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Joint Program in Oceanography/ Applied Ocean Science and Engineering

DOCTORAL DISSERTATION

Development and Functions of Signature Whistles of Free-Ranging Bottlenose Dolphins, *Tursiops truncatus*

by

Laela Suad Sayigh

September 1992

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Cambridge, Massachusetts 02139

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DEVELOPMENT AND FUNCTIONS OF SIGNATURE WHISTLES OF FREE-RANGING BOTTLENOSE DOLPHINS, *TURSIOPS TRUNCATUS*

by

Laela Suad Sayigh

B.A., University of Pennsylvania
(1985)

Submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

at the

MASSACHUSETTS INSTITUTE OF TECHNOLOGY

and the

WOODS HOLE OCEANOGRAPHIC INSTITUTION

September 1992

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For A. B. S., and the memory of A. A. R. S.

DEVELOPMENT AND FUNCTIONS OF SIGNATURE WHISTLES OF FREE-RANGING BOTTLENOSE DOLPHINS, *TURSIOPS TRUNCATUS*

by

Laela Suad Sayigh

Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the Massachusetts Institute of Technology and the Woods Hole Oceanographic Institution.

ABSTRACT

This thesis presents data on the development and functions of individually distinctive signature whistles of free-ranging bottlenose dolphins, *Tursiops truncatus*. Research was conducted at a study site near Sarasota, Florida, where a resident community of bottlenose dolphins have been the focus of a long-term, ongoing study. Through observations and censuses, researchers have gained information on home ranges and association patterns among individuals. A temporary capture and release program has provided opportunities to collect basic information regarding age, sex, genetic relationships, and life history of individuals, as well as to record vocalizations of known individuals. During the periods 1975-1976 and 1984-1992, 134 different individuals were recorded during temporary capture. More than half of these were recorded on two or more (up to 10) different occasions. These recordings demonstrate that free-ranging dolphins produce individually distinctive signature whistles, as was previously documented for captive dolphins. Each dolphin produced a distinctive frequency contour, or pattern of frequency changes over time, and this whistle comprised a large portion of all whistles produced. Comparisons of whistles recorded from the same individuals over periods of more than a decade indicate that these signature whistle contours are markedly stable. This extensive database of recordings of signature whistles produced by known individuals formed the basis for much of the work described in this thesis.

Playback experiments conducted during temporary capture-release projects indicated that free-ranging dolphins were able to discriminate among signature whistles of familiar individuals. When these results are taken in the context of what is known about dolphin societies, which are characterized by stable individual associations intermixed with fluid patterns of association among many individuals, it appears highly likely that dolphins use signature whistles to recognize one another as individuals.

Sex differences in whistle production were documented through analysis of whistles recorded during temporary capture. Naive judges rated the similarity of signature whistle contours of 42 Sarasota calves and their mothers, and found that males were more likely than females to produce signature whistle contours highly similar to those of their mothers. Conversely, females were more likely than males to produce contours highly distinct from those of their mothers. In addition, preliminary results indicated that male calves were more likely than female calves to produce whistles other than the signature whistle (called "variant" whistles). It was hypothesized that these sex differences may relate to the different roles males and females play in the social structure of the community.

Comparisons of whistle contours of parents and offspring, both in the wild (Sarasota) and in captivity (Miami Seaquarium), do not indicate that signature whistle structure is strictly inherited. Instead, it appears that learning plays a role in determining whistle structure. This contrasts with other non-human mammalian species, where learning does not appear to be involved in vocal development. Focal observations and acoustic recordings of four free-ranging Sarasota mother-calf pairs were conducted in order to examine the effects of the early social and auditory environment on signature whistle development. Although there was considerable individual variability among these four calves, this study provided some preliminary insights into factors affecting the time course and outcome of signature whistle development in the wild. Two calves which exhibited relatively rapid whistle development and produced contours that resembled those of their mothers also heard proportionately more of their mothers' signature contours than did the other two calves. The other two calves exhibited more prolonged whistle development and produced contours that did not resemble those of their mothers. Preliminary data indicated that these two mothers may have actively taught their calves to produce a distinctive whistle contour by producing "model" contours while their calves were very young. Strength of the mother-calf association, number of associates other than the mother, overall number of whistles heard, and number of whistles produced by the mother all may affect the time course of whistle development and whether or not a calf develops a contour similar to that of its mother.

Thesis supervisor: Peter Lloyd Tyack, Associate Scientist

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I will always remember fondly about my years in Woods Hole. More recently, Kathleen Ledyard has become a close and valued friend. I know I will not lost touch with any of them. My mother, sisters Sophia and Sara, brother Allen, brothers-in-law Rick and Mark, and cousin Carol have all provided support, love and friendship which I could not imagine being without. My nephews and niece have shown me that there is a life to look forward to after graduate school!

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CHAPTER 1: INTRODUCTION

Bottlenose dolphins, *Tursiops truncatus*, are among the best-studied species of delphinids. Most of the available information on dolphin communication has been derived from studies of this species. The sounds produced by *Tursiops* have been divided into three main categories (Herman and Tavolga 1980, Popper 1980): broadband clicks used in echolocation, narrow band whistles, and a diverse, mostly undescribed category called burst-pulse sounds. There is an extensive literature on the extremely precise echolocation abilities of these animals; they "can resolve differences in size, distance or texture of very similar targets" (Popper 1980, p. 43). Whistles and many burst-pulse sounds appear to be communicative in nature. There is a wide variety of types of burst pulse sounds; these promise to provide a rich resource for further research. Because of their greater tractability, whistles have been the focus of most research on dolphin communication to date. Several researchers in the 1960's presumed that whistles were context specific, with different whistle contours, or patterns of frequency versus time, having different meanings, like words (e.g., Dreher 1966, Dreher and Evans 1964, Lilly 1963). Convinced that the large brain of *Tursiops* signified the potential for complex linguistic abilities, John Lilly brought the study of dolphin communication into the realm of the sensational. He published many books (e.g. Lilly 1961, 1967, 1975), and widely popularized the notion that dolphins possess a language, and that they could perhaps learn to communicate with humans.

1.1 Signature whistles

The research of David and Melba Caldwell began to paint a different picture of the functions of dolphin whistles, however. Working with captive dolphins that had been isolated for various reasons, the Caldwells found that each dolphin produced an individually distinctive whistle, called a signature whistle, which accounted for over 90% of its vocalizations (Caldwell and Caldwell 1965, Caldwell et al. 1990). They found similar results for three other species of delphinids: common dolphins (*Delphinus delphis*; Caldwell and Caldwell 1968), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*; Caldwell and Caldwell 1970), and spotted dolphins (*Stenella plagiodon*; Caldwell et al. 1973). The Caldwells' work represented the first attempt to overcome the greatest obstacle in studying dolphin communication: identifying which individual is producing a sound. Earlier researchers put hydrophones near groups of wild or captive dolphins, and, upon hearing a wide variety of whistle contours, assumed that these represented some sort of language. Only through recording isolated animals were the Caldwells able to confirm the presence of individually distinctive whistle contours.

Since the Caldwell's pioneering study in 1965, surprisingly little research on signature whistles has been done. In fact, work on dolphin communication has lagged considerably behind studies of communication in many terrestrial animals, such as birds (e.g., Kroodsma and Miller 1982) and primates (e.g., Snowdon 1990).

However, several studies of captive dolphins (mostly bottlenose, because they adapt better to captivity than many other delphinid species) have begun to provide insights into how whistles may function in the communication system of these animals. Caldwell and Caldwell (1972) reported spontaneous mimicry of a man-made sound in a long-term captive isolate. Other researchers (Penner, cited in Evans 1967, and Richards et al. 1984) trained dolphins to imitate sounds on command. Richards et al. (1984) also trained dolphins to associate arbitrary sounds with objects. This ability to associate arbitrarily a signal and a referent could function in natural situations to associate a signature whistle with a particular individual. Imitation of signature whistles has been demonstrated in captivity (Burdin et al. 1975, Gish 1979, Tyack 1986), and Tyack (1986) suggested that these imitations may function to label individuals in the social group (Tyack 1986). A new technique (called a "datalogger") to identify which individual in a captive group is producing a sound should permit new insights into the functions of signature whistles and vocal mimicry (Tyack and Recchia 1991).

1.2 Studies of free-ranging dolphins

Study of communication in free-ranging dolphins has recently become feasible due to an increase in available information about their behavior, social structure, and life history. Several long-term research programs (e.g., Connor and Smolker 1985, Connor et al. 1992a, 1992b, Shane 1990, Wells et al. 1980, 1987, Wells 1991, Würsig 1978, Würsig and Harris 1990) have found that different ecological conditions can result in variability in social structure and residence patterns, but that in general bottlenose dolphins live in "fission-fusion" type societies, wherein stable associations among individuals are intermixed with highly fluid patterns of association (Shane et al. 1986). This dynamic nature of bottlenose dolphin societies necessitates longitudinal studies; cross-sectional studies are likely to provide only a partial, if not an inaccurate, picture.

1.2.1 The Sarasota dolphin community

The work presented in this thesis is based almost entirely on data collected from a resident dolphin community of approximately 100 individuals in waters near Sarasota, Florida. This dolphin community has been the focus of a long-term study led by Randall Wells, Michael Scott, and Blair Irvine (Irvine and Wells 1972, Irvine et al. 1981, Scott et al. 1990, Wells 1986, 1991, Wells et al. 1980, 1987) which has involved numerous other collaborators. "The home range of the Sarasota community encompasses a 40-km stretch of coastline that includes a system of bays, protected by a series of barrier islands, and the waters of the Gulf of Mexico up to about 1 km offshore of the islands" (Scott et al. 1990, p. 237).

When the study began in 1970, the initial focus was to examine home-range patterns of free-ranging *Tursiops*, primarily for management purposes. Over the years, this research program has grown to include a wide variety of disciplines, including communication and behavior, life history, and population biology (Scott et al. 1990). Through extensive observations and censuses, researchers have gathered information on the social structure of the community and on patterns of association among specific individuals. Matrilineal relationships of many individuals are known, as are the birth date or season of birth of most calves (Wells 1986). Radio tracking of animals provided information on movement patterns and home range size (Irvine et al. 1981). The community structure of bottlenose dolphins near Sarasota has been defined by Wells (1986) using data on home range and patterns of association. These dolphins have well-defined home ranges. Individual dolphins from the same community have both much higher rates of interaction and much greater overlap in their home ranges than with dolphins from adjacent communities.

