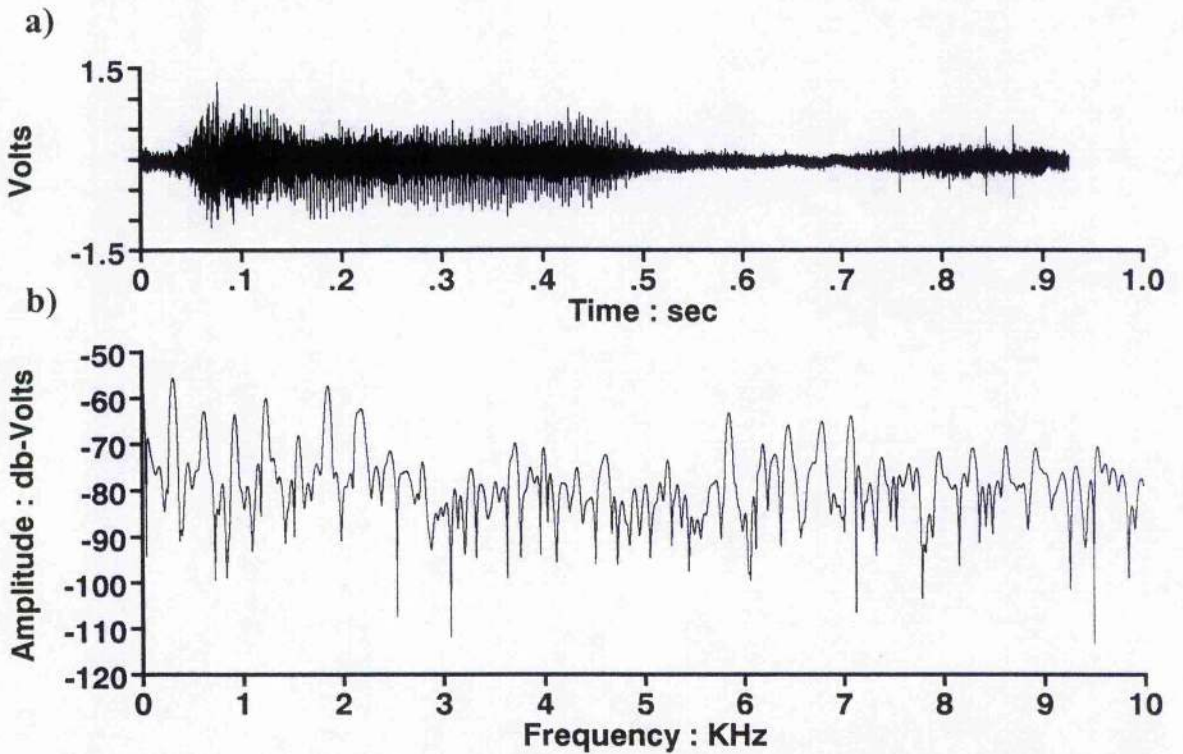
Feeding: A fish was seen either in a dolphin's jaws or swimming away from it at the surface. Only fast swimming fish were seen at this distance, since they sometimes broke the surface during their escape.

Surfacing: The back of a dolphin breaks the surface.

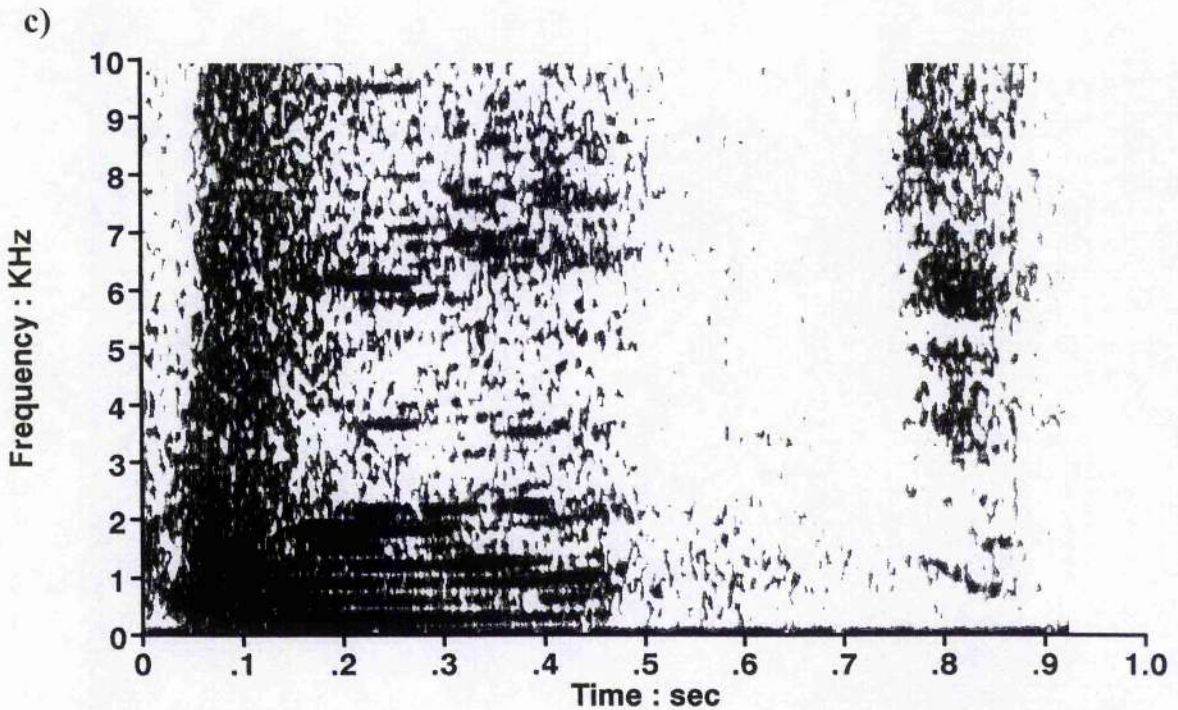
Except for feeding all these behaviour patterns were mutually exclusive. It is important to note that I could not identify individuals. Thus, a series of surfacings, for example, could have been produced by one or by several animals.

To investigate whether animals were attracted by braying, I compared the location and direction of all fast swims in relation to the position where a bray came from. To determine the position of an observed animal landmarks like houses and trees on the South shore were used. I noted in front of which landmark on the South shore the animal was seen. This limited the possible position of an individual to somewhere on a straight line between the observation point and the given landmark. Positions of landmarks were taken from admiralty charts of the area (scale: 1:2500). To determine an animal's distance from the observation point the channel was divided into three distance areas, one close to each shore and one in the middle of the channel. Each area was 175 m wide, so that the whole channel between the hydrophones was covered. Thus, for each surfacing there was a straight line in one of the three areas on which the animal could have been. The position of each surfacing was then compared to the location of the caller by using that point on the straight line that was closest to the caller's position as determined by acoustic localization. This is the most conservative estimate of non-caller/caller distance. I did not attempt to estimate the distance of a surfacing animal from the observation point more accurately to avoid observer bias.

If the position of a fast swim was less than 50 m from the caller the behaviour pattern was counted as occurring at the position of the caller. Otherwise the



DF: 3.05 Hz T-Lo: 0.ms T-Hi: 35.ms FFT:32768 Wind:HANN Sm: 0.



DF: 98 Hz DT: 10.2 ms T-Inc: 1.9 ms FFT:1024 Wind:HANN
Hi-Filt: OFF Lo:-40 db Hi: -6 db

Fig. 7.1: (a) Waveform of a bray. Each bray consists of two parts, a long multiband part and a short downsweep. (b) Power spectrum of a short part in the first segment of the bray. (c) Frequency spectrogram of the bray.

direction of fast swimming was noted as either towards the caller (decreasing distance to caller position) or away from the caller (increasing distance to caller position). All statistical tests were calculated by using the SPSS statistical package (Version 7.5).

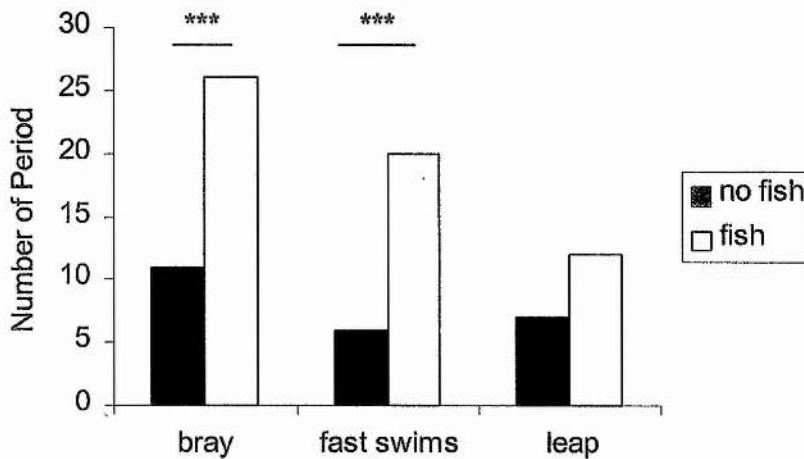


Fig. 7.2: Occurrence of braying, fast swims, and leaping in periods when feeding was observed compared with control periods. $N = 28$ for each condition (Cramer's V test: $***P < 0.001$).

Results

Fig. 7.1 shows an oscillogram, a frequency spectrogram and a typical power spectrum of a bray. Between 3/7/96 and 31/7/96 I recorded 132 braying events in a total of 51h 15 min observation time with dolphins present. This yields a rate of 2.58 events per hour. The number of dolphins present varied from 3 to over 15. To investigate whether braying could be food-related I investigated what other behaviour patterns could be observed when feeding occurred. Twenty-five feeding events were found in this sample. Three additional feeding events were observed in other ad libitum samples in 1996. The fish taken by the dolphins in these events were relatively large. Only two fish species of that size and shape are common in the Kessock Channel in the summer, salmon (*Salmo salar*) and sea trout (*Salmo trutta*). Using one-zero sampling I noted whether braying, fast swimming, or

leaping occurred anywhere in the area during one minute before and after feeding was observed (Fig. 7.2). As a comparison for this test another 28 randomly chosen two minute periods were examined for the occurrence of all the registered behaviour patterns. Fast swimming (Cramer's V test: $V = 0.5$, $P < 0.001$) as well as braying ($V = 0.57$, $P < 0.001$) occurred significantly more often during feeding than during non-feeding periods while leaping did not ($V = 0.19$, NS). Braying was observed in association with 93% of all feeding events, while fast swimming only occurred in 71% of cases. However, fast movements could only be observed if they occurred at the surface. Thus, fast movements could be more common than this during foraging but simply occur fully submerged.

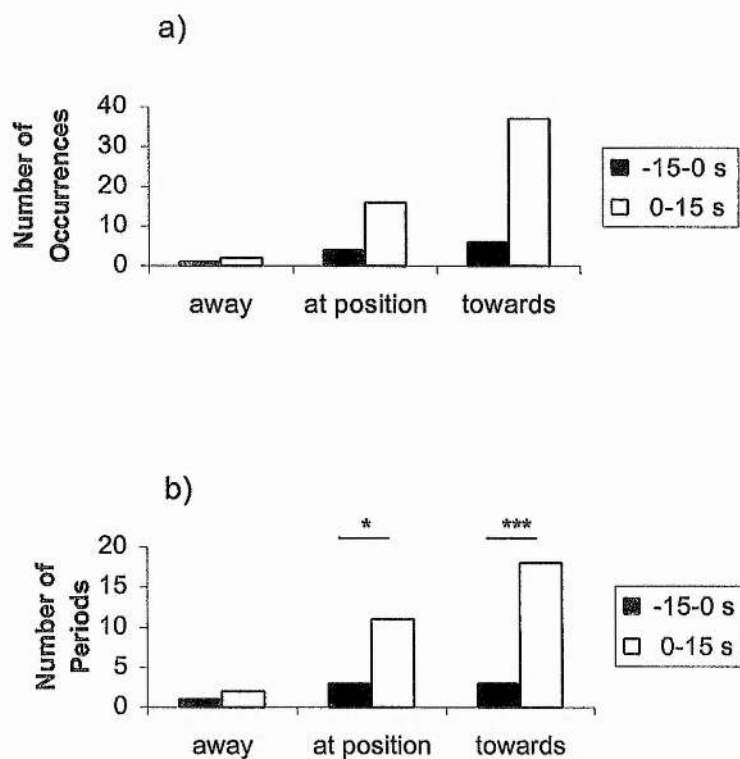


Fig. 7.3: Frequency of fast swimming before and after a bray. The bray occurred at time 0 s. (a) Total number of fast swimming surfacings. Test not conducted since it is not clear how many animals accounted for surfacings. (b) Number of 15 second periods that contained fast swimming surfacings (one-zero sampling). An Asterisk indicates a significant difference (McNemar test: * $p < 0.05$, *** $P < 0.001$).