A temporary capture and release program has provided a wealth of information that could not otherwise be obtained. During the periods 1975-1976 and 1984-1992, dolphins were captured temporarily with a large net in shallow (< 2 m) water, generally once or twice per year. A commercial fishing boat deployed a 300 m X 4 m seine net in a circle around the dolphins, enclosing them in a net corral (Wells 1991). The dolphins were able to swim freely in the net corral and were then briefly isolated one or two at a time to be measured, sampled, marked, and then released. Procedures included weighing and measuring the dolphins, taking blood samples, removing a tooth for age determination (through analysis of tooth growth layers (Hohn et al. 1989)), and recording their vocalizations. This sampling yielded basic information regarding sex, age, genetic relationships among individuals, and life history.

Genetic analyses have begun to provide new insights into the social structure of the community. For example, so-called "bands" of closely associating females consist of individuals from several different matrilines that have been in close association for several generations (Duffield and Wells 1991, Wells 1991). Different female bands are loosely associated with particular home ranges, such as the "Palma Sola" and the "Anna Maria" female bands (which spend large amounts of time in Palma Sola Bay and Anna Maria Sound, respectively, (Wells et al. 1987, Wells 1991)). All members of a particular band are rarely sighted together at once, and patterns of association among different females vary over time from relatively stable to transient. One of the determinants of female association patterns appears to be reproductive condition, wherein females with similar-aged calves tend to associate together (Wells et al. 1987, Wells 1991).

After calves leave their mothers, generally between 3 and 6 years of age, they join subadult groups (Wells et al. 1987, Wells 1991). Upon reaching sexual maturity, females tend to return to their natal group. Adult males may be solitary, or they may form strong, long-term bonds with one or more other unrelated, similar-aged males (Wells et al. 1987, Wells 1991). These long-term male-male associations are stronger than any others with the exception of those between mothers and their young calves.

1.3 Introduction to thesis research

Similar long-term associations among individuals, some stable and some fluid, have been observed in a long-term study of free-ranging bottlenose dolphins in Shark Bay, Western Australia (Connor and Smolker 1985, Connor et al. 1992a, 1992b), and have encouraged comparisons with better-studied non-human primate species with similar fission-fusion societies (Booth 1989, Connor et al. 1992a, 1992b).[1] Many studies of primate behavior have revealed complex, individual-specific associations, which require knowledge of the nature and history of relationships among many individuals (e.g., Essock-Vitale and Seyfarth 1986, Dasser 1985, de Waal 1982). Such systems require learning and memory of one's own relationships with other individuals, as well as of the relationships of other individuals. Thus, communication systems in such societies must provide means to convey information regarding kinship and/or individual identity. The question of whether or not signature whistles are used for individual recognition in bottlenose dolphins was explored by means of playback experiments in Sarasota (Chapter 3).

Although vocal learning is critical to the development of human speech, there is a surprising lack of evidence for learning in non-human mammalian vocal development. Signature whistles of Sarasota mothers and offspring were compared to look for possible effects of learning, and a sex difference was discovered which is

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[1] Since many non-human primate species have been the focus of intensive behavioral research, such comparisons may provide insights into areas that are less well understood for dolphins. Future research with other taxonomic groups may provide additional, and perhaps even more useful, sources of comparison.

described in Chapter 4. In Chapter 5, further parent-offspring comparisons are presented, followed by data on effects of the early social and auditory environment on signature whistle development. The latter was explored by means of observations and recordings of undisturbed mother-calf pairs.

The extensive background information that is available for the Sarasota dolphin community was critical for every aspect of the work on signature whistles presented in this thesis. General data on signature whistles recorded during the temporary capture-release program are described in Chapter 2. Knowledge of the relationships among individuals was essential in order to effectively design and interpret the playback experiments described in Chapter 3. Whistles that had been recorded during capture-release projects were utilized as stimuli in these experiments, as were whistles used in parent-offspring comparisons (Chapters 4 and 5). Knowledge of the signature whistles of most individuals in the Sarasota community through recordings made during capture-release projects was crucial for interpreting recordings made of undisturbed animals (Chapter 5). Background information on age, sex, matrilineal relationships and association patterns of individuals in the Sarasota community greatly enhanced the potential for examining social and behavioral factors that might affect whistle development.

This thesis represents a preliminary effort at describing the functions of signature whistles, and factors affecting their development. Further studies of the Sarasota dolphin community and other free-ranging dolphin communities promise to increase significantly our current understanding of the natural communication system of these animals.

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CHAPTER 2: GENERAL BACKGROUND AND METHODS

2.1 INTRODUCTION

The Sarasota dolphin project (Scott et al. 1990, Wells 1991; described in Chapter 1) has provided the first opportunity to overcome the greatest difficulty in studying communication of free-ranging dolphins: identifying which individual is producing a sound. Most studies of free-ranging dolphins to date have been limited to describing categories of sounds produced in general behavioral contexts (e.g., Tyack 1976). In the Sarasota capture-release project , whistles of known individual dolphins have been recorded year after year. Since 1975, 134 individuals have been recorded (67 male, 67 female) from one to ten times each (Figure 2.1), for a total of 398 animal/year combinations. Since these recordings were integral to the results presented in each chapter of this thesis, background on the Sarasota whistle database will be presented in this chapter. Recording and analysis techniques will be described, followed by background data on signature whistle structure from this study and from the literature.

2.2 METHODS

2.2.1 Recording techniques

During capture-release projects in 1975-1976, animals were typically held in the water in a floating stretcher. Recordings of whistles were made in air by M. D. Scott and by Paul Graycar (see Graycar, 1976) with a microphone held near the

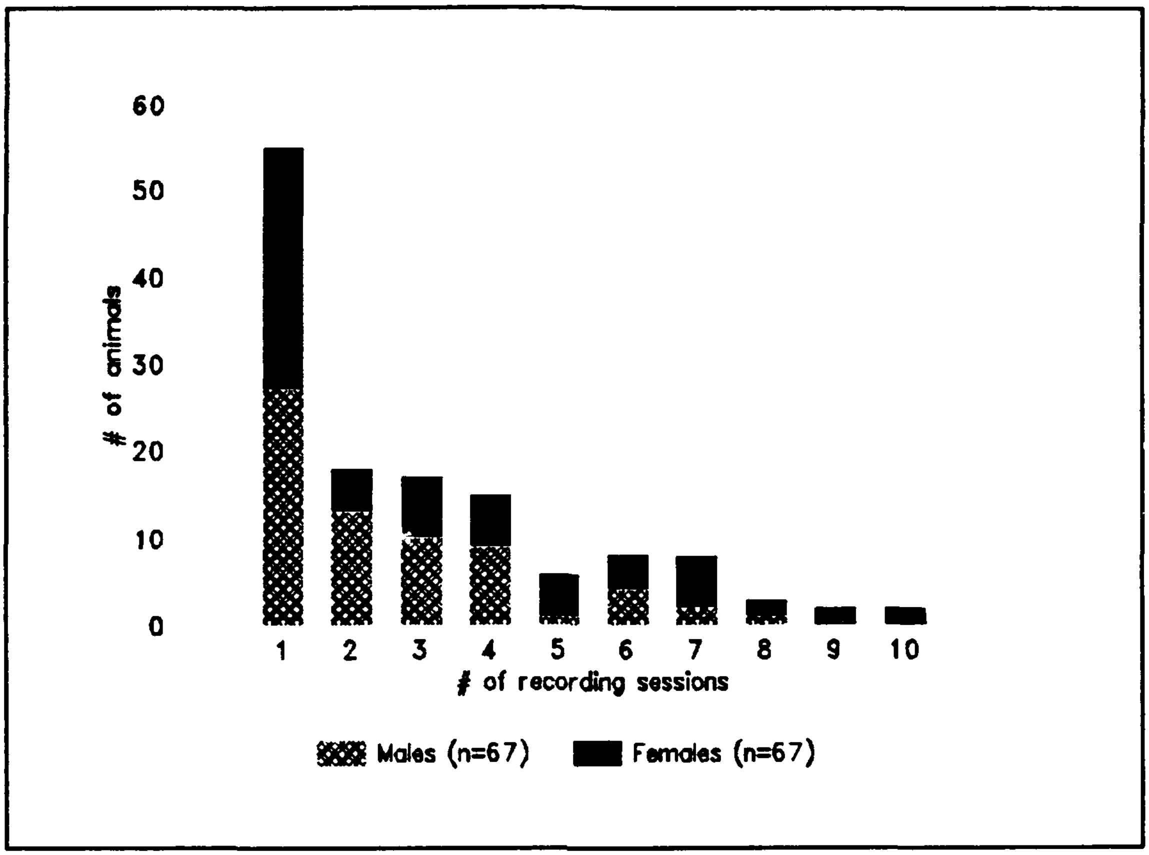

Figure 2.1. Number of different individuals recorded during the Sarasota capture-release projects since 1975. The number of recording sessions per individual varied from 1 to as many as 10, for a total of 398 animal/year combinations.

dolphin's head, using a Uher Report L or Report IC reel-to-reel tape recorder with a frequency response of 40-20000 Hz when operated at a speed of 7.5 in./s (Graycar 1976). From 1984 to 1990, animals were usually placed in a raft for processing. Since 1991, animals were processed on the deck of a large boat. A hydrophone with a suction-cup attached to it was usually placed on the head of each animal to obtain recordings of vocalizations, although occasionally a hydrophone was held in the water nearby. Hydrophones were designed by Peter Tyack (Tyack 1985); these recorded from about 1000 to 25000 Hz. On rare occasions, recordings were made in air using a microphone.

If a mother-calf pair were present, typically one member of the pair was processed while the other was held a few meters away in the water. In this way, the animals were usually in acoustic contact even when they could not see each other. Mothers and calves, or other pairs of animals that were caught together, were recorded on separate channels to enable analysis of whistle exchanges. From 1984 to 1988, whistles were recorded on either a Sony TC-D5M or a Marantz PMD-430 stereo cassette recorder, both of which have a frequency response of 30-15000 Hz, using Maxell UDXLII cassette tapes. Since 1989, a Panasonic AG-6400 stereo hifi VCR with a frequency response of 20 to 20000 Hz was used, with standard VHS tapes. In 1984 and 1985, recordings were made by P. L. Tyack. Since 1986, recordings were made by P. L. Tyack and myself.

In capture sessions from 1975 to 1992, single animals were usually held for 1/2 to 1 hour and mother-calf pairs for 1-2 hours. Recording sessions generally lasted for the duration of this period. In 1975-6, mother-calf relationships were surmised using information on size and association. Beginning in 1984, the identities of all mother-calf pairs were known from observations prior to capture (Wells, pers. comm.). Analyses presented in this thesis have relied heavily on the available background information on matrilineal relationships (Wells 1986, 1991; Wells et al. 1987; Wells, pers. comm.). Animal identification numbers used are those that were assigned to each individual by R. S. Wells.

2.2.2 Analysis techniques

Analysis of tapes recorded during the capture-release projects involved classifying whistles as signatures, variants (whistles other than the signature), deletions (portions of the signature) and imitations (contours resembling those of other individuals present). Between one and six different recording sessions of 81 individuals have been analyzed. The overall pattern of frequency modulation over time of a whistle can be represented visually as a spectrogram, and these patterns are called frequency contours. Before 1988, tapes were monitored by ear, and spectrograms of whistles were made with a Kay Elemetrics Corp. Sonograph Model 7029A Spectrum Analyzer with a narrow band (90 Hz) filter setting and a frequency range of 160-16000 Hz. Later analyses were performed on a Kay Elemetrics Corp. Model 5500 Digital Signal Processing system, with an upper frequency limit of 32000 Hz. Most analyses were performed with a sampling rate of 81,920 Hz, a 256 point FFT, and a Hamming window. With this system, all whistles could be viewed in real time, allowing for more accurate detection and classification of whistle contours.

Many whistles were digitized and incorporated into a sound database (Watkins et al. 1991). These digitized signals have been used in the development of many signal processing techniques, including contour extractions and quantitative contour comparisons (Buck and Tyack, submitted).

Throughout these analyses I focused only on the fundamental frequencies of the whistles and did not evaluate harmonics or patterns of concurrent echolocation pulses. It is likely that these and other features (such as amplitude modulation, see Tyack 1991) of whistles carry information and may be varied systematically, thus promising a rich area for future research.

2.3 SIGNATURE WHISTLES - Background

In a summary analysis of 22,278 whistles from 126 captive bottlenose dolphins, Caldwell et al. (1990) found that whistles tended to range from about 5 to 15 kHz, although extremes as low as 1 kHz or as high as over 24 kHz (how much over 24 kHz was not specified) were recorded. Signature whistles of the Sarasota animals generally ranged in frequency from about 5 to 25 kHz, although whistles starting as high as 14 kHz, or ending above 32kHz (the limit of our system) have been found. These values are in general accordance with several other published frequency ranges (cited in Caldwell et al. 1990: e.g., Kellogg et al. 1953, Dreher 1961, Dreher and Evans 1964, Herman and Tavolga 1980, Lilly and Miller 1961).

Caldwell et al. (1990) found that overall average duration was 0.96 seconds, although values ranged from 0.2 to 5.5 seconds. Repetitions of the signature whistle of a given animal can vary greatly in duration, depending to a large extent on the number of repetitive elements, called loops (Caldwell et al. 1973, 1990), that are produced. Number of loops is highly dependent on age, with younger animals producing fewer loops than older animals (Caldwell et al. 1990). In some cases the first and last loops are distinctive in structure; these are called introductory and terminal loops. Although dolphins tend to favor a certain number of loops per signature whistle, they often vary the number of central loops. Loops are often separated by silent intervals, but the timing of these is much more consistent than that of the intervals between separate whistles (Caldwell et al. 1990). Thus, there is seldom confusion as to what unit constitutes a separate whistle.

In a sample of signature whistles from 81 Sarasota individuals[1], 72.8% were multilooped in structure, as described above. However, only 17.3% contained introductory, central and terminal loops, while 14.8% contained introductory and "central" loops only, and 12.3% contained "central" and terminal loops only. Whistles consisting of repetitive elements with no obviously different introductory or terminal loops comprised 28.4%. The remaining 27.2% of individuals in this sample produced a non-looped, non-repetitive whistle contour. As described above, repetitions of such non-looped whistle contours can be differentiated from loops of one whistle, because

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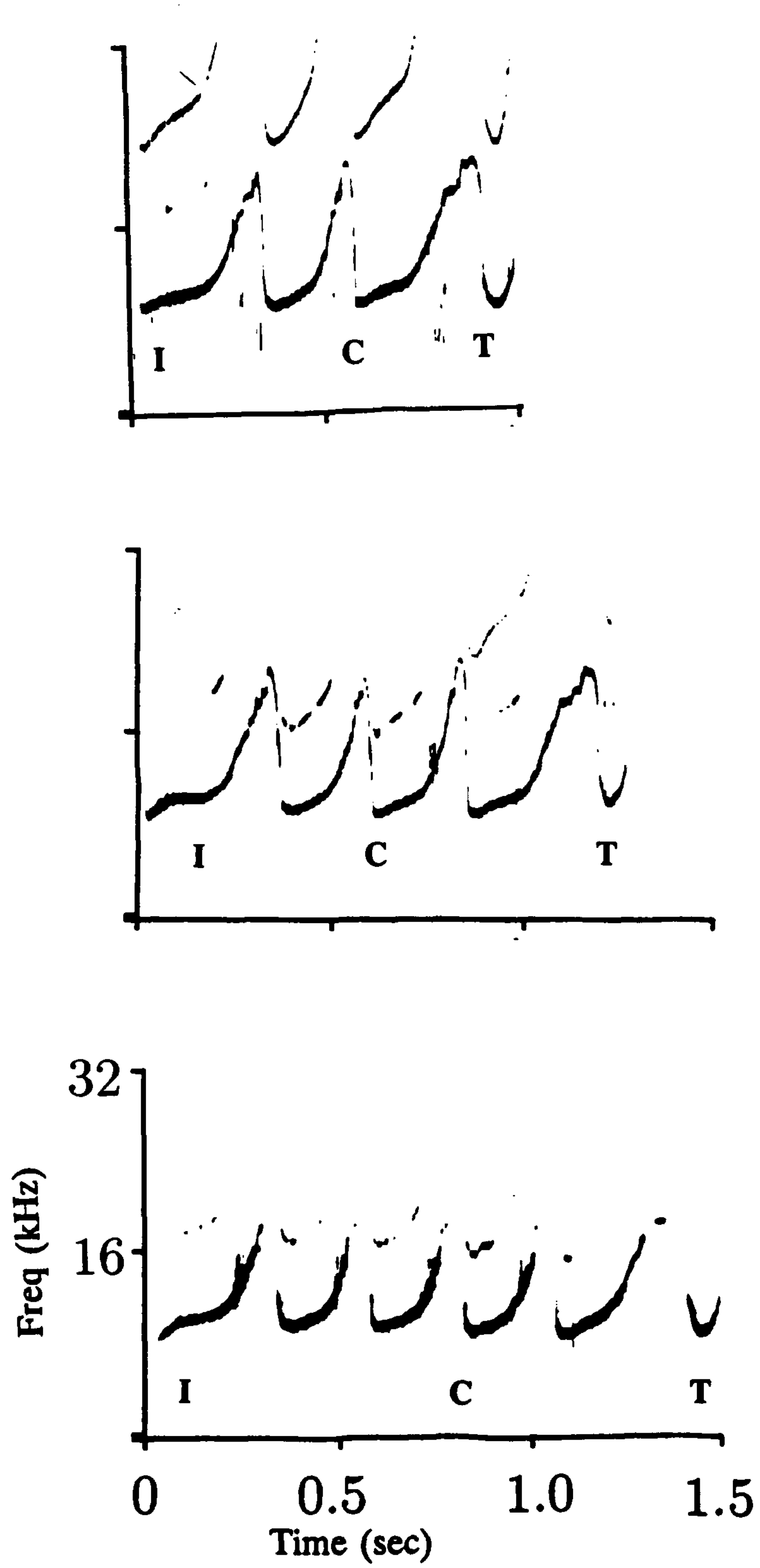
[1] All of the individuals in this sample were at least 1 year of age, at which time multilooped whistles were already occurring.

the intervals between repetitions are not constant. Examples of each of these types of whistles are shown in Figures 2.2-2.4.

The patterns of frequency changes over time that comprise signature contours are remarkably consistent across repetitions (e.g., see Figure 2.2). Although features such as absolute duration, maximum frequency and minimum frequency may vary considerably among repetitions, naive observers still have little difficulty sorting spectrograms of different signature contours by eye. A good example of this can be seen in Figure 4.1; although duration and frequency are not held constant, these repetitions are still easily recognized as the same overall contour.

Stability in signature whistles, determined by visually comparing spectrograms of whistles recorded from the same individuals over time, has been documented over periods of more than a decade in both captive (Caldwell et al. 1990) and wild (Sayigh et al. 1990) dolphins. Several examples of whistle stability can be seen in Figures 4.5-4.12.

Figure 2.2. Examples of a signature whistle of Sarasota female no. 35 (recorded during capture-release sessions in 1988 and 1989) with introductory, central, and terminal loops. Shown are whistles with 1, 2, and 3 central loops. Spectrograms were made with a Kay Elemetrics Corporation Model 5500 Digital Signal Processing system, with a sample rate of 81,920 Hz, a 256 point FFT, and a Hamming window.


I
C
T
I
C
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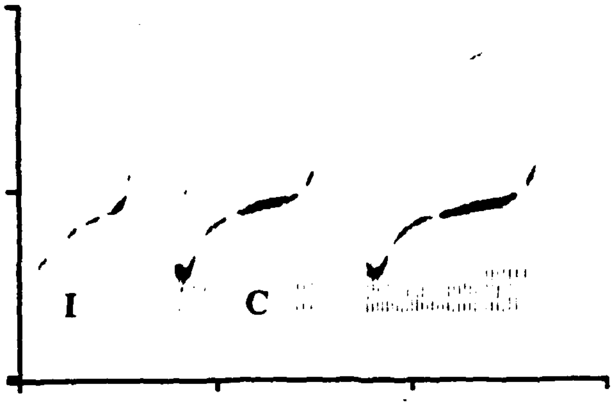
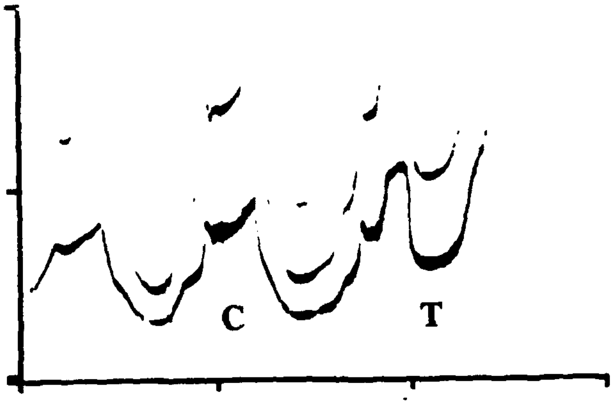
32
16
Freq (kHz)
I
C
T
0
0.5
1.0
1.5
Time (sec)

Figure 2.3. Examples of different types of repetitive, "looped" signature contours; #1 has only an introductory and "central" loops, #2 has only "central" and terminal loops, and #3 has neither introductory nor terminal loops. These are whistles produced by Sarasota females no. 16, no. 195, and no. 159, respectively, recorded during capture-release sessions in 1989 (#1 and #2) and 1987 (#3). Settings are as in Figure 2.2.