Tab. 7.1: Numbers of changes in the occurrence of fast swimming at the caller position before and after brays

Fast swimming before brays	Fast swimming after bray	
	No fast swims	Fast swims
No fast swims	2	9
Fast swims	1	13

Tab. 7.2: Number of changes in the occurrence of fast swimming towards the caller position before and after a bray

Fast swimming before brays	Fast swimming after bray	
	No fast swims	Fast swims
No fast swims	7	15
Fast swims	0	3

If brays indicate feeding, fast swims could either be chases of fish that occur at the caller position or rapid approaches by conspecifics that are attracted by a bray. However, if braying indicates social interactions that involve chases between individuals we would expect them to occur primarily at the caller position. In the second phase of the study I investigated whether fast swimming that was observed before and after a bray, occurred at the caller position or whether it involved other animals that approached or avoided the caller. Only fast swimming could be used as an indicator of animal movement since dolphins could not be identified individually. I compared the occurrence of fast swimming in a 15 second period before and after the first bray of a braying event again using one-zero sampling. Fast swimming in these periods occurred in association with 36% of all braying events in July 1996. Acoustic localization together with behavioural observations was carried out in 1995. In 25 cases between 14/7/95 and 21/9/95 fast swimming was observed in at least one of these periods and the first bray could be localized acoustically (total observation time 37h 45 min). I also counted the total number of fast swims (Fig. 7.3a). However, since it was not clear whether one or more animals were responsible for the observed fast swim surfacings in a 15 second observation period tests were conducted on the one-zero sampling data. The

results showed that fast swimming at (McNemar test: $P < 0.05$) as well as towards the caller position (McNemar test: $P < 0.001$) increased significantly after a bray (Tab 7.1 & 7.2). Fast swimming away from the caller position was rare (once before a bray, twice after a bray) and its frequency did not change after a bray (McNemar test: NS) (Fig. 7.3b). The binomial distribution was used for all McNemar tests. However, it is important to note that not all animals in the area reacted with an approach. Even animals near the caller position sometimes did not seem to react. They continued to surface normally without showing any acceleration.

Discussion

The results presented here showed that braying is a food-related call that attracts conspecifics in the area. An increase in fast swims also occurred at the position of the caller. This could be for two reasons. Firstly, feeding on large fish is likely to involve chases leading to fast swims at the caller position. Secondly, all surfacings within 50 m of the caller were considered to be at the caller position and the distance between a caller and a non-caller was determined in a very conservative way. Thus, this distance could have been underestimated in many cases. It could have been that some animals that were considered to be at the caller position were actually non-calling animals near-by that were also attracted and accounted for the fast swimming that was observed in this area.

But is this call used to signal to conspecifics or to manipulate prey behaviour? Several hypotheses that have been brought forward for other animals are less likely in dolphins. Since fish are very mobile and it is unlikely that other dolphins would find the same food spot at the same time, explanations that involve the avoidance of increased aggression by other group members can be discarded. Furthermore, dolphins do not have many predators, so that a decrease in predation pressure due to the presence of more individuals does not seem to be a likely reason for food calling. Four hypothesis may explain braying. (1) Brays could attract closely related kin that are near-by. Female bottlenose dolphins tend to associate with their kin (Wells et al. 1987). However, dolphins have very fluid

association patterns and the probability that other unrelated individuals are also attracted is high. (2) Attracting conspecifics is a strategy to increase the feeding success of the caller. In cliff swallows (*Hirundo pyrrhonota*) a caller benefits from the presence of other individuals because insect swarms disperse more slowly if more animals are present (Brown et al. 1991). In dolphins the approach of conspecifics could chase fish back towards the caller and thus increase its probability of a catch. (3) The caller could benefit by an increase of its social status. This is a possibility that we know little about, since the dynamics of status changes in dolphin societies are virtually unknown. In this and the other hypotheses mentioned so far the bray would be a signal to conspecifics, as has been suggested for food calls in other species. However, (4) another possible function of brays could be to change prey behaviour. The design features of a bray suggest that it has not evolved as a long distance signal to conspecifics. Most energy in it is below 1 kHz. Even though low frequencies travel better underwater, the hearing sensitivity of a dolphin is low in this frequency range (Johnson 1967). An alternative explanation is that brays can either stun a fish or change its behaviour so that it is easier to catch. Salmon can be disorientated by exposing them to low frequency sound (VanDerWalker 1967). The mechanism of this effect is not understood. Possible explanations are that the acceleration in the water affects the lateral line system, that the sound hits the resonant frequency of the fish or parts of it, that the sound pressure level overloads the hearing of the fish, or that the sounds actually cause tissue damage. It has been argued that high frequency clicks are less likely to stun prey because the sound pressure levels required would be too high (Zagaeski 1987; Marten et al. 1988). However, if it is not the pressure but another parameter that elicits the reaction in the fish, clicks might still stun prey. (Marten et al. 1988) argued that low frequency sounds are likely candidates for prey stunning because they fall in the auditory range of fish and they last long enough to overload their hearing. Further studies are needed to investigate this possibility. Looking at the facts from this study it seems more likely that brays are used to manipulate prey behaviour than that they are designed to attract conspecifics. If this is true the attraction of conspecifics would be a by-product of braying.

Playback studies of brays to salmon as well as dolphins would shed light on their functional significance. It would enable us to observe the reactions of salmon to a bray and also show whether it is the bray that attracts other dolphins. Presently it is still possible that the actual attraction is caused by other sounds produced during these feeding events. Such other sounds are whistles and clicks, which are found in many contexts, but also feeding sounds caused by the impact of the dolphin's teeth. Even slight variations in whistles or clicks could indicate a feeding event to other dolphins. However, the distinct approach reaction in the 15 s after a bray was heard suggests that this sound is the actual indicator to other dolphins. Furthermore, brays are a lot rarer than other dolphin sounds. We know that whistles and clicks are used in many different contexts. This relative rarity could mean that brays are used exclusively during feeding. It would be interesting to know how context-specific the use of brays is. Braying occurred several times in the randomly selected control periods. However, controls were simply times in which feeding could not be observed from above the surface, and it is possible that subsurface feeding occurred during these periods. In fact, the small amount of feeding observed at the surface suggests that most feeding occurred underwater. Thus, playback experiments as well as closer underwater observations are needed to test these hypotheses.

Chapter 8

General Discussion and Conclusions

The results of this thesis have shown that bottlenose dolphins use sounds in a wide variety of contexts. They used individually-specific, stereotyped signature whistles primarily when they were separated, but sometimes copied those of other individuals. The captive animals used a lot of non-signature whistles, on the classification of which different methods disagreed. In wild dolphins that were dispersed, matching of stereotyped whistles occurred more often than expected by chance. The active space of these whistles was a lot larger than that of terrestrial animal signals. Finally, wild bottlenose dolphins used low-frequency bray sounds in the context of feeding. These sounds attracted conspecifics, but their characteristics suggest that they might function mainly to modify prey behaviour and facilitate capture. These are just a few examples of how dolphins use sounds. Many other applications as in echolocation (Norris et al. 1961) or in aggressive interactions (Overstrom 1983) have been described elsewhere.

Certain patterns that underlie the communication system of dolphins emerge from these studies. The idea that stereotyped signature whistles are used as cohesion or individual identification sounds has been supported. Furthermore, it seems likely that vocal learning evolved in dolphins in response to the constraints that the marine environment imposed on their communication system. To investigate these two questions further we need work on whistle classification and recognition. Most studies on dolphins have concentrated on the sound producer and rarely on the reaction of the receiver. But only classification experiments can answer some of the questions that have arisen from previous studies. One of the main questions is how dolphins classify non-signature whistles. While we have good evidence for the biological significance of signature whistles as defined by human observer classification (see Chapters 3 and 4), human observers as well as different

computer methods disagree strongly on the classification of non-signature whistles. If human observers use their criteria for signature whistle classification on non-signature whistles the whistle repertoire of an individual seems vast. It is very rare that two non-signature contours resemble each other as closely as two signature whistle contours do. In an experiment in which an animal is conditioned to press a paddle if it hears the same sound twice, one could make the two test sounds more and more dissimilar to test classification thresholds or test how a dolphin classifies pairs of non-signature whistles. Similar experiments have been carried out with birds (e.g. Shy et al. 1986). Another method to investigate this question is the measurement of response times or response strength. In meadowlarks (*Sturnella neglecta*), for example, response times become shorter if playback songs are made more different (Falls et al. 1990). If animals tend to match playbacks this can also be used in classification experiments (e.g. Falls et al. 1988). If the stimulus is made more and more variant the threshold at which the animal still classifies it as its own call can be found. It remains to be seen whether dolphins match playbacks of their own whistles, so that this method could be used. The results of this study make this seem likely. Finally, habituation experiments can be used to determine whistle type boundaries. This has been used in various bird species like red-winged blackbirds (*Agelaius phoeniceus*) (Searcy et al. 1994) and song sparrows (*Melospiza melodia*) (Searcy et al. 1995). If an animal habituates to sound A and dishabituates to sound B a difference has been detected. However, results of such experiments have to be compared to perception experiments. Dishabituation could occur to any perceivable change and, in this case, would give only information on perception thresholds. However, if an animal does not dishabituate to sounds that have been shown to be distinguishable to the animal, this paradigm can be used to gather information on whistle type boundaries. It has been used successfully on the perception of alarm calls in vervet monkeys (*Cercopithecus aethiops*) (Cheney & Seyfarth 1988).

Another question that experiments of this sort could answer is whether dolphins can recognize each other by voice. Individual recognition can be based on various parameters. All animals have individually shaped vocal tracts that cause unique voice characteristics. The question is whether these are sufficient for individual recognition at all distances. In dolphins, the use of signature whistles suggests that

it is not. But identity information that is encoded in a learned contour is unreliable if animals copy each other's signature whistles. So far it has only been hypothesized that signature whistles are necessary for the maintenance of group cohesion and individual recognition. A test of this hypothesis is badly needed. In vervet monkey habituation studies have shown that individuals generalize over different alarm calls emitted by the same individual suggesting voice recognition (Cheney & Seyfarth 1988). In birds this question has also received a lot of attention. Song similarity should, in theory, make individual recognition more difficult (Krebs & Kroodsma 1980). Great tits (*Parus major*) (McGregor & Avery 1986) and song sparrows (Beecher et al. 1994a) have problems in distinguishing between individuals singing the same song type. However, both species can learn to distinguish shared songs sung by different individuals. Female great tits can distinguish between their own mate and another male singing songs that are shared between them (Lind et al. 1996), and song sparrows can be trained to distinguish between shared songs (Stoddard et al. 1992). Dolphin whistles are more similar to the tonal song of birds than to the low frequency calls of primates. Low frequency calls are theoretically better for transmitting voice characteristics over long distances since they are not attenuated as quickly and since more harmonics are found in the low frequency range. Harmonics are influenced by vocal tract morphology and can be used to transmit identity information. The more harmonics reach the receiver the more redundancy there is in the signal and the more likely it is to transmit the encoded identity information. However, the auditory sensitivity of dolphins is tuned towards higher frequencies even though they also produce low frequency sounds. It could be that this is a result of the necessity for good hearing in the frequency range of above 100 kHz (Au et al. 1974; Au 1993) that is used for echolocation. The use of this high frequency range is probably an adaptation to prey size. Killer whales (*Orcinus orca*), for example, feed on larger prey and use echolocation clicks that are usually below 50 kHz (Diercks et al. 1971; Evans 1973). Their low frequency hearing is better than that of the bottlenose dolphin (Hall & Johnstone 1972). Killer whales only rarely use whistles (Ford 1989). They have pod specific burst-pulsed calls with many harmonics (Ford & Fisher 1983), but so far no individual recognition signals have been found. Thus, killer whales may be able to use these harmonics for individual

recognition by voice. To date no study has addressed this question, but it could explain the difference in the vocal repertoire of these two dolphin species.