1.



2.



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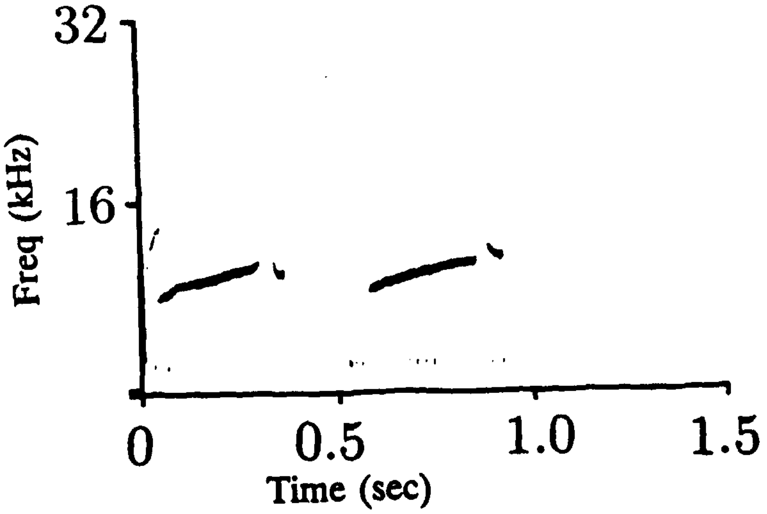
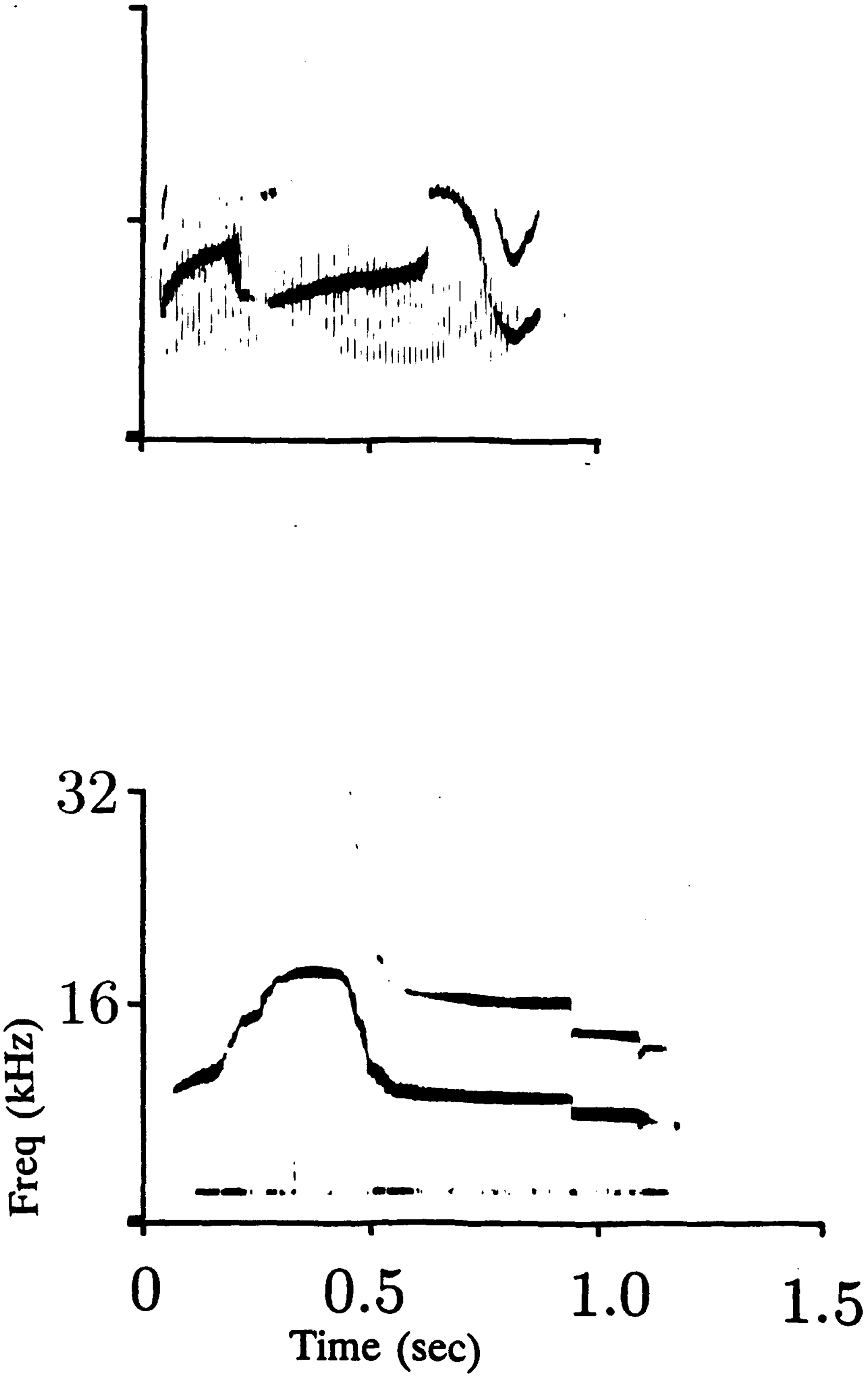


Figure 2.4. Two examples of whistles with non-looped, non-repetitive contours. The upper whistle was produced by Sarasota male no. 67, and the lower one was produced by Sarasota female no. 194. Both were recorded during capture-release sessions, in 1987 and 1989 respectively. Settings are as in Figure 2.2.


32
16
Freq (kHz)
0
0.5
1.0
1.5
Time (sec)

It is possible that the stress of the capture process resulted in atypical whistle production. For example, Caldwell et al. (1970) reported that captive animals under stress produce whistles with less frequency modulation. If the stress of capture were biasing our whistle sample, however, we would expect the whistles of the same individuals, recorded up to 10 times between 1975 and 1992, to have changed with increasing habituation to capture. Although most animals do become habituated (Scott et al. 1990), we have not noticed any associated change in whistle production. Furthermore, signature whistles recorded from undisturbed animals are indistinguishable from those produced by the same individuals during temporary capture (e.g., Figure 2.5).

Any whistles produced by a particular individual that do not closely resemble its signature contour are called variant whistles.[2] At the present time, next to nothing is known about variant whistles. Both recurrent variants and one-time occurrences have been noted (pers. obs.). Their functions are unknown, although it is likely that some recurrent variants are imitations of another individual's signature contour (e.g. Tyack 1986, Chapter 4). In analysis of tapes from the capture-release sessions so far, whistles were only scored as imitations if they resembled the signature contour of another individual present in the same capture. It is possible that some variant whistles are imitations of whistles of individuals not present. Techniques are

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[2] Caldwell et al. (1990) call these "aberrant" whistles.

being developed (e.g., Buck and Tyack, submitted) which will allow quantitative assessments of similarity of variant whistles to a catalogue of signature and variant whistles of individuals in the Sarasota community. This should significantly enhance our understanding of the functions of variant whistles. Chapter 4 presents preliminary data on a sex difference in variant whistle production (Figures 4.13-4.14).

This thesis utilizes the extensive database of whistles recorded from the Sarasota animals, in conjunction with detailed background information about the individuals in the Sarasota community. Data are presented on: 1) the possible use of signature whistles for individual recognition (Chapter 3); 2) sex differences in mother-offspring similarity of signature whistles and in variant whistle production (Chapter 4); and 3) factors affecting signature whistle development (Chapter 5).

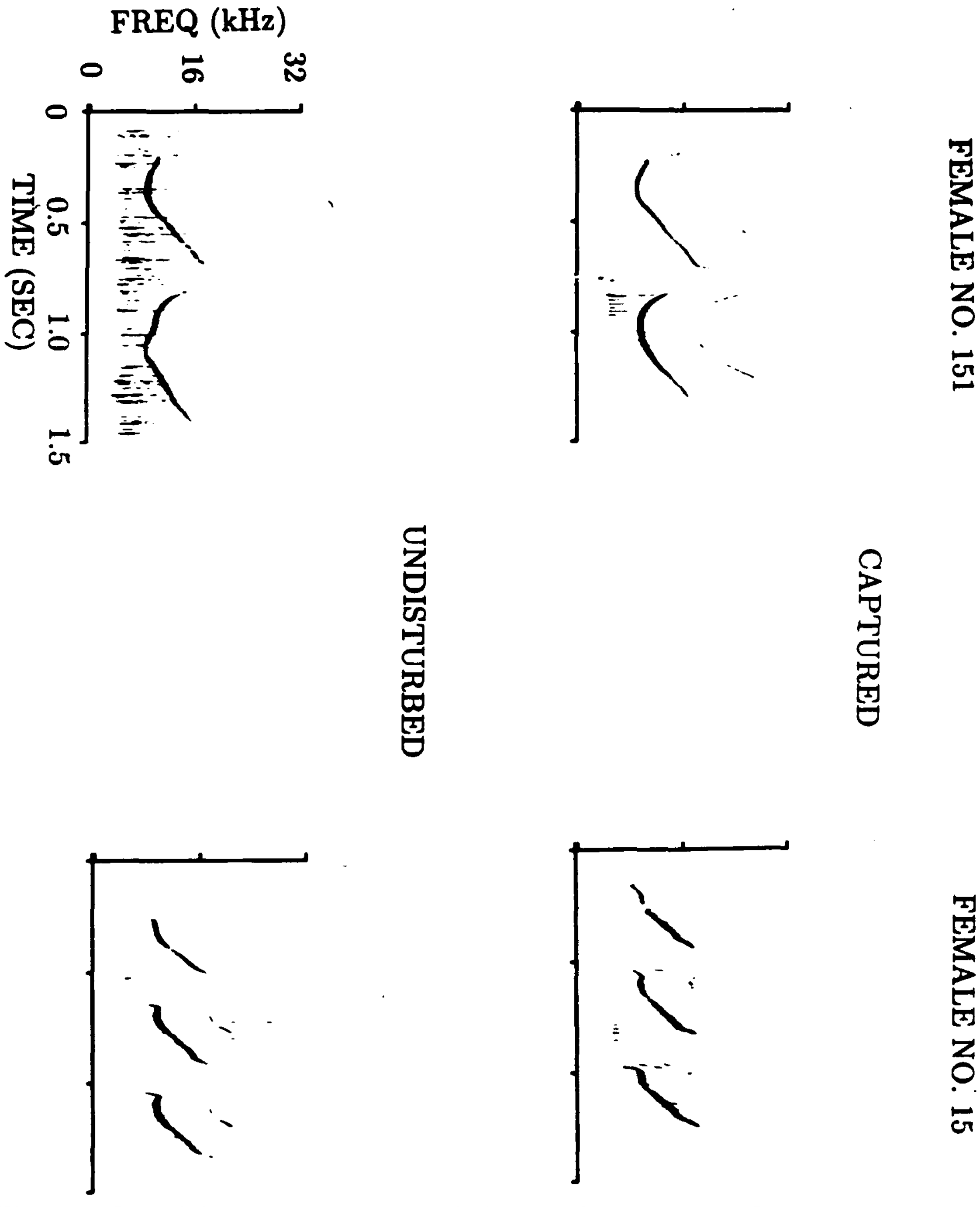

Figure 2.5. Whistle contours recorded from females no. 15 and no. 151 during temporary capture and under undisturbed conditions. Note the similarity in contours recorded in these different contexts. Settings are as in Figure 2.2.

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CHAPTER 3: INDIVIDUAL RECOGNITION IN FREE-RANGING BOTTLENOSE DOLPHINS: A FIELD TEST USING PLAYBACK EXPERIMENTS

3.1 INTRODUCTION

The term "signature" whistle implies the function of signalling individual identity. For such signalling to be of any use, individuals must have a parallel ability to recognize one another. The societies of bottlenose dolphins, typified by fluid association patterns intermixed with long-term stability in overall associations (Shane et al. 1986), would appear to require that individuals recognize one another. Acoustic recognition is the most likely sensory channel, given the poor visibility that often characterizes coastal marine habitats. This chapter explores whether or not bottlenose dolphins use signature whistles for individual recognition, by presenting data from playback experiments conducted with free-ranging dolphins in the Sarasota community. First, a review of studies of individual recognition involving auditory stimuli will be presented.

Early research on animal communication focused largely on innate, inflexible behaviors, many of which were involved in species recognition. Mechanisms for species recognition should be unambiguous, in order to minimize losses to reproductive success resulting from hybridization. However, many early researchers also observed the wealth of individual variability in some animal signals (primarily birds; e.g., Beer 1969, 1970a, 1970b, 1970c, Evans 1970, Hutchison et al. 1968, Marler 1960, Stevenson et al. 1970, Thorpe 1968, White 1971, White and White 1970, etc.) and thus began to investigate the more ontogenetically open (Mayr, 1974) systems for individual recognition. A majority of these studies have investigated individual variability in auditory stimuli, and they have encompassed a diversity of taxa. Some examples are listed in Table 3.1; see also reviews by Colgan (1983), Falls (1982), Gould (1983), Marler (1960), and Thorpe (1968).

Table 3.1. Examples from the literature of studies of individual recognition using auditory cues. In the "Study focus" column, "PO" refers to parent-offspring recognition, "NS" refers to neighbor stranger recognition, "SG" refers to individual recognition in social groups, and "VV" refers to studies which only demonstrated vocal variability among individuals, not perception by conspecifics. These categories are discussed in detail in the text. Other categories noted in this table are "M" for mate recognition, and "G" for recognition of group or flock members.

TAXA	STUDY FOCUS	REFERENCE
<u>Amphibians, Fish</u>		
Bullfrog	NS	Davis 1987
Damsel fish	NS	Myrberg and Riggio 1985
<u>Birds</u>		
Bank swallow	PO	Beecher et al. 1981, 1985
Barn, cliff and tree swallows	PO	Burtt 1977 Loesche et al. 1991 Medvin and Beecher 1986 Sieber 1985 Stoddard and Beecher 1983
White-throated sparrow	NS	Brooks and Falls 1975 Falls and Brooks 1975
Song sparrow	NS	Stoddard et al. 1991
Piñon jay	VV,M PO	Berger and Ligon 1977 McArthur 1982

TAXA	STUDY FOCUS	REFERENCE
Great tit	NS VV	Krebs 1971 Weary et al. 1990
Chickadee	VV,G	Mammen and Nowicki 1981
Striped-back wren	NS	Wiley and Wiley 1977
Royal tern	PO	Buckley and Buckley 1972
Crested tern	PO	Davies and Carrick 1962
Sandwich tern	VV	Hutchison et al. 1968
Common tern	PO	Stevenson et al. 1970
Laughing gull	PO,M	Beer 1969, 1970a, 1970b, 1970c, 1979
Black-billed gull	PO	Evans 1970
Ring-billed gull	PO	Miller and Emlen 1975
Gannet	VV,M	White 1971, White and White 1970
Pukeko	NS	Clapperton 1987a, 1987b
Blue grouse	NS	Falls and McNicholl 1979
Ancient murrelet	PO	Jones et al. 1987
European bee-eater	PO	Lessells et al. 1991
Adelie penguin	PO	Thompson and Emlen 1968
<u>Mammals</u>		
Sperm whale	VV	Backus and Schevill 1966 Watkins and Schevill 1977
Humpback whale	VV	Hafner et al. 1979
Bottlenose dolphin	VV	Caldwell and Caldwell 1965
Common dolphin	VV	Caldwell and Caldwell 1968
Pacific whitesided dolphin	VV	Caldwell and Caldwell 1970
Spotted dolphin	VV	Caldwell et al. 1973
Northern elephant seal	PO	Petrinovich 1974
Galapagos fur seal and sea lions	PO	Trillmich 1981

TAXA	STUDY FOCUS	REFERENCE
Bats	PO	Balcombe 1990
	PO,VV	Balcombe and McCracken 1992
	VV	Gelfand and McCracken 1986
	PO	Turner et al. 1972
Squirrel monkey	G,NS	Biben and Symmes 1991
	PO	Kaplan et al. 1978
	VV	Lieblich et al. 1980
	PO	Symmes and Biben 1985
	VV	Symmes et al. 1979
Spider monkey	SG	Masataka 1986
Pygmy marmoset	SG,NS	Snowdon and Cleveland 1980
Vervet monkey	PO,NS, SG	Cheney and Seyfarth 1980, 1982, 1986
Rhesus monkey	PO	Hansen 1976
Stumptail macaque	VV	Lillihei and Snowdon 1978
Japanese macaque	PO	Pereira 1986
Mangabey	NS,SG	Waser 1977
Chimpanzee	VV	Marler and Hobbett 1975
Ringtailed lemur	VV	Macedonia 1986
Pika	NS	Conner 1985
Reindeer	PO	Espmark 1971, 1975
Raccoon	PO	Sieber 1986
Timber wolf	VV	Tooze et al. 1990
Sheep	PO	Walser et al. 1981, 1982, Walser and Walters 1987

This is not meant to imply, however, that studies on vocal communication are alone in demonstrating such recognition; odor (in arthropods: Johnson 1977, Jutsum et al. 1979, in amphibians: Jaeger 1981), footdrumming (in kangaroo rats: Randall 1989), and electric organ discharges (in fish: McGregor and Westby 1992) are examples of other modalities capable of conveying individuality.

A variety of evidence indicates that the mechanisms of individual recognition in a species are related to its social organization. For example, many authors (e.g., Beecher et al. 1981, 1985, Beer 1970a, Colgan 1983, Falls 1982, Loesche et al. 1991, Medvin and Beecher 1986, Thorpe 1968) present data showing that individual recognition is more highly developed in colonial or group living species, where there is extensive contact among individuals, than in solitary species, where individuals encounter one another less often. In group living species, individual recognition between parents and offspring could be essential to ensuring reproductive success. Without such recognition, parents may not be able to provide care selectively to their own offspring. Similarly, territorial animals could prevent unneccessary aggressive encounters by learning to differentiate between sounds of non-threatening neighbors and intrusive strangers. By contrast, animals that do not defend a territory may not need to make such discriminations.

Both parent-offspring and neighbor-stranger recognition have been documented extensively in the literature, and are discussed in more detail below.

Other studies have looked at recognition between mates (e.g., Beer 1970a, Berger and Ligon 1977, White 1971), nestmates (e.g., Schimmel and Wasserman 1991), and fellow group or flock members (e.g., Biben and Symmes 1991, Clapperton 1987a, 1987b, Mammen and Nowicki 1981). A related area that has received a great deal of emphasis is kin recognition, wherein individuals discriminate among kin versus non-kin, sometimes without previous exposure to kin (e.g., Waldman 1981, Holmes and Sherman 1982, see Waldman 1987 for a review). There has been much controversy about the mechanisms by which kin recognition occurs, although in most cases familiarity, either through association or with an individual's own phenotype ("phenotype matching"), can account for discriminations. Grafen (1990) argued that virtually all cases of kin recognition in the literature can be explained as byproducts of either species, group or individual recognition mechanisms.

Studies of individual recognition have often focused on discriminations between familiar versus unfamiliar classes of individuals; e.g., kin versus non-kin, offspring versus non-offspring, neighbors versus strangers. These can be contrasted with studies of recognition in long-lived social animals that maintain relationships with related and non-related individuals over periods of many years (e.g., Cheney and Seyfarth 1980, 1982, 1986, Dasser 1985, Essock-Vitale and Seyfarth 1986, de Waal 1982). "...[P]rimates can remember past interactions, seem able to predict the behavior of others on the basis of prior observations (Kummer 1982), and discriminate among their own and other individuals' close associations" (Essock-

Vitale and Seyfarth 1986, p. 452). Indeed, it is widely accepted that most, if not all, primate species exhibit such "true" individual recognition (Essock-Vitale and Seyfarth 1986, Snowdon 1990). Although familiarity undoubtedly plays a role in these recognition systems as well, they provide examples of recognition on a truly individual basis, akin to how it occurs in humans.

Bottlenose dolphins, *Tursiops truncatus*, which are the subject of this thesis, are a social species with long-lasting, close associations among individuals (Chapter 2; Wells et al. 1987, Connor et al. 1992). These animals use acoustic communication extensively, indicating that this would be the most likely channel for individual recognition, if it were to occur. Their vision, although excellent (Dawson 1980), is of limited usefulness in many turbid, coastal habitats, and their olfactory lobe is absent (Herman and Tavolga 1980). Individual recognition through vocal whistle "signatures" (Chapters 1 and 2) has been suggested by several authors (Caldwell and Caldwell 1965, Tyack 1986a, Sayigh et al. 1990). However, so far only an ability to discriminate among whistles of different individuals (an important prerequisite to individual recognition) has been demonstrated experimentally (Caldwell et al. 1971, 1972).