Recognition experiments will also have to consider voice recognition over the different distances that correspond to separation distances between individuals. While voice recognition might be possible at close range it could be difficult at a distance. Another issue related to this is the change of air-filled cavities under different water pressures and how this affects recognition. The findings of Ridgway et al. (1997) suggested that beluga (*Delphinapterus leucas*) sounds changed drastically at different depths. It would be important to trace such changes in dolphins more systematically and investigate whether parameters that are thought to be important for individual recognition by signature whistles, such as the overall contour of the whistle, can be kept constant at varying depths.

The question of how dolphins recognize each other by sounds is directly related to the issue of whistle type matching. As pointed out several times in this thesis this is theoretically a contradictory phenomenon. However, all the results presented here suggest that on the one hand dolphins use signature whistles for group cohesion and individual recognition and on the other that matching is an important aspect of their communication. There are two possible solutions to this problem. One is that deception does not pay and therefore does not occur (Grafen 1990). This could either be because the costs for producing a deceptive signal outweigh the achieved benefit, or because the same goal can be achieved with a different strategy that is inherently less costly, or because deceivers are sanctioned by conspecifics. In the last case the occurrence of deception would depend on the probability of being found out. So far deception has not been demonstrated to occur in dolphins, but it is a theoretical possibility. One of the main contexts in which it is likely to be used is where resources are monopolized, in which case deception could be one strategy to gain access to such resources. Since dolphins are not territorial and food patches form and dissolve relatively quickly in the sea, this seems unlikely to be of advantage. However, male bottlenose dolphins sometimes monopolize females (Connor et al. 1992b). In this context deception could be a fruitful strategy if herding males could be lured away from the females. Just as with individual recognition the solution for the contradiction between

learned individual recognition calls and the possibility of deception could involve both pressures in a stable equilibrium. Deception can be evolutionarily stable if it is rare and if the advantages of using learned calls in individual recognition outweigh the disadvantages of being deceived occasionally (Wiley 1994).

Matching can have many advantages too. It allows animals to address specific individuals. Considering the vast active space of a dolphin whistle this is probably a lot more important than in most terrestrial animals. A similar case can be found in bat roosts where several thousand individuals occupy a very small area and frequently depart and arrive to feed their young (Janik & Slater 1997). It is interesting that bats are also vocal learners and that they use learned sounds in individual recognition contexts (Jones & Ransome 1993). This parallel supports the idea that vocal learning evolved in the context of individual recognition. Again playbacks as well as more observational studies in the wild are needed to investigate in what contexts this addressing is used.

We have seen throughout this thesis the arguments that can be brought forward to explain the complexity of dolphin communication. It is important to note that most of these arguments also apply to terrestrial animals to a certain extent. However, the degree to which dolphins are deprived of visual and olfactory cues, together with their high mobility, predatory life style, and the long phase of dependency of their infants is unparalleled. The acoustic channel is the only one available for communication and to maintain group cohesion. Thus, acoustic background noise caused by other dolphins must be high. The finding that the active space of a bottlenose dolphin whistle can have a radius of up to 38 km shows that they are exposed to a lot more noise than we would expect from their group sizes. Apart from the problem of masking noise, this finding has two very important implications. Firstly, it means that we possibly have to readjust our views on the structure of dolphin societies. Studies that have employed boat surveys and photo identification techniques to determine social association patterns found that bottlenose dolphins tend to associate with specific individuals, but that these patterns are very fluid and that an individual often does not associate with one interaction partner for several days (Wells et al. 1980,1987; Wells 1991). This conclusion is based on the assumption that animals in the same

group interact socially while those in different groups do not. Wells and his colleagues considered all animals that are within 100 m of each other as belonging to one group. Given the long range over which individuals can be in acoustic contact and the dynamics of fish aggregations it is reasonable to take an alternative viewpoint. Since dolphins rely heavily on acoustic communication it could be that a group definition based instead on the acoustic space of dolphin signals would shed new light on social structures. Individuals that interact acoustically might be more closely associated than those that are only swimming in the same general area. Animals that happen to feed in the same area need not necessarily interact socially. Dolphins seem to use the Kessock Channel primarily for foraging during rising tides (Lütkebohle 1995). Small clusters of dolphins often arrived together and also left together, but mixed with other individuals in the area during their stay (pers. obs.; Lütkebohle 1995). Even though this is a preliminary observation based on very obviously marked individuals, it could indicate that such feeding aggregations are not well suited to investigate the social structure of these animals. Acoustic data are often difficult to get, but group definitions that are based on close proximity between individuals (e.g. Smolker et al. 1992), and if possible on the behavioural context, might be more useful for the study of association patterns.

The second implication of the large acoustic space of dolphin signals also concerns their social behaviour. This large range enables an individual to collect information on a lot of interactions without being itself involved. McGregor (McGregor 1993; McGregor & Dabelsteen 1996) pointed out that eavesdropping is likely to occur in large communication networks and that its role in animal communication has been underestimated in many studies. Indeed we know almost nothing about whether and how dolphins use such information. However, it would be very interesting to investigate its possible effects on social interactions and the dominance structure in dolphin societies. If the food-related calls described in Chapter 7 are used to stun prey, the finding that dolphins are attracted to feeding sites after braying was recorded could be an example of how animals benefit by eavesdropping on others. However, currently we do not know what the primary function of braying is.

It becomes clear that the study of dolphin communication is still far behind that of other animals. Now that acoustic localisation techniques are more easily available I hope that more researchers will take these into the field and study functional aspects of this important part of their social behaviour. Dolphins have a complex social systems and exhibit cognitive abilities that equal those of non-human primates. Thus, they are a very promising group for the comparative study of the evolution of cognition and communication in mammals. The comparison of dolphins, seals, bats, and primates has already helped to recognize some of the likely factors that were responsible for the evolution of vocal learning in mammals (Janik & Slater 1997). Similarly, as pointed out in Chapter 2, the similarities in the complexity of the social structure and in the opportunistic feeding habits of dolphins and some apes make comparisons between these animals particularly interesting for the study of the evolution of intelligence. The fact that dolphins, unlike non-human primates, are also very versatile at vocal learning gives us a chance to observe in what ways these skills interact and how such interactions affect the structure of animal societies.

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Vocal Learning in Mammals

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I. INTRODUCTION

In this chapter we survey the occurrence of vocal learning in mammals and discuss possible reasons it has evolved. But first it is important to be clear about what we mean by "vocal learning." The term has been used to describe the influence of learning on a variety of different aspects of vocal communication. Learning can affect the generation of sounds, their usage, and their comprehension. While modifications in sound generation as a result of experience can be described as learning sounds, those in comprehension and usage are rather different phenomena, which are perhaps better described as learning about sounds. Vocal learning, as we discuss it here, refers only to learning sounds, that is, to instances where the vocalizations themselves are modified in form as a result of experience with those of other individuals. Learning that affects usage and comprehension of sounds will be referred to as contextual learning as opposed to vocal learning. Contextual learning in relation to vocal communication is relatively common among mammals. The list of animals in which the utterance of a vocal signal has been brought under conditional control, i.e., which have learned to change the context in which they are using sounds, comprises rats (Lal, 1967), guinea pigs (Burnstein and Wolff, 1967), dogs (Salzinger and Waller, 1962), cats (Molliver, 1963), sea lions (Schusterman and Feinstein, 1965), primates (Myers, Horel, and Pennypacker, 1965; Randolph and Brooks, 1967; Wilson, 1975; Aitken and Wilson, 1979), and dolphins (Lilly, 1965). Other forms of contextual learning in vocal communication involve learning to recognize particular sounds, or learning to react to sounds differently as a result of experience. These are important ways in which learning may influence vocal communication, and the behavior associated with it, but they are not examples of vocal learning in the strict sense in which we use the term here.

Some types of modification through learning are likely to be easier to achieve than others because different sound parameters are controlled by different mechanisms. Overall duration and amplitude of a sound can be altered by simple modifications of exhalation alone. A longer exhalation phase or higher air pressure while producing the sound is all that is required to cause such changes. For learning to occur here, only the activity of respiratory muscles need be modified by experience. Such changes in duration or amplitude do not affect the overall form of a call. On the other hand, the detailed matching of a sound pattern requires much more complicated alterations. The fundamental frequency of a sound can be altered only if the activity of muscles controlling the vocal apparatus itself can be modified by experience. In tonal signals this is required to achieve change in the frequency contour of a call. Of course, other more complex processes can be involved in sound production. Rapid amplitude modulation, for example, can cause additional frequency bands in a call. Seemingly subtle changes that require a high degree of coordination between respiratory, laryngeal, and articulatory muscles, like those leading to differences in voice-onset time, can also be involved. Where possible we look at modifications in duration and amplitude and those in frequency parameters separately, and point to these different levels of motor control as they occur in the vocal learning of different groups.

Vocal learning has been described only in birds and mammals, and even among these the evidence is patchy. It has been found in all songbirds (Oscines) studied to date (Kroodsma and Baylis, 1982), but appears not to occur in the closely related Suboscines (Kroodsma, 1984, 1989). Convincing evidence comes from only two of the twenty or so other orders of birds: the hummingbirds (Apodiformes) (Baptista and Schuchmann, 1990; Gaunt, Baptista, Sanchez, and Hernandez, 1994) and the parrots (Psittaciformes) (Todt, 1975; Pepperberg, 1981). The three groups showing vocal learning are only distantly related to each other, suggesting that it has evolved among birds on at least three separate occasions. In mammals, the importance of vocal learning in our own species contrasts remarkably with the scarcity of evidence elsewhere. Part of the reason for this may be the lack of relevant studies. Absence of evidence for vocal learning in a particular species is certainly not evidence for its absence.

In our review of the literature on vocal learning in mammals we attempt to determine the extent to which it occurs in species other than our own, and whether it is widespread or patchily distributed as in birds. This survey enables us to compare and contrast birds and mammals, and to consider the possible functional significance of vocal learning. It may perhaps also shed some light on why it occurs in humans. But first we discuss the methods

that have been used in various studies and the extent to which these can give unequivocal evidence for or against vocal learning.

II. EVIDENCE FOR VOCAL LEARNING

There are several pitfalls in trying to show vocal learning in a particular species. A fundamental problem is the question of whether a particular call was in an animal's repertoire before it was first noted. Apparent changes in the call repertoire of an animal often relate to other changes in its environment. Examples are alterations in social context, because of the introduction of foreign animals or a change in status, changes in the habitat that alter its sound transmission characteristics, or seasonal events that influence the diurnal behavior patterns of the animal. If a new call arises at the time of such an event, it could be because of a change in the frequency of occurrence of calls that were already present in the repertoire rather than vocal learning.

But even a truly new call could arise for different reasons. Maturation processes or improvisation could be responsible, rather than copying from other individuals. Maturation processes lead to changes in vocal tract morphology that can influence sound characteristics. Thus, simple observations of changes in the call repertoire during ontogeny are difficult to interpret. Vocal learning may or may not be involved.

Improvisation is another process that leads to the production of new calls. Various different mechanisms can be used to achieve improvisation, and vocal learning, again, may or may not be involved. One possibility is the production of completely new sounds through random sound generation. This form of improvisation would be an interesting case of vocal flexibility. According to our definition it does not involve vocal learning, however, since experience is not required. As we see in our survey, completely random sound production has so far never been the only possible explanation for an observed change in call structure. But there are other forms of improvisation that do involve learning. If an animal produces a completely new call that avoids overlap with calls of other individuals, experience might be used to achieve this avoidance. This would be a case of vocal learning according to our definition. A more restricted form of improvisation might involve a recombination of given subunits of a call. If these units can be produced on their own, this form of improvisation represents a special case of contextual learning. It is simply a matter of calls that are already present in an individual's repertoire being produced in a new context. Finally, an animal could learn different parts of other individuals'

calls and combine them to form a new call. This sort of improvisation would be a clear case of vocal learning.

Vocal learning is obviously difficult to investigate if changes in calls do not result in matching those of other individuals or model sounds. The most clinching evidence for vocal learning comes from experiments in which animals are trained to imitate sounds that have not been in their repertoire before. If animals are able to copy sounds that are very different from sounds in their natural repertoire, like human speech or computer-generated sounds that were designed to be different, vocal learning has clearly been demonstrated. In animals that are not capable of imitating such sounds, vocal learning within the natural repertoire can nevertheless be shown by rearing experiments, if infants that were raised with different acoustic stimuli are found to match the sounds they heard in detail. It is unlikely that selective reinforcement of randomly produced sounds could result in detailed matching of sounds produced by other animals.