Falls (1982) noted that features of a signal used for species recognition should exhibit low inter- and intra- individual variability, whereas features used for individual recognition should exhibit high inter-individual variability, but low intra-individual variability. Beecher (1982, see also Loesch et al. 1991) expanded this concept, and noted that selection for individual recognition could increase inter-individual variability, decrease intra-individual variability, or increase perceptual sensitivity to signature traits. Many studies have demonstrated individual variability in vocalizations without testing whether this variability is perceived by conspecifics (Table 3.1, studies marked "VV" for vocal variability). As outlined by Beer (1970a), demonstrating individual recognition should be a three-part process, where vocal variability is shown, evidence for individual recognition is noted in natural behavior, and discrimination among individuals is confirmed through playback experiments. Studies which involved at least some experimental testing of recognition (usually by means of playback experiments) will be discussed below in more detail.

3.1.1 Parent-offspring recognition

The vast majority of studies of individual recognition have focused on parent-offspring recognition (Table 3.1, studies marked "PO"; see Colgan 1983, Falls 1982 for reviews). Many of these studies have found that the occurrence of individual recognition and the timing of onset is closely tied to the ecology of each species. For example, mutual parent-offspring recognition in colonial nesting bank swallows (Beecher et al. 1981) and cliff swallows (Beecher et al. 1985, Stoddard and Beecher 1983), which associate in groups of hundreds of birds, was found to be highly developed. Conversely, solitary nesting barn swallow chicks showed only a weak ability to recognize their parents, and parents were not able to recognize chicks (Medvin and Beecher 1986). In general, in cases where recognition occurs, its onset is closely tied to mobility of the offspring (e.g., Beecher et al. 1981, 1985, Beer 1969, 1970a, 1970c, Burtt 1977, Davies and Carrick 1962, Evans 1970, Lessells et al. 1991, Miller and Emlen 1975, McArthur 1982, Stevenson et al. 1970). Presumably, location is a sufficiently reliable cue before the young are able to move around. Among mammals, raccoon cubs began to recognize calls of their mothers at the time that they began to venture from the den (Sieber 1986).

In royal terns, which live in extremely dense colonies, parents were able to recognize eggs visually (Buckley and Buckley 1972). Vocal recognition between parents and/or chicks in this species and in black-billed gulls, which also live in crowded colonies, began much earlier than for many other species (Buckley and Buckley 1972, Evans 1970). Group living bats (Balcombe 1990), reindeer (Espmark 1971), fur seals (Trillmich 1981), sea lions (Trillmich 1981), and northern elephant seals (Petrinovich 1974) all exhibit parent-offspring recognition within the first days of life. Without recognition, the potential for losing track of offspring would be very high. Beer (1970a, 1970c) found that development of recognition of various adult calls by laughing gull chicks closely matched the ecological needs of the chick; e.g., very young chicks responded positively only to "crooning" calls, which are associated with feeding of the nestlings, but as the chicks began to venture from the nest, they began to discriminate the "kehah" and "long calls" of their parents. Beer (1970) speculated that the adult "kehah" and "long calls", which function in greetings and nest relief, are better indicators of both individual identity and location than are "crooning" calls, and thus are more useful cues for older, more independent chicks.

Many studies have focused on either parent or offspring recognition, leaving open the question of whether recognition is mutual. For example, among primates, Hansen (1976) showed that juvenile rhesus monkeys recognize their mothers, but he did not investigate maternal recognition. Researchers have found that squirrel monkey (Kaplan et al. 1978, Symmes and Biben 1985) and Japanese macaque (Pereira 1986) mothers recognize young, but they did not investigate recognition by offspring. However, mutual recognition has been demonstrated in reindeer (Espmark 1971), sea lions (Trillmich 1981), fur seals (Trillmich 1981) and possibly bats (Balcombe 1990, Balcombe and McCracken 1992). In addition, several species of birds have been found to exhibit mutual recognition (e.g., cliff swallows: Beecher et al. 1985, Stoddard and Beecher 1983, bank swallows: Beecher et al. 1981, piñon jays: McArthur 1982, and ancient murrelets: Jones et al. 1987). In one case, however, Beer (1979) showed that what appeared to be mutual recognition in laughing gulls was actually chicks' recognition of parents and subsequent vocal cueing of the parents. Chicks responded vocally only to their own parents, and thus solicited their parents' response.

Playback experiments that do not demonstrate individual recognition may indicate that recognition is not based solely on vocal cues. Visual or olfactory cues, or timing of response (e.g., in sheep: Walser et al. 1981) could play roles in recognition.

As discussed earlier, data in virtually all studies of parent-offspring recognition could result from discrimination of familiar versus unfamiliar stimuli, wherein individuals habituate to stimuli heard most frequently. Parents discriminate between offspring and non-offspring; offspring discriminate between parents and non-parents. Beer (1970a, 1970b) attempted to control for the effect of familiarity by playing back calls of parents versus familiar neighbors to chicks. However, it is likely that the parents' calls were still a more dominant component of the chicks' acoustic environment, since they were generally closer, and therefore louder, than neighbors' calls. In addition, the calls of parents would usually be associated with positive reinforcement (i.e., feeding). These factors might increase the salience of the parents' calls. For many birds and non-social mammals, there may not be a need to distinguish individuals other than parents and offspring. Therefore, recognition between parents and dependent young may not be the best context in which to look for true individual recognition. A system in which something closer to true individual recognition has been documented is territorial species' discrimination of neighbors versus strangers.

3.1.2 Neighbor-stranger recognition

It is obvious why neighbor-stranger recognition would be advantageous for territorial species. In many cases, a song of a familiar neighbor does not represent a territorial intrusion, whereas an unfamiliar song probably does. Aggression is energetically costly; it would behoove individuals not to engage in unneccessary aggressive encounters. A large number of studies of neighbor-stranger recognition have been reported in the literature. Ydenberg et al. (1988) compiled a list of 40 such studies conducted in the past 30 years (not all involve acoustic recognition); several studies are also listed in Table 3.1 (marked "NS"). The primary focus has been on territorial birds. Blue grouse (Falls and McNicholl 1979), great tits (Krebs 1971), and white-throated sparrows (Brooks and Falls 1975) are examples of species that have been shown to respond more strongly to playbacks of songs of strangers versus neighbors. Again, such recognition could result from discriminations of familiar versus unfamiliar sounds. Individuals may become habituated to sounds of neighbors that are heard frequently, enabling them to discriminate these from unfamiliar sounds. However, in some cases discrimination is strongly tied to locational cues, and several authors have suggested that this represents true individual recognition, rather than discrimination of familiar versus unfamiliar sounds. For example, Falls and Brooks (1975) showed that white-throated sparrows responded in the same way to the songs of strangers as to the familiar songs of neighbors broadcast from the wrong location. Wiley and Wiley (1977) documented the same phenomenon for striped-back wrens, which responded differentially to playbacks of duets of neighbors broadcast from different locations. Stoddard et al. (1991) also found a location effect in playback of neighbors' songs to song sparrows. They noted that song sparrows need to recognize changes in location of particular neighbors, since neighbors are frequently responsible for territorial invasions. In all of these cases, if the songs of neighbors were perceived as simply a familiar class of sounds, then location of playback should not affect the response. It could be argued (Falls 1982), however, that the familiarity of the stimulus has two components: song structure and location. If either of these are altered, the stimulus is no longer familiar.

Perhaps more compelling evidence for individual recognition comes from studies by Clapperton (1987a, 1987b) of group living, forest dwelling, territorial pukeko (a non-passerine bird), and by Conner (1985) of territorial pikas (a small mammal). Male pukeko discriminated among calls of strangers, neighbors, and group members. Within a cooperative group, there was some evidence that male calls were further distinguished according to dominance rank. This type of discrimination may be essential for effective functioning of a cooperative breeding group. Territorial pikas responded more strongly to unfamiliar short calls of strangers than to familiar calls of neighbors. However, as in song sparrows, strangers did not always represent the greatest threat to an individual's territory. Pikas were also able to discriminate between calls of different familiar individuals, and response strength was correlated with the likelihood of intrusion by a particular individual.

3.1.3 Individual recognition in social groups

Even though some studies of neighbor-stranger discrimination arguably demonstrate true individual recognition, many of the studies that have been discussed so far represent a level of recognition that is functionally different from, for example, that which is so commonplace in the daily lives of human beings. For us, individual recognition is an integral part of daily existence; reaching far beyond recognition of kin and neighbors, or even of frequent associates. Note that this is not a qualitative, but rather a quantitative difference from the studies of parent-offspring and neighbor-stranger recognition already discussed. In many of these cases, individually distinctive features of signals may be learned and classified into two categories: familiar and unfamiliar.[1] Perhaps other information, such as location, is tied into making these discriminations. In general, the literature indicates that the level of classification matches the ecological needs of the animals. Most monogamous birds need only distinguish mate from non-mates, offspring from non-offspring. Territorial species need to distinguish neighbors from non-neighbors; they need not know which

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[1] Even if finer level discriminations do occur, most studies of parent-offspring or neighbor-stranger recognition have not been designed to look for them.

particular birds fit into these categories. In some cases, such as for pukeko and pikas, finer discriminations may enhance an individual's reproductive success. As demands of group living increase, advantages to recognizing other individuals increase as well.

True recognition of individuals, for example, is a prerequisite for reciprocal altruism (Trivers 1971), which has been documented in baboons (Packer 1977), vervet monkeys (Seyfarth and Cheney 1984), and bats (Wilkinson 1984). Connor and Norris (1982) suggested that dolphins display many of the characteristics presumed to be associated with reciprocally altruistic behavior (e.g., long-term, close associations; care-giving behavior). Cheney et al. (1986) stated that "nonhuman primates cultivate relationships with particular members of their groups and ... such relationships contribute to individual reproductive success" (p 1362). Individuals which interact repeatedly with one another over their lifetimes may need to classify their associates into many categories: e.g., as individuals in their own group versus a neighboring group; or according to their relationship to themselves or to other associates. For example, mangabeys recognized vocalizations of individual males from their own and neighboring groups (Waser 1977). Vervet monkeys recognized vocalizations of individuals in neighboring groups. Individuals responded more strongly to vocalizations of individuals from neighboring groups that were played back from the wrong locations than to those played back from the correct locations (Cheney and Seyfarth 1982). Snowdon and Cleveland (1980) found that pygmy marmosets responded differently to vocalizations of the same individual originating from familiar and unfamiliar locations. The similarities here to studies of neighbor-stranger recognition, where location played a role in recognition, emphasizes that these various contexts of individual recognition differ in degree, rather than in kind.