Such rearing experiments have commonly been carried out on birds, but few have been attempted on mammals. There are probably two main reasons for this. First, many of the mammalian species involved, such as whales and dolphins, are difficult to keep in the highly controlled acoustic environments necessary for such studies. Second, the species involved are highly sociable and subjecting individuals to experimental treatments involving deprivation likely to lead to suffering is not easy to justify. Because of these difficulties, for many mammals the evidence for or against vocal learning is more circumstantial.

The main source of such less direct evidence comes from geographic variation in vocal signals. Where neighboring animals, or those in a social group, share sounds that differ from more distant individuals or those in other groups, vocal learning is a probable reason. This is most obvious where groups are not geographically isolated from each other. However, one has to be careful in interpreting such observations. Geographic variation in vocalizations can also arise because of ecological differences. Transmission characteristics of the environment may influence the extent to which a particular sound in an animal's repertoire is used. Differences in social structure in different locations could have the same effect on the usage of different call types that are present in the repertoire of all members of the species. Even different preferences for certain call versions can be the reason for geographic variation. In what he called action-based learning Marler (1991) suggested that an animal may produce only those sounds from its repertoire that are selectively reinforced by social stimulation. If there are different preferences for particular call types in different populations, action-based learning may result in geographic variation of their call repertoires. This would be a case of contextual learning, but not vocal

learning. Finally, if animals tend to stay in their maternal groups, genetic transmission is a possible reason for differences in call repertoires. Further research is needed in such cases to show vocal learning unequivocally.

III. SURVEY

A. BATS

In many bat species the isolation calls of pups exhibit vocal "signatures" (significant individual differences that remain constant over time) and these are used by mothers to find their offspring when they return to the colony to suckle them. Variation in the isolation calls of young big brown bats (*Eptesicus fuscus*) is as great within as between colonies, and between twins as between less close relatives (Rasmuson and Barclay, 1992). The production of a completely new call could be achieved either by producing a call at random, which need not involve learning, by active avoidance of matching the calls of neighboring individuals, or by composing a call mixing different parts of heard calls. Although the last two mechanisms would involve learning, there is no conclusive evidence that they are involved here. However, it is interesting that there are closer similarities in echolocation calls within families than between them in this species (Masters, Raver, and Kazial, 1995), suggesting that echolocation and isolation call development are controlled by different mechanisms.

In the lesser spear-nosed bat (*Phyllostomus discolor*) mothers and infants exchange calls when they reunite, and Esser and Schmidt (1989) suggest that the infant's isolation call becomes progressively more like the mother's call over the first few weeks of life. Esser (1994) argues that this is due to learning: he found that the calls of isolated pups that were played a tape-recorded call over the first 50 days of life tended to become somewhat similar to it, while those of unstimulated controls remained highly variable. However, one problem with isolation experiments is the general lack of stimulation. Bats might simply need auditory input of some nonspecific sort to develop normal calling behavior. An experiment with two groups hearing different calls would clarify whether learning is involved.

The most convincing evidence for vocal learning in bats comes from the development of echolocation calls in greater horseshoe bats (*Rhinolophus ferrumequinum*) (Jones and Ransome, 1993). This call is an almost pure tone of around 83 kHz. Its sound frequency is higher in summer than in winter, but it also rises in the first year or two of life, and later falls off in old age. When young bats first start to hunt for themselves at a few weeks of age the frequency of the calls they adopt is strongly correlated with that

of their mother. In both males and females young bats with mothers over five years old have significantly lower echolocation calls than those born to younger mothers. This correlation with maternal age strongly suggests that learning is involved.

B. PINNIPEDS

Most authors place the pinnipeds in the order carnivora. They are classified into the true seals (phocids), the sea lions and fur seals (otariids), and the walruses (odobenids). Evidence for vocal learning has so far been found only in phocids. The most conclusive evidence that seals can learn new sounds comes from the imitation of human speech by captive animals. Two male harbor seals (*Phoca vitulina*) at the New England Aquarium were able to mimic speech sounds (Ralls, Fiorelli, and Gish, 1985). The more impressive of the two, Hoover, spontaneously developed imitations of a variety of phrases typically produced by visitors to the aquarium, such as "hello there" and "come over here," as well as his own name and an imitation of laughter. In a controlled conditioning experiment, the second seal was trained to imitate its own name.

Evidence in the wild is not so easily obtained. Geographical variation has been described in several species, but authors vary in whether they attribute this to learning. Thomas and Stirling (1983) examined Weddell seal (*Leptonychotes weddelli*) calls at Palmer Peninsula and McMurdo Sound, two sites on the edge of the Antarctic continent some 4000 km apart. Weddell seals have a large repertoire of vocalizations that they use extensively in the mating season (Thomas and Kuechle, 1982). Although some call types were found at both sites, each colony also had several unique ones. Marked spectral and temporal differences were found in some of the shared calls. Furthermore, seals at McMurdo had more call types in their repertoire than those at Palmer Peninsula. The authors suggest that the combination of fidelity to breeding sites and learning may account for these differences. The problem is to differentiate between these ideas: over a long period of time geographical isolation may lead to genetic differences affecting calls just as learning may give rise to call differences over shorter periods. Morrice, Burton, and Green (1994) compared vocal repertoires of two Weddell seal colonies located in adjacent fjords only 20 km apart. Despite the close proximity of these two colonies they had only 5 of 44 described vocalization types in common. Of the five shared call types two showed significant differences in their start or end frequency between colonies. Furthermore, a song type recorded in 1984 in one of the fjords (Green and Burton, 1988) could not be found again in 1989/1990 (Morrice *et al.*,

1994). Such strong dialects between adjacent colonies are rare in mammals and make vocal learning a likely explanation for their occurrence.

All other studies on geographic variation in seal calls have concentrated on very distant sites. Thomas and Golladay (1995) studied geographic variation in leopard seal (*Hydrurga leptonyx*) underwater vocalizations at Palmer Peninsula and McMurdo Sound, the same sites as in the Weddell seal study by Thomas and Stirling mentioned earlier. They found that seals at Palmer Peninsula had more call types in their repertoire and that shared calls varied in frequency and time parameters between the two sites. Bearded seals (*Erignathus barbatus*) at six distant sites north of Canada and Alaska also differed in various temporal and spectral features of their underwater "trill" vocalizations (Cleator, Stirling, and Smith, 1989). Again, the authors suggest that this may be because of strong fidelity to specific breeding areas, but they do not discuss learning. Terhune (1994), in a study of harp seal (*Phoca groenlandica*) underwater calls in the Gulf of St. Lawrence and on Jan Mayen Island, sites some 3500 km apart, found spectral and temporal differences in shared call types. Each colony also had one unique call type not found at the other study site. Terhune attributes differences between sites to reproductive isolation. Given the possible role of learning, this seems somewhat sweeping. It is interesting, though, that different samples at each of the two sites were collected on occasions 18–20 years apart and only slight differences, probably attributable to sampling error, were found between the recordings at the same place (Terhune, 1994). This suggests that call repertoires at a particular place are conservative in a way that would be less likely if learning were involved. However, harp seals can live up to 35 years (Reeves, Stewart, and Leatherwood, 1992), so that 20 years might not be enough time to pick up changes caused by copying errors in a learning process.

Differences in the pattern of northern elephant seal (*Mirounga angustirostris*) threat vocalizations between several islands off California were interpreted by Le Boeuf and Peterson (1969a) as evidence for learning. There were marked differences in the pulse rate of threat calls between the colonies, one of which, with its distinct dialect, had been in existence only for a few years. However, later studies showed that, even though there were still clear individual differences in pulse rates, colony differences had disappeared (Le Boeuf and Petrinovich, 1974; Shipley, Hines, and Buchwald, 1981). Note that to change pulse rate the animal has to produce the same sound in quicker or slower succession. It does not change the form of the call. Therefore, this would not qualify as an example of vocal learning according to our definition, unless pulse sequences represent minimum units of call production and single pulses cannot be produced on their own. However, the disappearance of geographic differences in calling behavior

is an interesting phenomenon that is relevant for our interpretation of geographic variation in other cases. By the end of the 19th century, northern elephant seals were reduced to less than 100 animals all living on Isla de Guadalupe 243 km west of Baja California (Bartholomew and Hubbs, 1960). The population was then protected and started to grow again and to recolonize old breeding sites (Le Boeuf and Petrinovich, 1974). There are two ways in which differences between colonies could have arisen in the first phase of recolonization. The first is a founder effect. The small number of males that emigrated to recolonize a particular breeding site could have had pulse rates on average different from those of the original colony. Once an elephant seal has chosen a breeding site in the first year of its reproductive life, it tends to return to that same site each year (Le Boeuf, Ainley, and Lewis, 1974). A difference in pulse rates between colonies would therefore be likely to persist as long as no further migration occurred. The second possibility is that a few males monopolized most of the females and spread their pulse rate, either through being imitated by younger animals or through genetic transmission. If young males return to their natal rookery to breed, a particular pulse rate could thus establish itself and persist. In small colonies only a few males do indeed monopolize all the females and are the only ones that breed (Le Boeuf, 1974), but there is no clear evidence on whether males return to their natal rookeries to breed. Dispersion from the island of birth after 1968 was considerable (Le Boeuf *et al.*, 1974), but of 400 males tagged as juveniles on Año Nuevo Island between 1964 and 1969 none were sighted at any of the other breeding sites in their first breeding season at the age of 5–6 years (Le Boeuf, 1974). If there is continuing immigration from other colonies, pulse rate in a recolonized site would change and eventually the differences in pulse rate between colonies would disappear. The subsequent studies during rapid population expansion showed this to be the case. Such a process would occur as long as there was no isolating mechanism between populations, whether or not learning has a role in pulse rate development. The longevity of elephant seals made it possible to witness these changes occurring. The observed differences cannot therefore be regarded as a result of learning.

C. CETACEANS

1. *Toothed Whales (Odontocetes)*

As with seals, the smaller cetaceans can be kept in captivity, and observations there provide some evidence of vocal imitation. There is anecdotal evidence, largely from keepers, that these animals can modify the broad-band frequency squeaks that they produce so as to imitate human speech (*Tursiops truncatus*, Caldwell and Caldwell, 1972; *Delphinapterus leucas*,

Eaton, 1979). The most extensive experimental evidence comes from the bottlenose dolphin (*Tursiops truncatus*), as this is the cetacean most commonly kept in captivity. They produce whistles, clicks, and burst-pulsed sounds that are all modifiable by experience. Most of the evidence of vocal learning concerns their whistles. Caldwell and Caldwell (1972) recorded a case of spontaneous whistle mimicry when their study animal matched a whistle that was being used to test its sound localization abilities. Reiss and McCowan (1993) also found bottlenose dolphins mimicking whistle sounds spontaneously. Two young males were given control over stimuli by means of an underwater keyboard. Pressing a symbol on this released a sound linked to it and also the presentation to the dolphin of an object or activity, such as a ball or being rubbed. The animals learned to mimic the sounds and later produced them frequently without having pressed the key to hear the appropriate stimulus, but often while playing with the object or engaged in the activity with which it had been linked.

When it comes to training, there is no doubt that dolphin whistles can be modified by experience. Richards, Wolz, and Herman (1984) trained a dolphin to imitate computer-generated sounds using food or petting by the trainer as rewards. The animal matched a variety of sounds that were quite different from those it produced before the training. In some cases it produced passable copies the first time a sound was introduced. In further training the animal was rewarded for producing particular whistles when specific objects were shown to it, and would do so with a high degree of reliability. Thus, the dolphin effectively learned vocal labels for those objects. In a subsequent series of experiments, Sigurdson (1993) also successfully trained two dolphins to match computer-generated whistles.

A few studies have described the changes in whistle repertoires of infant bottlenose dolphins over time (Caldwell and Caldwell, 1979; Sayigh, 1992; McCowan and Reiss, 1995). However, even though the species is clearly capable of vocal learning, the role of vocal learning in whistle development of infants has not been demonstrated so far.

Wang and his colleagues (Wang, Würsig, and Evans, 1995) found marked geographic variation in spectral and temporal features of bottlenose dolphin whistles in the wild at sites only a few hundred kilometers apart. Each site had its own resident population with some individuals moving between them. Since dolphins produce individually specific whistle contours, the study did not look at different call types separately, but simply compared general parameters like start and end frequency in all recorded whistles at each site.