Abilities for much finer discriminations are evident from studies by Cheney and Seyfarth (1980) and Masataka (1986). Vervet monkey mothers not only recognized screams of their own juveniles, but they also associated a particular juvenile's scream with the appropriate mother. In playback experiments, control females were significantly more likely to look at the mother of the juvenile whose screams were played back than to look at any other nearby individual (Cheney and Seyfarth 1980). In a study virtually identical in experimental design, Masataka (1986)[2] showed that individual spider monkeys not only discriminated among vocalizations of different individuals, but also that they were able to recognize calls that had originally been directed toward them. Even more striking was evidence that control individuals also recognized which individual was the intended recipient of the played back calls. Spider monkeys live in dense forest habitats, where vocal cues may provide the only clues to individual identities of group members.

An even finer level of recognition among individuals has been documented by Dasser (1988) and Cheney and Seyfarth (1986). In an experiment involving

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[2] In fact, sections of the text describing the methods in this paper were identical to sections in Cheney and Seyfarth (1980).

photographs, not vocal cues, Dasser (1988) showed that Java monkeys apparently categorized group members with respect to mother-offspring affiliations. Vervet monkeys were aware not only of the types of relationships that they themselves have with other individuals, but also that other individuals share analagous types of relationships. Individuals were more likely to threaten a particular individual either if 1) they had recently fought with that individual's close kin; or 2) their own close kin and that individual's close kin had recently fought (Cheney and Seyfarth 1986). These data also indicate that interactions among individuals depend on memories of the histories of interactions among individuals in a social group (Dasser 1985, Essock-Vitale and Seyfarth 1986, de Waal 1982).

3.1.4 Individual recognition in cetaceans

Five species of cetaceans (bottlenose dolphins: Caldwell and Caldwell 1965, common dolphins: Caldwell and Caldwell 1968, Pacific whitesided dolphins: Caldwell and Caldwell 1970, spotted dolphins: Caldwell et al. 1973, and sperm whales: Backus and Schevill 1966, Watkins and Schevill 1977) have been found to produce individually distinctive vocalizations. In many other species it has not yet been possible to attribute sounds to particular individuals; thus, more such "signature" vocalizations may be discovered. Of the five known species, all are long-lived, social animals, for which individual recognition seems likely to play an important role in social interactions (Tyack 1986b).

Tyack (1991) pointed out that variations in the vocal tracts of terrestrial animals may lead to vocal variability among individuals, which, as it does in humans, can lead to individual recognition. Tyack (1991) speculated that such gas-filled cavities may not provide reliable cues for individual recognition in diving mammals, in which pressure changes can change the shape of the vocal tract. Therefore, these mammals may have to produce signals that are individually distinctive in temporal patterns, such as sperm whale "codas", or in frequency modulation, such as dolphin whistles, to reliably signal individual identity.

3.1.5 Individual recognition in bottlenose dolphins

In the remainder of this chapter, I explore the potential for individual recognition in free-ranging bottlenose dolphins using the criteria suggested by Beer (1970a): 1) inter-individual variability in vocalizations, 2) evidence for individual recognition in natural behavior, and 3) discrimination among individuals in playback experiments.

3.1.5.1 Vocal variability

Individual variation in bottlenose dolphins vocalizations has been thoroughly documented through analyses of individually distinctive signature whistles of captive

(Caldwell et al. 1990) and wild (Sayigh et al. 1990, Chapter 2) dolphins. Background information on signature whistle structure of captive and wild dolphins was presented in Chapter 2.

Several lines of evidence support the idea that bottlenose dolphin signature whistles provide information on individual identity. First, inter-individual variability is much higher than intra-individual variability (Buck and Tyack, submitted), a prerequisite for signature signals (Beecher 1982). Second, Caldwell et al. (1971) demonstrated that one bottlenose dolphin was capable of extremely accurate discrimination of different exemplars of two naturally occurring signature whistles. Spectrograms of the two signature whistles used as stimuli in this experiment were visually quite similar. A later study (Caldwell et al. 1972) showed that the same dolphin was capable of distinguishing among signature whistles of at least eight different individuals, using many different exemplars from each individual. Discrimination among many different whistle contours would be important if signature whistles were used for individual recognition in fluid social groups. Further studies on cognition by Herman and co-workers (Herman 1986, Herman et al. 1984, Richards et al. 1984) have shown that dolphins are capable of discriminating among many different computer generated whistle-like sounds. In this "language" training, dolphins were able to learn to associate arbitrary sounds with arbitrary objects, a skill that would be necessary for association of specific signature whistles with particular individuals.

3.1.5.2 Observational evidence for individual recognition

Observations of wild bottlenose dolphins provide compelling evidence for individual recognition. Extremely stable individually-specific relationships have been extensively documented in at least two wild communities of bottlenose dolphins (Wells et al. 1987, Connor et al. 1992, see Chapter 1). For example, coalitions of two to three unrelated males can have coefficients of association that are close to 1.0, meaning that they are together in approximately 100% of all sightings of either individual (Wells et al. 1987). Mothers and calves remain in close association for 3 to 6 years (average: 5), and one 10 year association was observed (Wells et al. 1987). One case where a mother and calf reunited after a prolonged separation was described by Wells (1991).

In addition to these long-term, stable associations among individuals, dolphins interact repeatedly with many other individuals over the course of their long lives[3]. In environments where visibility of 30-50 meters is exceptional, it is almost impossible to imagine how else these individually-specific relationships could be maintained if not acoustically. Whistles can travel several kilometers and are omnidirectional. Furthermore, whistles are known to be used extensively in natural contexts (Chapter 5).

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[3] Free-ranging dolphins can live to at least 50 years of age (Wells, pers. comm.).

3.1.5.3 Playback experiments

Playback experiments were designed to test the ability of dolphins to use signature whistles for individual recognition. As mentioned previously, playback experiments have been utilized extensively in studies of individual recognition. In behavioral research on cetaceans, which has traditionally lagged behind research on terrestrial animals, playback experiments have proven to be a powerful technique for documenting the general functions of vocalizations (Clark and Clark 1980, Mobley et al. 1988, Tyack 1983).

However, experimental design of playback experiments has recently been the focus of a lively debate (Kroodsma, 1989a, 1989b, Searcy, 1989, Catchpole, 1989). Kroodsma (1989a, 1989b) claimed that many studies involving playback experiments with birds suffered from a design flaw termed pseudoreplication (Hurlbert 1984). He outlined an example of an experimental design containing pseudoreplication, wherein one exemplar from each of two song dialects are presented to a number of birds, and a differential response to the two exemplars is taken as evidence for differential response to the respective dialects. In this experiment, the "replication" occurs at the wrong level; this study can only provide evidence for a differential response between two particular songs, rather than between two dialects. A differential response to two songs could be due to a factor other than that which is being tested; for example to different states of arousal in the two birds from which the exemplars were recorded. Though Searcy (1989) argued that such an experiment is still valuable, it cannot be contested that experiments with greater external validity are highly desirable. These factors were taken into consideration in design of the present experiments. They were conducted in pairs, in which the same two stimuli were predicted to evoke opposite responses from a pair of target animals (see section 3.2.1). This controlled for any unknown cues that may have been present in the stimuli.

The primary target groups for playback experiments were mothers and independent offspring who were no longer associating together continuously. During the period of close association between mothers and offspring, the signature whistle often appears to function as a contact call (e.g., McBride and Kritzler 1951, Sayigh et al. 1990). Mother-offspring recognition could result purely from discrimination of familiar versus unfamiliar stimuli, as has been discussed previously. This would result if mothers and offspring simply habituate to the whistles that they hear most frequently, which are likely to be those of one another. A better test for individual recognition, although still not conclusive, is: do mothers continue to recognize (i.e., respond differently to) signature whistles of independent offspring? Likewise, do independent offspring recognize signature whistles of their mothers? In these cases, simple habituation to frequently heard stimuli could not account for discrimination of whistles, since mothers and independent offspring tend to associate at low levels.

In these experiments, each target animal was presented with two familiar stimuli, with one predicted to elicit a stronger response than the other. In tests with mothers as target animals I compared responses to a whistle sequence from an independent offspring with responses to a whistle sequence from a familiar, similar-aged non-offspring; in tests with independent offspring as target animals I compared responses to a whistle sequence from the mother with responses to a whistle sequence from a familiar adult female. Offspring used as target and stimulus animals had been independent from their mothers for periods ranging from one to fourteen years. Target mothers and independent offspring associated with both animals whose whistles were used as stimuli at similarly low levels.

A third set of experiments targeted females from different bands (Wells 1991, see Chapter 1), in order to test whether adult females preferentially respond to whistles of closely associated females, compared to whistles of familiar, but less closely associating females. Since all females in a band are not matrilineally related, recognition can not be based on a simple matrilineal "signature", such as was found for pigtail macaques by Gouzoules and Gouzoules (1990). In addition, even the whistles of matrilineally related females are quite distinct from one another (Sayigh et al., 1990, Chapter 4). Thus, it is of interest to determine whether females recognize signature whistles of their individual group members.

The Sarasota capture-release project (Chapter 1), although an artificial setting for wild animals, was otherwise ideal for conducting playback experiments, since responses were easily observed and the context was easily controlled. Playbacks with completely undisturbed animals are not feasible without better underwater viewing capabilities than are typical of Sarasota waters. In addition, the immediate context of the target animals would be likely to affect the outcome of the experiments. In playbacks to temporarily captured animals, recordings used as stimuli in the experiments were made during captures in previous years. Therefore, if contextual information (e.g., state of arousal or stress) is contained in signature whistles, and if the animals are sensitive to this information, then playback of these stimuli during capture should be plausible to the animals.

Caldwell et al. (1990) studied changes in whistles as a function of four general behavioral contexts: "isolated when first captured and placed in a tank; isolated but habituated to captivity and undisturbed; stranded in air while subjected to venipuncture; and isolated and habituated to captivity and receiving human attention which appeared positively reinforcing (feeding and play)" (p. 221). However, there were few consistent changes among the individuals studied, leading them to conclude: "[f]or another dolphin to learn what a particular pattern of whistling predicts, it may need to learn how the individual it is hearing tends to vary its whistles in different contexts" (Caldwell et al. 1990, p. 232). It is still unclear, however, whether dolphins are capable of discerning contextual information present in signature whistles.

Caldwell et al. (1971) trained one dolphin to discriminate between signature whistles of two different animals, using whistles recorded in different behavioral contexts as stimuli. The study animal did not differentiate among signature whistles recorded in different behavioral contexts, but this could easily have been due to the training paradigm, which required only that the subject differentiate the two signature whistles.

In order to control for possible discrimination of any contextual cues that might be present in the whistle stimuli, a paired playback design was used. Pairs of target animals were predicted to respond in opposite directions to two playback stimuli, based on their relationships to the individuals that produced the stimulus whistles. But if animals responded to whistles based on the level of arousal of the individual that produced them, rather than on the identity of the vocalizer, then both target animals should respond in a similar manner to a given pair of stimuli. Thus, this paired playback design also eliminated problems associated with pseudoreplication that were discussed earlier.