Experimental work by Moore and Pawloski (1990) provided evidence that vocal flexibility applies to click sounds used in echolocation as well. They succeeded in training a bottlenose dolphin to shift the peak frequency

of its broad-band ultrasonic echolocation clicks. The anecdotal evidence of dolphins mimicking speech sounds also suggests that clicks can be modified, as they use very rapid click trains called burst-pulsed sounds to produce these imitations.

Turning to larger odontocetes, there is also evidence in favor of vocal learning. Pods of killer whales (*Orcinus orca*) off British Columbia have repertoires of 7–17 call types, which appear to be shared by most individuals in the pod (Ford and Fisher, 1983; Ford, 1991). Groups of pods can be placed in “clans,” which share some call types, although shared types still have pod-specific features; there is no sharing of calls between clans. New pods appear to form by splitting of preexisting ones, with slow divergence of calls thereafter, though there is evidence that pod repertoires can persist for 25 years with little change. Since all animals within a pod are closely related (Bigg, Olesiuk, Ellis, Ford, and Balcomb, 1990), such differences could be caused by genetic differences. However, Ford (1991) reports that individuals occasionally seem to mimic the calls of other pods, suggesting that learning is involved.

Studies on captive killer whales have not addressed the question of vocal learning directly. However, Bain (1986) gave an anecdotal report that a female killer whale from Iceland started to mimic calls of a female from British Columbia, Canada, after they had been housed together for a few years. Differences in the vocal repertoire of killer whales between such distant sites are larger than those between sympatric pods (Awbrey, Evans, Jehl, Thomas, and Leatherwood, 1982). However, no spectrographic analysis was provided in Bain's study. Bowles, Young, and Asper (1988) described the vocal development of a captive killer whale calf, but the role of vocal learning in call development could not be addressed. As discussed earlier, changes in the vocal repertoire during ontogeny can be maturational, genetic, or learned. Van Heel, Kamminga, and van der Toorn (1982) reported an experiment in which a killer whale seemed to spontaneously imitate computer-generated tonal signals that were used in training the animal to perform different tasks. However, these signals were designed to resemble the whale's own vocalizations, so that vocal learning was not necessary to produce them.

2. *Baleen Whales (Mysticetes)*

Perhaps the best known example of vocal learning among whales in the wild is that of male humpback whales (*Megaptera novaeangliae*) in which individuals produce long and elaborate songs lasting up to 20 minutes before repetition (Payne and McVay, 1971). Recordings of the songs of this species off Bermuda over a period of 18 years showed that they changed with time but that at any one time the songs of different individuals were

similar (Payne and Payne, 1985). Detailed study of songs recorded around Hawaii in two singing seasons (mid-November to mid-May) demonstrated progressive change from month to month through the season, with little difference between the end of one season and the start of the next, the period when the whales are away on their feeding grounds and sing little (Payne, Tyack, and Payne, 1983). This suggests that change is an active process rather than one of forgetting sounds with the passage of time. Nor can the changes be attributed to changing group membership, as Guinee, Chu, and Dorsey (1983) obtained two recordings from each of three identified individuals and found both that they changed and that they did so in parallel with each other. These detailed short-term changes, both within and between individuals, can be accounted for only if animals are imitating one another. However, songs of different humpback whale populations differ completely (Winn, Thompson, Cummings, Hain, Hudnall, Hays, and Steiner, 1981). But even though this species is clearly capable of vocal learning, geographic variation could have evolved because of genetic isolation between populations in different oceans.

Bowhead whales (*Balaena mysticetus*) studied during their spring migration have also been found to sing (Cummings and Holliday, 1987). Their song consists of repeated phrases that can be categorized into one to three themes. A song lasts about one minute but is usually repeated several times. As with humpback whales, all animals in the study population off Alaska sang the same song but the song was different in each singing season (Würsig and Clark, 1993). Cummings and Holliday (1987) always heard one animal singing at a time but another one often started as soon as the first stopped. It is not clear yet whether individuals change their song over the season, but, if so, it would be strong evidence for vocal learning.

D. PRIMATES

As we get closer to humans, one might imagine that the evidence for vocal learning would become more and more impressive. As we shall see, this is far from being the case.

1. Monkeys

"There is no conclusive evidence of vocal learning in monkeys" (Snowdon, 1990, p. 225). Perhaps the strongest evidence against vocal learning is in squirrel monkeys (*Saimiri sciureus*), where isolation-reared animals (Winter, Handley, Ploog, and Schott, 1973), and even deafened ones (Talmage-Riggs, Winter, Ploog, and Mayer, 1972), show normal vocal development. In the squirrel monkey there is also a good example of a dialect that is not based on learning. Two distinct phenotypes of squirrel monkeys,

the Roman Arch and the Gothic Arch population, named after characteristics of their supraorbital color pattern, show differences in the structure of their isolation calls (Winter, 1969). The unique call structure of each population was present in infants from the first day of their lives (Lieblich, Symmes, Newman, and Shapiro, 1980). Given the normal vocal development of both deafened and isolated individuals, these differences are clearly not based on vocal learning. Furthermore, Struhsaker (1970), who investigated geographic variation in the call structure of vervet monkeys (*Cercopithecus aethiops*) in various parts of Africa, could not find any differences between populations.

Marmosets and tamarins have been studied extensively, mainly by Snowdon and his colleagues. In the field, Hodun, Snowdon, and Soini (1981) measured four parameters of the long call of saddle-backed tamarins (*Saguinus fuscicollis*). They found differences in the long calls of different subspecies, with that of one individual having features both of its own subspecies, *S. f. nigrifrons*, and of an adjacent one, *S. f. illigeri*, suggesting that learning might be involved. To find out whether this animal could have been a hybrid between the two subspecies, the same four call parameters were measured from two known hybrids of these subspecies in captivity. The hybrids developed a long call with one of the sound frequency parameters being closest to that of a third subspecies, which they had been able to hear in the room where they were housed, while the other parameters resembled those of *nigrifrons*. The wild animal, on the other hand, resembled the *illigeri* subspecies in this frequency parameter and in its call duration. The data were not given in detail, and concern up to only 12 calls of each of the three different animals, so it is difficult to assess whether differences in long-call structure reflected vocal learning, genetic differences, or different motivational states during recording sessions.

Maeda and Masataka (1987) found variation in long calls of red-chested moustached tamarins (*Saguinus labiatus labiatus*), that had been caught at two sites 27 km apart. In a subsequent study, a third group, which was caught only 15 km from one of these sites, produced a third call variant (Masataka, 1988). Each particular variant of the call was used by animals living within 6 to 15 km of each of the original catching sites, while animals from further away used different variants. Masataka (1988) reported that there were no geographical barriers between sites where different call variants were found, but there are no data on whether interbreeding between these sites occurs. It is also possible that tamarins adjust their calls according to the habitat by using different forms that are already present in their repertoire or that the variations found belong to particular matriline. In either case learning need not be involved.

In a more recent study, Elowson and Snowdon (1994) showed that members of pygmy marmoset (*Cebuella pygmaea*) colonies modified the structure of their individually distinctive trill contact calls after being placed in a cage adjacent to another colony. The modifications did not result in converging or diverging call structure. This, again, could be evidence for learning, but introducing new animals, even if contact is only acoustic, might shift social relationships within and between colonies. Thus, the modification of calling behavior over time might not be due to learning but could be related to a change in the role or dominance structure of each colony. In this example it is not clear whether call variants that were found after the introduction of the other colony were in the call repertoire before. They simply could have occurred less often because of the different social status of the individual before the introduction.

Whether or not macaque food calls are learned has been the cause of some controversy. Field observations by Green (1975), in which he found differences between troops in Japanese macaques (*Macaca fuscata*), suggested that food calls might be learned. However, in all three locations studied by Green, extensive food provisioning might have conditioned monkeys to produce only a particular version of their food call from a range present in their repertoire before provisioning started. Subsequently, Masataka and Fujita (1989) carried out cross-fostering experiments between Japanese and rhesus monkeys (*Macaca mulatta*), and found that the young developed calls more typical of their foster species. However, their result was based on only three animals that might have been atypical (Snowdon, 1990). Owren, Dieter, Seyfarth, and Cheney (1992) failed to replicate Masataka and Fujita's result. They argue that the calls of adult females of the two species vary a great deal and that there was no significant difference between species in any of the measures used. Even though infants of both species differed significantly in several parameters, calls developed by the cross-fostered infants fell within the distribution range for normally raised members of their own species in most cases. Despite this, it seemed that cross-fostered Japanese macaques did become more similar to rhesus monkeys in several frequency measures after 2 years of age. Given the variability of calls within species and the overlap between them, this is not an easy system in which to test for vocal learning.

In training experiments it has been shown that rhesus monkeys can be conditioned to increase overall call duration and amplitude (Sutton, Larson, Taylor, and Lindeman, 1973). Therefore, primates seem to have control over these basic call parameters. However, as pointed out earlier, such shifts do not require any changes in the setting of the sound production organ, but only a longer or stronger expiration phase. In another report about these experiments, Larson, Sutton, Taylor, and Lindeman (1973)

described changes in the spectral components of the trained calls in the 5–8 kHz range. It is important to note that these changes were not a requirement of the conditioning procedure but occurred independently of the selective rewards used in the experimental setup. Therefore, they do not represent evidence for vocal learning in the frequency domain. Larson *et al.* argue that they reflect a decrease in stress over the period of the experiment. Hauser (1992) found differences in the “coo” social contact vocalization of rhesus monkeys between different matriline on Cayo Santiago. Again, it is not clear whether these are caused by learning, genetic predisposition, or differences in parental behavior that might affect the extent to which a particular call version in an animal’s repertoire is used. Hauser mentioned that some animals changed their coo calls after migrating into another group, but did not provide further details. As in other studies, such changes could also be the result of a change in usage of calls that were present in the animal’s repertoire before.

2. Gibbons

Among the primates, gibbons are undoubtedly the most elaborate singers. Both male and female sing, and they often do so in the form of coordinated duets in which the female, with her “great call,” may take the leading role. Gibbons are monogamous and territorial, and the song duets are assumed to function in territory maintenance and pair bonding. In playback experiments, Mitani (1985) showed that females do not approach singing males, but males and females react strongly toward new duets in or close to their territory. Despite their complexity and intricacy, gibbon songs are highly stereotyped with little geographic variation (Marshall and Marshall, 1976). The major role of experience in the development of gibbon vocalizations lies not in copying but in coordination between members of a pair. A newly introduced pair of siamangs (*Hylobates syndactylus*) completed their great call sequences on only 24% of occasions, the songs terminating because one or the other animal produced a call that was inappropriately placed or timed. However, in recordings made after they had been together for 18 weeks, some 79% of sequences were completed (Maples, Haraway, and Hutto, 1989). There is also evidence, some anecdotal (Marshall and Marshall, 1976) some better documented (Geissmann, 1983; Srikosamat, 1982), that females deprived of a male or with one that does not sing can produce the male contribution to the duet as well as their own.

When it comes to development in gibbons, there is no evidence that individuals copy from each other, but there is strong evidence for a genetic influence. This comes from hybrids in nature and in captivity. White-handed gibbons (*Hylobates lar*) and pileated gibbons (*H. pileatus*) hybridize in a contact zone in central Thailand. Brockelman and Schilling (1984) found

that daughters of mixed parentage develop great calls unlike those of their mothers, but intermediate between the two species. This occurs despite the fact that the calls develop during mutual singing sessions between mothers and daughters. A similar conclusion has been reached from studies of hybrids between the two species in captivity (Geissmann, 1984, 1987). Tenaza (1985) also found that the song of two young, a male and a female, from a cross between *H. lar* and *H. muelleri* included characteristics typical of their own sex in both species despite having heard those elements from only one of these, that of their own sex parent.

Although these hybrid studies appear to argue strongly against a role of learning in gibbon song development, Marler and Mitani (1988) press for caution. If, as has been suggested in birds, young animals are born with a species-specific template that constrains what they will learn, the template in a hybrid might not be well matched to the sounds it experiences, so that it fails to learn parental calls. Mitani (1987) also presented evidence that agile gibbons (*Hylobates agilis*) show geographic variation in their calls. The populations involved were on separate islands very distant from one another. Therefore, genetic differences could be responsible. Further studies focusing on possible dialects in the wild are needed to evaluate whether some learning could be involved in gibbon call development.

3. Great Apes

Of the great apes, the vocalizations of chimpanzees have been the most extensively studied (e.g., Marler and Tenaza, 1977). It was natural that those interested in whether apes could master language first turned to humans' closest relatives. Although subsequent efforts with various media, ranging from sign language to computer keyboards, met with considerable success, early attempts to "teach chimps to speak" were almost fruitless. Vicki, the common chimpanzee (*Pan troglodytes*) trained by Hayes (1951), eventually seemed to produce four English words after 7 years of language training. However, no data on the similarity of these sounds with actual words were presented. The bonobo (*P. paniscus*) called Kanzi, studied by Hopkins and Savage-Rumbaugh (1991), developed a variety of species-typical vocalizations but, despite extensive interactions with humans, only four calls not shared with control animals. However, the different rearing of Kanzi could have delayed the development of certain bonobo calls, so that these four sounds could have been left over from his call repertoire as an infant. Therefore, they do not represent evidence for vocal learning in bonobos either.

When it comes to imitation of conspecific sounds, there is little evidence. Mitani, Hasegawa, Gros-Louis, Marler, and Byrne (1992) describe differences in the pant hoot of chimps between two sites in Tanzania, Mahale

and Gombe. In a subsequent analysis, Mitani and Brandt (1994) demonstrated that population differences in these calls were largely encoded in only one parameter, namely frequency range. The differences seem, however, quite subtle, which may explain why there are no other reports of geographical variation in chimp sounds. Mitani *et al.* (1992) argue that these differences could result, not from copying, but from contextual learning stemming from the selective reinforcement within each population if an animal produces sounds that match the population norm. This would be what Marler (1991) called action-based learning, in which an individual produces only those sounds from its repertoire that have been selectively reinforced by social stimulation. In this case the difference in call structure between recording sites would have been caused by different preferences for certain call versions by each population. Alternatively, food provisioning by humans at both sites may have had a conditioning effect that resulted in the observed differences, if individual humans were more responsive to certain call variants. Again, this may have led the animals to use another call variant that was present in their repertoire before without vocal learning being involved.

Mitani and Brandt (1994) presented interesting evidence that male chimpanzees match the acoustic characteristics of each other's pant hoots when calling together. This was statistically significant for the one individual for which a sufficient sample size was available. Depending on its chorusing partner this animal changed the spectral structure of its calls to match those of the other caller. Further research is needed to investigate the flexibility of pant hoot matching and assess whether these changes are learned or a side effect of subtle differences in calling contexts.

E. OTHER MAMMALIAN ORDERS

A few studies of other mammalian orders have shown similar phenomena to those discussed for primates, although they have not so often been interpreted as evidence for vocal learning. Romand and Ehret (1984) studied the development of sound production in the domestic cat (*Felis catus*). To investigate the influence of auditory feedback, motivation, and ontogenetic changes in the vocal tract, they compared calls of normally raised, deafened, and isolated kittens. The three groups differed in certain call parameters but individual variability was great. The authors interpret these differences as resulting from the lack of auditory feedback in deafened kittens and from different motivational states in isolated ones. Call parameters of isolated individuals indicated a delayed development of the vocal apparatus and a higher stress level than in normally raised kittens. Romand and Ehret come to the conclusion that call development in cats "follows

a 'self-centered strategy' rather than an 'open and environmentally dependent' one" (Romand and Ehret, 1984, p. 648). Molliver (1963) successfully trained cats to increase the duration of their calls in an operant conditioning procedure. As discussed earlier, this does not require any changes in the setting of the sound production organ, but only a longer expiration phase. It is a demonstration of a limited form of vocal learning that has also been found in primates.

Slobodchikoff and Coast (1980) found geographic variation in various time parameters of alarm calls given by groups of Gunnison's prairie dogs (*Cynomys gunnisoni*) living 13 km apart. An alarm call in this species is a series of several barks. Groups differed in total call length, number of barks per call, duration of each bark, and the time intervals between barks in a series. Again, these parameters describe the timing and duration of a call but not its frequency structure. Pikas (*Ochotona princeps*) in the United States also show geographic variation in duration and in the fundamental frequency of their short calls (Somers, 1973; Conner, 1982). The two populations studied by Somers are geographically separated by the Colorado River. However, there is an overlap zone at the source of the river where he found individuals with calls intermediate between the two variants. Conner (1982) only found differences between widely separated populations. He argued that variations do not represent vocal dialects but are the result of independent evolutionary histories. As with other cases of geographic variation, further studies are needed to clarify the origin of these differences. Finally, a recent study on banner-tailed kangaroo rats (*Dipodomys spectabilis*) has shown that they adjust their footdrumming signatures to differ from new neighbors after they change their territory (Randall, 1995). This is an interesting case of plasticity in sound production, although it concerns signals that are not produced by the vocal apparatus and concerns only the timing of signals, so it is not strictly relevant to our purpose.

IV. FUNCTIONAL SIGNIFICANCE AND ORIGIN

In this section we will consider possible reasons why vocal learning evolved in mammals. In discussing this it is important to bear in mind two separate problems. First is the question of why vocal learning arose in the first place, the answer to which may be far back in time and within a different functional context to that in which it occurs today. Second is the more accessible question of why vocal learning persists in certain species. Similar hypotheses may be relevant to both contexts, so that a discussion

of all possible reasons for vocal learning may shed light on both its origin and its current advantages for a particular species.

We will consider each of the main hypotheses that have been put forward to account for vocal learning. Earlier discussions have been largely in relation to birds, as vocal learning in this group has been extensively studied. Before discussing the possible relevance of each hypothesis to mammals, we will make brief mention of how these hypotheses measure up to the bird evidence.

A. INTERSEXUAL SELECTION

In many animals male songs attract females. If a longer or more elaborate song is more effective in this respect, then sexual selection could result in the evolution of very complex displays. Different mechanisms could account for an increased response in the female. Complex auditory input might lead to greater stimulation of the reproductive system of a female or it might simply prevent habituation by females. From a functional perspective, song complexity might be a cue used by females to assess male fitness, if it is costly for males to achieve complexity. Whatever its causal and functional basis, however, if complexity is advantageous, vocal learning may be favored as a means of achieving it. The copying of song elements from conspecifics allows an animal to incorporate new elements into its song, while still retaining the species-specific pattern. The development of completely new sounds without such copying would risk the loss of species recognition. Furthermore, the generation of vocal complexity through an increase in genetic information would undoubtedly be a slow and costly process. Thus, vocal learning could well have been favored as a means of acquiring an elaborate song.

Many songbirds have complex song repertoires built up by learning, and sexual selection has frequently been proposed as a reason for this complexity. In line with this suggestion there is evidence that female birds of various species solicit more to repertoires of songs than to single song types (e.g., red-winged blackbird, *Agelaius phoeniceus*, Searcy, 1988; starling, *Sturnus vulgaris*, Eens, Pinxten, and Verheyen, 1991), and that the reproductive system of female canaries (*Serinus canaria*) may be more stimulated by complex than by simple songs (Kroodsma, 1976). In the field, male sedge warblers (*Acrocephalus schoenobaenus*) with large syllable repertoires have been found to attract females earlier than those with smaller ones (Catchpole, 1980). Thus, several lines of evidence point to the importance of sexual selection in the generation of complex song repertoires in birds.

Turning to mammals, we know little about the functions of many male vocal displays. In phocids they are often highly varied, and several observations suggest that some of them may be sexual displays. During the mating season male harbor seals produce repetitive vocal displays underwater for up to several hours (Hanggi and Schusterman 1994; Van Parijs, Thompson, Tollit, and MacKay, in press). Male Weddell seals defend small underwater territories against other males; they sing on these territories and stop doing so if a female enters the territory to mate (Bartsh, Johnston, and Siniff, 1992). A large part of the species' repertoire is produced only by males (Thomas and Kuechle, 1982). Bearded seals and leopard seals, the vocalizations of which vary geographically, also produce underwater songs in the breeding season (Ray, Watkins, and Burns, 1969; Stirling and Siniff, 1979). Further studies of these and other "singing" seals, like the crabeater seal (*Lobodon carcinophagus*) (Stirling and Siniff, 1979), the Ross seal (*Ommatophoca rossi*) (Watkins and Ray, 1985), and the walrus (*Odobenus rosmarus*) (Stirling, Calvert, and Spencer, 1987), should clarify the role of vocal learning in the acquisition of song.

Behavioral observations of humpback whales, and the fact that it seems to be only males that sing (Tyack and Whitehead, 1983) and then mainly during the breeding season, suggest that song is a reproductive advertisement display and/or a territorial one. However, even though humpback whale and bowhead whale songs are very complex and change over the singing season, all males in a population sing the same song at any particular time. We can only speculate on the origin of this phenomenon but, if songs are used to attract females, sexual selection holds a possible explanation. If a maximal response in the female was elicited by presenting the same acoustic pattern repetitively, the singing behavior of humpback whales could represent a communal vocal display that increases the responsiveness of females. The synchronized changes in song over time combined with song complexity could then be a result of conflicting pressures on individual males to make their own song more attractive by introducing new variations, but to maintain a communal display at the same time. Although whales are not easy to study, there is a clear need for more information about how their songs relate to other aspects of their behavior if we are to understand their functional significance.

Other baleen whales that produce their sounds in repetitive songlike sequences are fin whales (*Balaenoptera physalus*) (Watkins, Tyack, Moore, and Bird, 1987) and blue whales (*Balaenoptera musculus*) (Cummings and Thompson, 1971). However, mysticetes also produce a variety of other social sounds. Repetitive sequences of the same sound could also be used to coordinate group movements. Since low-frequency sounds of whales can travel long distances (e.g., Cummings and Thompson, 1971), it is hard to

determine whether widely spaced animals belong to one social group or are solitary individuals that happen to be within hearing range.

The calls of some bats, like the hammer-headed bat (*Hypsignathus monstrosus*) (Bradbury, 1977) and the African false vampire bat (*Cardioderma cor*) (McWilliam, 1987), are used to attract females or act in territorial defense. Studies of whether and to what extent these species learn their calls would be interesting given the small amount of information on vocal learning in bats.

B. INTRASEXUAL SELECTION AND RESOURCE DEFENSE

Vocal learning could also have evolved in relation to territory maintenance and defense. In birds, small song repertoires are often used in matched countersinging between neighboring males on their territories, and the precise matching of songs that learning allows may confer a reproductive advantage. Payne, Payne, and Doehlert (1988) showed that male indigo buntings (*Passerina cyanea*) that share songs with neighbors do better in various measures of reproduction, including fledging more young. Song learning might enable birds to mimic established and successful individuals (Payne, 1981). This could discourage intruders and result in improved intruder detection if shared songs cannot be reproduced by foreign birds (see also Section IV,D on group recognition). Furthermore, the development of varied song repertoires, which seems to depend on learning, as they have been recorded only in species where vocal learning occurs, can also have a deterrent effect as far as intruders looking for territories are concerned. This has been shown most clearly in the speaker replacement experiments carried out by Krebs, Ashcroft, and Webber (1978) on great tits (*Parus major*). Krebs (1976) argued that this might be because repertoires give the impression that there are several birds present rather than just one. If repertoire size is a measure of fitness, it could also be used to assess a male's fighting ability in territorial conflicts.

In animals that defend territories it is often unclear whether females choose a particular male because of his vocal display or because of territory quality. In contrast to many terrestrial animals, underwater territories of marine mammals do not hold useful resources for the raising of offspring. The mating system of most singing marine mammals resembles more that of a lek. Therefore, if singing territories are positioned on the migration routes of females, the choice of a territory might have a considerable influence on breeding success. In that case vocal learning might have evolved through intrasexual selection. In marine mammals, there is some evidence that song might be used in male spacing on the breeding grounds. Weddell seals defend small underwater territories next to female haul-out

sites while they are singing (Watkins and Schevill, 1968; Bartsh *et al.*, 1992). Distances between singing humpback whales are about 2.4 times bigger than between nonsinging whales, suggesting a spacing function of song (Frankel, Clark, Herman, and Gabriele, 1995).

No evidence for vocal learning has been found in mammals that defend females or resource-based territories against other males. Examples are elephant seals and gibbons. Elephant seals defend breeding territories around their harems on land and produce threat vocalizations to defend these territories against other males (Le Boeuf and Peterson, 1969b). In gibbons song is thought to function in territory maintenance and pair bonding but not in mate attraction (Mitani, 1985, 1988).

In social groups vocal learning could be used in a variety of ways to gain access to resources. In highly social animals the ability to match sound features of other individuals might help to establish and maintain social relationships, or even raise the possibility of deception through the mimicry of sounds made by dominant animals. In bottlenose dolphins the formation of alliances between males has been observed (Connor, Smolker, and Richards, 1992). Imitation of their signature whistles could be used to maintain social bonds or deceive other individuals alike. In primates increasing sociality and the formation of complex social relationships could provide reasons for vocal learning to arise. Chimpanzees are known to form alliances against other group members (Harcourt, 1988) and the behavior of monkeys in social interactions sometimes involves what appears to be deception (reviewed in Cheney and Seyfarth, 1990). However, they do not seem to be capable of vocal learning. There are two possible explanations for this difference between primates and cetaceans. It could mean that vocal learning did not evolve because of advantages in social interactions. Alternatively, it may be because primates use other modes of communication (e.g., facial/gestural displays) to achieve similar results. Poor underwater visibility and the limited ability to use gestures and facial expressions in cetaceans could have favored the use of vocal communication more than in primates.

C. INDIVIDUAL RECOGNITION

Nottebohm (1972), in a classic paper on the origins of vocal learning, argued against individual recognition being an important factor in the evolution of vocal learning in birds. Learning, as he points out, often leads to precise similarities between animals, and these would hinder rather than aid individual recognition. Furthermore, slight individual differences in the morphology of the sound production apparatus within a population, if consistent over time, usually introduce enough variability in unlearned sounds to allow individual recognition (Beer, 1969). Individual recognition

on the basis of simple unlearned calls has been demonstrated to occur in many bird species, such as auks (Tschanz, 1968) and gulls (Beer, 1969), in which vocal learning is unknown. However, set against these arguments, there are ways in which vocal learning may enhance differences between individuals and, especially in high-background-noise environments, this may be important as an aid to discrimination. Even though birds learn their songs from conspecifics, they frequently learn different songs from different individuals so that their repertoires differ. New elements may also appear in their songs as a result of copying errors, or a bird may combine elements from different songs to form a new song (Slater and Ince, 1979). Thus, learning can lead both to new repertoires and to new songs within a bird's repertoire, so that it is not correct to assume that learning necessarily leads to greater call similarity between individuals. Indeed, one route to individually specific calls may be by combining features learned from several other animals.

All groups of mammals that show evidence for vocal learning do live in high-background-noise environments. Bat roosts, in which thousands of animals vocalize in the same frequency range, are one example, sea mammals provide another (Spiesberger and Fristrup, 1990). Additionally, in diving animals air-filled cavities that are involved in sound production get distorted with changing pressure. This could change voice characteristics considerably and mask individually specific cues that could otherwise be used for individual recognition (Tyack, 1991). If individual recognition requires more variability in calls than arises from differences in vocal tract morphology, or if such cues become unreliable during diving, improvisation rather than vocal learning might provide the answer. But there are theoretical reasons for thinking that this way of producing a completely new behavior pattern is a very difficult task. Every pattern that is generated reflects in some way the mechanism by which it is produced. For this reason, computer programs can create only pseudo-random numbers (Morgan, 1984). Even though some birds seem to produce completely new songs in their ontogeny (Marler, Mundinger, Waser, and Lutjen, 1972), improvisation has rarely been reported, suggesting that composing a new sound out of parts of others is an easier way to produce a unique individually specific call. It also ensures that the new call is not accidentally similar to that of other group members. Vocal learning may thus lead to individual distinctiveness by allowing the individual to produce a distinctive new call type that has not been present in the repertoire of its social group before. Examples of mammals that seem to make their signals different from those of other group members are dolphins (Caldwell and Caldwell, 1965, 1968), big brown bats (Rasmuson and Barclay, 1992) and banner-tailed kangaroo rats (Randall, 1995). However, if individual recognition is why vocal learn-

ing evolved, it must be supposed that there are benefits to the individual in allowing itself to be identified.

Investigations of vocal learning in bats have concentrated on call similarities between mothers and pups. All species mentioned in Section III,A are colonial. Mothers leave the roost every night to feed and have to find their offspring on return. Here, the gain in being identified is clear because the offspring will die if not fed frequently. Interestingly, infant greater horseshoe bats of 5 to 7 weeks of age that are still suckled do not have specific isolation calls (Matsumura, 1979), but show learned modifications in their echolocation calls. Perhaps their ability to match the main frequency of the mother's echolocation call is sufficient for mother-pup recognition so that specific isolation calls are not needed. The need for effective individual recognition does seem to be the most likely reason why vocal learning has evolved in these bats. However, more studies, especially on species that do not breed in big roosts, are needed to assess whether this is the only possible explanation.

Information on functions of odontocete sounds is still scarce, but the evidence we have points toward their use in individual recognition and group cohesion. These animals use most of their calls in social interactions, and have never been observed to show singing behavior like that of mysticetes. Even though evidence for vocal learning has been found in every cetacean that has been examined, mysticetes and odontocetes have very different social systems. While mysticetes seem to live alone most of the time, odontocetes live in relatively stable social groups (Tyack, 1986a). Bottlenose dolphins have a large repertoire of whistles, but most of those produced by an isolated individual are of a particular form more or less peculiar to itself and thus termed its "signature whistle" (Caldwell and Caldwell, 1965, 1968; Caldwell, Caldwell, and Tyack, 1990). These signature whistles can remain stable for at least 12 years (Sayigh, Tyack, Wells, and Scott, 1990). This stability of signature whistles and their frequent production by isolated individuals supports the idea that they have a role in individual recognition. Tyack (1986b) found that 77% of all whistles of two interacting dolphins fell into two categories. One whistle was largely produced by one animal and the second mainly by the other. Tyack suggested that these were the signature whistles of the two animals, and that the fact that both individuals could produce both whistles may represent mimicry.

Bottlenose dolphins have been shown to hunt cooperatively (Hoese, 1971) and support each other if injured (Lilly, 1963). In these situations it is certainly of advantage to a vocalizing animal to be individually identified by its allies. In a playback experiment Sayigh (1992) showed that mother bottlenose dolphins were also more likely to turn toward the signature

whistles of their independent offspring (and vice versa) than toward those of other dolphins. Smolker, Mann, and Smuts (1993) presented evidence for use of signature whistles in mother-calf reunions. Individually specific signals are very common in odontocetes (e.g., *Delphinus delphis*, Caldwell and Caldwell, 1968; *Lagenorhynchus obliquidens*, Caldwell and Caldwell, 1971; *Physeter macrocephalus*, Watkins and Schevill, 1977; *Stenella plagiodon*, Caldwell, Caldwell, and Miller, 1973) and add to the evidence that vocal learning might have evolved in this group because of benefits it brought to individual recognition and group cohesion.

D. FAMILIAL OR GROUP RECOGNITION

In familial or group recognition we encounter the same problem as in individual recognition. There must be some benefit to each individual to be recognized by its group or family members for vocal learning to evolve. Possible reasons are avoidance of inbreeding, cooperation between group members, or the identification and exclusion of strangers. All these arguments have been put forward for birds. Inbreeding avoidance is unlikely to be important, as male birds do not often sing the same songs as their fathers, as would be necessary if females were to use song as a cue. In Darwin's finches (*Geospiza* spp.), which include some of the small number of species where fathers and sons are known to sing the same songs, females have been found to mate randomly in relation to song type (Millington and Price, 1985). Group recognition is perhaps more likely as birds usually respond more aggressively to alien songs than to those of neighbors, and, in colonies and in groups of territories, sharing of vocalizations through learning is common. This led Feeles (1977, 1982) to put forward the idea that shared songs might act as a "password" in the colonies of caciques (*Cacicus cela*) that she studied.

It is striking that most odontocetes show individually specific calls, while killer whales have group-specific ones. The social organization of killer whales, with their stable family groups, is very different from that of bottle-nose dolphins. Most dolphins live in fission-fusion societies with few stable associations between individuals (reviewed in Norris and Dohl, 1980). Killer whales tend to stay in their parental group throughout their lives (Bigg *et al.*, 1990). They hunt cooperatively on a variety of different prey, ranging from herring to other marine mammals (Smith, Siniff, Reichle, and Stone, 1981; Similä and Urgate, 1993), and food sharing within pods has been observed (Hoelzel, 1991). Here, family-specific calls could help to avoid inbreeding or be used to maintain social bonds between group members and to exclude foreign individuals.

As with individual recognition, vocal learning could have been a good solution for marine mammals to the problems imposed on group recognition calls by the environment. High background noise could easily mask the subtle effect of differences in vocal tract morphology between different matriline, making them useless for group recognition. Learning would allow animals to produce completely new sounds that are different enough to be recognized even in noisy conditions. The production of new, very distinctive sounds could also compensate for changing voice characteristics caused by the effects of water pressure on the air-filled vocal tract at different diving depths.

In the more fluid social system of bottlenose dolphins, individual recognition to maintain social relationships is likely to be more important. These animals associate in temporary groups of variable size and composition. However, certain long-term associations have been discovered between related females (Wells, Scott, and Irvine, 1987). Small subgroups of two to three males also form relatively stable alliances (Connor *et al.*, 1992; Smolker, Richards, Connor, and Pepper, 1992). Vocal learning could be of advantage in alliance formation and maintenance in this species. Males have been shown to cooperate with other males in aggressive interactions and in herding of females (Connor *et al.*, 1992). Male alliances could use signature whistle mimicry or learned alliance specific calls to maintain their bonding and exclude strangers.

Off Sarasota, Florida, approximately half the male bottlenose dolphins develop signature whistles that are very similar to those of their mother, while most females produce signature whistles highly distinct from those of their mothers (Sayigh *et al.*, 1990; Sayigh, Tyack, Wells, Scott, and Irvine, 1995). It seems unlikely that only males develop family-specific calls as a kinship label that facilitates inbreeding avoidance because, while females tend to associate in matriline later in life, males do not associate closely with their female relatives, though remaining in the same general area. Females may need to develop a signature whistle as different as possible from their mother's to avoid misidentification. The higher degree of similarity of signature whistles between mothers and sons could stem from the lack of this requirement or it could benefit males if matriline affects dominance in dolphin societies. There is some evidence that it is the sons of only certain females that produce signature whistles like those of their mothers (Sayigh *et al.*, 1995), but further investigation is needed.

E. POPULATION IDENTITY

The development of dialects between neighboring populations of potentially interbreeding individuals could lead to assortative mating; this in turn

might benefit individuals if there are local genetic adaptations that can thereby persist. Nottebohm (e.g., 1972) suggested that dialects that are common in birds might have this effect. Although the idea has received some subsequent support, particularly in the white-crowned sparrow (*Zonotrichia leucophrys*, Baker and Cunningham, 1985), the weight of evidence is against it. For example, white-crown dialect boundaries do not seem to limit dispersal, song learning in males may occur after dispersal, and females often mate with males singing a different dialect from their natal one (see Catchpole and Slater, 1995, pp. 205–209 for a more detailed discussion). Even though this idea is now generally discounted in birds, it could still be true for marine mammals and bats that possess a similar potential for quick dispersal. If these animals return to their home area to mate, dialects might help to maintain local adaptations. Even in the relatively homogeneous marine environment, differences in local adaptations could exist between coastal and pelagic populations or between areas with different prey species.

In many of the examples of geographic variation in mammal calls the actual extent of each population is unknown. Even though some of the locations where seals have been found to differ in their vocalizations are several thousand kilometers apart, these species are mobile as well as widely distributed and could easily cover such distances in their migrations. Humpback whale populations in different oceans on the other hand may well be truly isolated and their dialects are therefore unlikely to be adaptive in maintaining population identity. Variations in call structure of different primate populations have been interpreted as possible evidence for vocal learning by several authors. If call variations between neighboring populations are actually learned, a function in population recognition might be a reason. However, there is no clear evidence for learned differences yet.

F. INTENSE SPECIATION

Nottebohm (1972) discussed intense speciation as one possible factor in the development of vocal learning in birds. He argued that, with large numbers of species in small geographic areas, vocal learning might have evolved among passerine birds because of the need for rapid change in signals. Subsequently, it was suggested that vocal learning might itself have enhanced speciation in passerines, if learned signals acted to restrict gene flow. However, Baptista and Trail (1992) argue that there is little evidence that differences in bird vocal signals act as a barrier to interbreeding.

In mammals, vocal learning does not appear to correlate with rapid speciation, making either of these ideas unlikely to apply. Marine mammals could have gone through a phase of intense speciation when they returned

from land to sea. However, this seems unlikely to have put any pressure on the development of vocal learning for species recognition, as the available space for dispersal was so great and the habitat was relatively homogeneous.

G. HABITAT MATCHING

Different habitats can have very different sound transmission characteristics (Marten and Marler, 1977; Marten, Quine, and Marler, 1977; Wiley and Richards, 1978; Waser and Brown, 1986). If a species lives in various different habitats, or if the transmission characteristics of its habitat change frequently, vocal learning could help to optimize its vocal signals. This idea was originally put forward by Hansen (1979) for birds, many species of which disperse widely and live in a variety of habitats. Data in support of it have been obtained on two species: the great tit (*Parus major*, Hunter and Krebs, 1979) and the chingolo sparrow (*Zonotrichia capensis*, King, 1972; Nottebohm, 1975). Particularly detailed studies by Handford (1981, 1988; Handford and Loughheed, 1991) suggest that trill rates in this last species in agricultural areas match the habitat that was present before cultivation began, thus pointing to a very slow rate of change.

Studies on primates have shown that some species do have calls that are matched to the transmission qualities of their habitat (Brown, Gomez, and Waser, 1995). However, there is no clear evidence for vocal learning in primates. In marine mammals it is unlikely that vocal learning has evolved because of advantages in habitat matching because, compared to most terrestrial environments, the sea has very stable sound transmission characteristics (Spiesberger and Fristrup, 1990). In bats all evidence for vocal learning involves mother-pup interactions. However, it could be possible that vocal learning enables them to match their echolocation calls to particular habitats. Further studies are needed to investigate this possibility.

V. CONCLUSIONS

A. FLEXIBILITY IN VOCAL LEARNING

We have identified several different levels of complexity in vocal learning. The most simple, in which animals can be trained to alter the overall duration and amplitude of a sound, seems to be a relatively common feature of mammalian communication systems (e.g., bottlenose dolphin, Lilly, 1965; domestic cat, Molliver, 1963; rhesus monkey, Sutton *et al.*, 1973). It is likely that this form of sound alteration is closely linked to contextual learning

of sounds. If an animal has learned to withhold or produce a sound in different contexts, it has a certain degree of learned control over the onset and offset of calling. An alteration of temporal parameters, like intercall intervals in sound sequences, in relation to auditory experience would thus become possible. This control over the muscles of the respiratory system and their coordination with the vocal apparatus might also be sufficient for learning how to alter total amplitude and duration of single calls. A more elaborate form of this sort of learning might involve significant changes in voice-onset time in a call or complex amplitude modulations that superimpose additional frequency bands on a call. To our knowledge there are as yet no studies of the role of learning in modifying these parameters.

The second stage, in which an animal is able to learn how to alter certain frequency parameters to match another individual's calls, has been demonstrated only in greater horseshoe bats, marine mammals and humans. Here, the activity of muscles of the vocal apparatus itself needs to be modifiable by experience. This needs a different level of neural control and is a significant next step in the evolution of vocal learning. While there are other reasons why an animal might gain control over the respiratory system to make it modifiable by experience (e.g., contextual learning in relation to vocal communication, diving), the vocal apparatus is used only in call production. However, not many studies have looked at this relatively limited form of vocal learning yet. It may be more common than it seems at this point.

The ability to copy completely new sounds seems to be rare among mammals. Our review has shown that it is known to occur only in marine mammals and humans. However, we do not know whether the distinction between the ability to imitate new sounds and that to change only certain parameters in a limited way is a real one. More studies focusing on the extent to which calls are modifiable through vocal learning are needed. Bats, for example, might be capable of more drastic changes than the ones we know of so far.

B. FACTORS AFFECTING THE EVOLUTION OF VOCAL LEARNING: THE ROLE OF MOBILITY

Many bird species in three different orders (Passeriformes, Apodiformes, Psittaciformes) show vocal learning, suggesting that it evolved separately in each of these groups. In mammals it is known to occur in humans, cetaceans, phocid seals, and bats, taxa that do not share a unique common ancestor. Here, too, it seems vocal learning has evolved independently in each group. Given this lack of a direct phylogenetic connection, it is interesting to ask whether there is a common factor that could have caused a convergent evolution of vocal learning in these groups.

We have identified several possible reasons why vocal learning could have evolved in different mammalian groups. If we examine features that these groups have in common with each other and with birds, an obvious similarity is their high mobility. With the exception of humans, they all spend at least part of their lives swimming or flying in three-dimensional environments. The high mobility of animals living in air or water is a fundamental common factor that has influenced various different aspects of their lives. It is more difficult for males to monopolize females. Members of a social group are more likely to lose contact in three-dimensional space. Vocal signals are likely to be used more because animals can disperse more quickly and visual contact is difficult to maintain. The increased use of vocal communication instead of visual signals increases background noise in the acoustic frequency bands used for communication and adds pressure toward signal diversity. Thus, living in these environments could make the development of vocal learning in a species more likely. There are, of course, other mammals, like arboreal or nocturnal ones, that face similar problems to a lesser extent. However, the impact of such problems is certainly highest in flying and swimming animals, as they disperse much more quickly and are not limited to moving only along solid structures in their environment, as are tree-living species, for example.

C. IMPLICATIONS FOR THE EVOLUTION OF HUMAN LANGUAGE

In primates, researchers have been looking for evidence of vocal learning for a long time. Even though they clearly have considerable control over their vocal utterances, including the duration and amplitude of their calls, vocal learning has not been unequivocally established in primates other than humans. The fact that dolphins, seals, and many birds spontaneously start to imitate sounds from their acoustic environment in captivity suggests that imitation plays an important role in their lives. Such imitation of new sounds has never been observed in nonhuman primates.

It seems strange that our closest relatives show no evidence for vocal imitation, yet humans are so adept at it. The suggested environment of early humans does not seem to have been strikingly different from those of other primates. Thus, all the possible advantages of vocal learning mentioned in Section IV would have been present for other primates, too. Why then did the ability to imitate sounds evolve in humans and not in nonhuman primates? Jakobson (1941) claimed that all the sounds of the world's languages occur in infant vocalizations, suggesting that the learning of new sounds is not involved in language acquisition. However, today most researchers accept that humans are capable of vocal learning. More recent discussions on natural predisposition for language learning have concen-

trated on the acquisition of language as a communication system (Bickerton, 1990; Pinker and Bloom, 1990), not on whether vocal learning is involved in the acquisition of the sound repertoire. A convincing explanation for the difference between nonhuman and human primates relates to the evolution of language. It might seem difficult to imagine how imitating sounds could have been of any advantage to the first individual that did so. This is certainly true if we assume that the evolution of language relied on vocal learning. However, several authors have argued that language developed in gestures before it affected vocal behavior (Hewes, 1973; Parker and Gibson, 1979). Once a gestural communication system with learned signals had become established, vocal learning would have been greatly favored because it makes it possible to use language even where visual contact is absent. If this sequence of events is correct, the lack of evidence for vocal learning in nonhuman primates would not be so surprising. However, more research, especially on the possibility of a more limited form of vocal learning in nonhuman primates, is needed.

D. FUTURE RESEARCH

We have suggested that sexual selection, defense of resources, and individual recognition are the most likely reasons why vocal learning evolved in mammals, assuming that its functional significance has not changed since then. However, further studies are needed to find out how flexible the vocal system of each group is and what they are using this flexibility for. The body of evidence for vocal learning in mammals is still very small compared with that in birds. In many very vocal mammals, such as elephants, vocal learning has not been studied at all. We have already mentioned various other species that would be very interesting to study in this context.

The most powerful experimental approaches to the study of vocal learning are certainly conditioning experiments and studying the effects of keeping experimental animals in controlled acoustic environments. If an animal can be trained to imitate a new sound that has not been in its repertoire before or if infants that have been exposed to different stimuli match what they have been hearing in detail, we have found unequivocal evidence for vocal learning. As our survey has shown, many authors interpret less convincing results as evidence for vocal learning. Geographic variation, differences in vocalizations between different matrilineages or between normally raised and isolated individuals, changes in the vocal repertoire during ontogeny, and changes in vocal behavior after being housed with new individuals have all been interpreted as indicating vocal learning. All these examples could involve vocal learning, but they do not represent unequivocal

cal evidence for it. However, they give valuable information on species that could be interesting subjects in which to investigate its existence.

Recent investigations of primate communication systems have revealed a greater flexibility than previously thought. Elowson and Snowdon (1994), for example, found significant alterations in call parameters of pygmy marmosets in relation to changes in their social environment. Because individuals did not match conspecifics in this study, trying to show that vocal learning was responsible would be difficult, but it deserves further investigation. In chimpanzees, in which individuals seem to match the pant hoots of their chorusing partners (Mitani and Brandt, 1994), this might be easier. Cross-fostering experiments within this species might be able to give clearer results on whether a limited form of vocal learning exists in nonhuman primates. Concurrent investigations of gestural communication in wild great apes could give information on what role learned gestures play in their natural communication system. Such studies could indicate how likely it is that gestural or vocal communication was the basis for language evolution.

Even in those groups where evidence for vocal learning has been presented, information on its significance and flexibility is often lacking. The evidence in bats, for example, is still sparse, though it seems clear that their learning is not as versatile as that in marine mammals. Training bats with different stimuli would help to find out to what extent learning can influence the development of their communication and echolocation calls. More experiments on vocal learning in those marine mammals that show singing behavior are also needed. We still do not know how widespread vocal learning is in these groups and how they learn their songs. In seals, phocids seem to be capable of vocal learning, but there is no evidence for it in otariids. This could simply reflect a lack of studies, but there are also marked differences in the mating strategies of otariids and phocids that could explain the apparent discrepancy. Apart from the elephant seal, all the phocids that show geographic variation in their vocalizations breed at least partly on ice and copulate in the water (Stirling, 1975). This makes it difficult for a male to monopolize several females: they are either scattered on available haul-out sites or else in the water where there is poor visibility combined with increased mobility in all directions. Otariids, on the other hand, breed on land and males often defend harems against other males. The fact that singing behavior has so far been found only in phocids suggests that vocal learning may have evolved in relation to their mating strategy. However, the only clear evidence for vocal learning in seals comes from a harbor seal that imitated human speech spontaneously. There are as yet no further studies of vocal learning in seals, and there is a clear need for them.

Comparative studies of how background noise influences call development and usage might also shed light on the origin of vocal learning. While

odontocetes seem to use vocal learning to improve individual recognition, mysticetes apparently use it only in their singing behavior. We do not know whether vocal learning evolved once or twice in the lineage of cetaceans. Studies on how sexual selection on one hand and individual recognition on the other influence vocal behavior are needed to clarify how vocal learning evolved and persisted in these animals.

Further studies on the vocal communication systems of toothed whales would be especially valuable. Even though individual recognition seems to be a likely reason for vocal learning to have evolved in dolphins, vocal learning could be used extensively in their complex social systems, including the possibility to use it in vocal deception. A study of how dolphins use imitation in the wild might open up a new perspective on why their vocal learning evolved. Given that its function might have changed in a particular species, and that dolphins show remarkable cognitive capacities (review in Herman, Pack, and Morrel-Samuels, 1993), including the ability to process syntactical information in signal sequences (Herman, Richards, and Wolz, 1984), it is likely that, once evolved, vocal learning had profound effects on various aspects of their natural communication.

VI. SUMMARY

Vocal learning, as we discuss it in this review, refers to instances where vocalizations are modified in form as a result of experience with those of other individuals. While many birds are capable of vocal learning, unequivocal evidence for it is rare in mammals. The most versatile mammalian vocal learners are cetaceans, harbor seals, and humans, all of which are able to imitate new sounds. Greater horseshoe bats learn the main frequency of their echolocation calls from their mothers and are the only other mammals shown so far to be capable of learning to change frequency parameters in their calls. Nonhuman primates have been conditioned to alter the duration and amplitude of their calls but not their frequency parameters. We suggest that sexual selection, defense of resources, and individual recognition are the most likely reasons why vocal learning has evolved in mammals. However, we know little about the functional significance of vocal learning for these animals and more studies are badly needed.

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