The goal of these experiments was to test whether dolphins use signature whistles as a means to recognize individual group members. Many studies of individual recognition have demonstrated discrimination between familiar and unfamiliar classes of stimuli (e.g., see sections 3.1.1, 3.1.2). Other studies have linked this discrimination with recognition of individuals (e.g., section 3.1.3). Although earlier studies (Caldwell et al. 1971, 1972) demonstrated that a dolphin was capable of discriminating among different signature whistles, they did not show that the animal associated a particular whistle with a particular individual. Playing back whistles of two individuals that are both known to the target animals, and which associate at similar rates with the target animals, is a first step at making this distinction between discrimination and recognition. It is difficult to make generalizations about social functions of signature whistles involving individual-specific relationships without an understanding of whether these whistles are used in individual recognition.

3.2 METHODS

3.2.1 Experimental design

The experimental design of mother/independent offspring playbacks consisted of paired trials, wherein each of two target animals (mothers or independent offspring, T1 and T2) were played the same two stimulus tapes (S1 and S2), one of which was the independent offspring (or mother) of each of the target animals, and the other was a familiar individual of similar age (Table 3.2). For example:

		Stimuli (* indicates stimulus predicted to evoke a stronger response)	
Target animal	T1	S1*	S2
	T2	S1	S2*

In playbacks to females from different bands (T1 and T2), stimuli consisted of whistles from a member of the target animal's own female band (S1), and whistles from a member of another female band (S2), which was known to the target animal but was not as close an associate.

Table 3.2. Protocol for paired trials in playback experiments. For the purpose of illustration, the protocol for mother-independent offspring playbacks with mothers as the target animals is presented. The outline for other target groups is identical, as described in the text.

Target animal - mothers	Playback stimuli - Independent offspring
#16	#140*, #148
#22	#140, #148*
#5	#159*, #17
#10	#159, #17*
#52	#164*, #160
#50	#164, #160*
#35	#30*, #33
#26	#30, #33*
#16	#140*, #61
#32	#140, #61*

* Independent offspring of the target animal

Pairs of stimuli were chosen to control for familiarity. For example, in the mother-independent offspring playbacks, pairs were chosen such that individuals were from the same female band (Wells et al. 1987). Where possible, independent offspring were matched for age in both target and stimulus pairs. In most cases, this ensured a fairly high level of association between the paired animals, because within a band mothers with similar-aged calves tend to associate together. In addition, similar-aged independent offspring tend to associate together (Wells et al. 1987, Wells 1991). In all cases, the target animals were familiar with each of the animals whose whistles were used as paired stimuli. Coefficients of association[4] between target and stimulus animals for four playback pairs are shown in Tables 3.3 and 3.4. The period during which offspring were associating with their mothers ("Offspring dependent", Table 3.3) is obviously characterized by high association rates between mothers and offspring. It noteworthy, however, that during this period both target animals in a given pair showed comparable levels of association with the second stimulus animal (not the mother or independent offspring of the target animal; e.g., 0.24 and 0.26 for the first pair in Table 3.3). In the period since offspring became independent, which is when playback experiments took place, coefficients of association between target and stimulus animals are somewhat more variable, but are still similar across stimulus pairs ("Offspring independent", Table 3.3). As expected, coefficients of association between females in the same female band (calculated over the period 1984-1992) were higher than those between females of different bands, although the latter were non-zero values (Table 3.4).

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[4] Calculated as twice the number of sightings in which both individuals were present divided by the total number of sightings of each individual (Wells et al. 1987).

Table 3.3. Coefficients of association between target and stimulus animals for seven playback pairs. Values are shown both for the period of mother-calf association, and for the period since the offspring became independent (which is when playback experiments took place). Data were obtained from R. S. Wells.

	Offspring dependent		**Offspring independent**	
Target animal ID	**Stimulus #1**	**Stimulus #2**	**Stimulus #1**	**Stimulus #2**
Independent offspring				
#142 (Born 1984)	**0.99***	0.24	**0.00***	0.03
#144 (Born 1984)	0.26	**1.00***	0.17	**0.29***
#148 (Born 1984)	**0.96***	0.37	**0.16***	0.10
#140 (Born 1984)	0.38	**1.00***	0.08	**0.13***
#164 (Born 1985)	**0.98***	0.08	**0.25***	0.23
#160 (Born 1985)	0.08	**1.00***	0.00	**0.11***
#2 (Born ~1974)	**0.90***	0.17	**0.16***	0.16
#3 (Born 1973)	0.07	**0.98***	0.10	**0.12***
#144 (Born 1984)	**0.99***	0.24	**0.28***	0.44
#159 (Born 1986)	0.51	**0.99***	0.26	**0.41***

	Offspring dependent		**Offspring independent**	
Target animal ID	**Stimulus #1**	**Stimulus #2**	**Stimulus #1**	**Stimulus #2**
Mothers				
#22	**0.96+**	0.38	**0.16+**	0.08
#16	0.37	**1.00+**	0.10	**0.13+**
#61	**1.00+**	0.08	**0.14+**	0.06
#16	0.09	**0.97+**	0.04	**0.11+**

*** Mother of the target animal**
+ Independent offspring of the target animal

Table 3.4. Coefficients of association between target and stimulus females from different female bands used in a paired playback trial. Data were obtained from R. S. Wells.

Target animal ID	**Stimulus #1**	**Stimulus #2**
#48	**0.13***	0.03
#23	0.10	**0.14***

*** Member of the same female band as the target animal**

3.2.2 Stimulus preparation

The following procedure was used in preparing stimulus tapes:

1) Recording sessions of an individual whose whistles were to be used as stimuli were monitored on the Kay Elemetrics Corp. Model 5500 DSP Sonagraph.

2) Sessions that involved whistle exchanges with another individual were selected, so that the natural timing of whistle production in a capture situation could be preserved.

3) A portion of an exchange was selected that contained as little extraneous noise and/or feedthrough from the other channel as possible.

4) Frequencies below the minimum frequency of the whistle were filtered out, and a 47.5 second filtered section was stored in the buffer of the Kay (this is the maximum buffer size when analyzing at 32 kHz).

5) Any extraneous noise or feedthrough was then edited out, and sections of typical ambient noise of the same length were inserted, to preserve the original timing.

6) The audio output of the Kay was then recorded on a Marantz PMD-430 stereo cassette recorder.

In preparing the first set of experiments in 1989, I selected a 2 minute stimulus presentation for playbacks. Steps 4 and 5 were therefore repeated 3 times to achieve a 2 minute long stimulus, for each of 52 stimuli. For the 1989 tapes, loudness was controlled by attempting to maintain a relatively constant needle deflection on the gain meters of the cassette recorder. The level on the amplifier used to power the playback speaker in the experiments was selected after experimentation with a vocalight (Tyack 1985). Vocalights contain light-emitting diodes (LED's) which light up in proportion to the loudness of a sound. At the New

England Aquarium, Peter Tyack held a vocalight at a distance of about 1 meter from a dolphin whistling at typical levels, and observed the number of LED's (2-4) illuminated. The level on the amplifier was set (before the experiments) when the same number of LED's were illuminated at a distance of 1 meter from the playback speaker.

3.2.3 1989 Protocol

The initial protocol in 1989 was: 1) a 2 minute pretrial period; 2) the first 2 minute playback; 3) a 2 minute post-trial period; 4) the second 2 minute playback; 5) a 2 minute post-trial period. This design attempted to strike a balance between giving the animal enough time to respond during and after each stimulus presentation and minimizing the overall length of the experiment. The latter was an important consideration, since both the target animal and the people around it (see Final Protocol, Figure 3.1) had to remain in position for the duration of the experiment.

However, after the first few trials in 1989, it became apparent that the animals were still responding (with head turns toward the speaker - see section 3.2.5.1) to the first stimulus at the time the second stimulus was presented. Therefore, again in the interest of minimizing the overall duration of each experiment, stimulus presentations were shortened to 30 seconds each and the post-trial intervals were lengthened to 5 minutes. Subsequent trials in 1989 thus utilized only the first 30 seconds of each stimulus tape. However, it also appeared that there was considerable variation in amplitude of the 1989 stimulus tapes. So, in 1990, an entirely new set of 52 30-second stimulus tapes was made, taking extreme care in regulating amplitude. To guard against distortion on playback, a level was set on the waveform for maximum amplitude, and the loudest part of each stimulus sequence was constrained to that amplitude. Tapes were then all recorded at the same input levels. Again, the level on the amplifier was set through experimentation with a vocalight. It is worthy of note, however, that the amplitude variation noted in the 1989 tapes by no means negates the usefulness of the few experiments that were conducted with the final version of the protocol in 1989. The paired design of stimulus presentations should factor out attention to amplitude alone by any of the target animals. The tapes were remade in an effort to reduce variation in responses due to irrelevant variables.

3.2.4 Final Protocol

In the final protocol, experiments consisted of 5 phases: (1) a 2 minute, 5 second pre-trial period; (2) a 30 second playback; (3) a 5 minute, 5 second post-trial period; (4) another 30 second playback; (5) a 5 minute, 5 second post-trial period. Though there were only 30 seconds of sound on each stimulus tape, a 40-second period was allocated for the playback, to allow time for the leader on the tape and the response time of the experimenter. In general, this produced an extra 5 seconds in the pre-trial period and an extra 5 seconds in the post-trial period. Playback apparatus included a University Sound underwater speaker, and a Marantz PMD-430 stereo cassette deck attached to a 90 watt amplifier. The underwater speaker was the greatest constraint on the frequency response of the system, as it reproduced sounds faithfully only up to 11 kHz. However, since a great deal of energy of most *Tursiops* whistles is present below 11 kHz, and since the target animals did respond strongly (section 3.3.2.1), it appears that this speaker produced a satisfactory reproduction of the whistles. Recordings of each playback were made with a Panasonic AG-6400 hifi VCR, and hydrophones designed by Peter Tyack (Tyack 1985, Chapter 2). All five phases were videotaped for later analysis.

The layout for the experiments is shown in Figure 3.1. People stationed around the target animal held measuring tapes in air at right angles, which facilitated measurement of head turns toward and away from the speaker (see section 3.2.5.1). If the target animal was a female with a dependent calf, the calf was held in the position marked "DC" in Figure 3.1. It was held at a 90 degree angle to the playback speaker so that orientations of the target animal toward the speaker and toward the dependent calf could be differentiated. In one case, a pair of target animals was caught simultaneously with a third animal, which was held in the "DC" position for each of the playback experiments. This was done so that both experiments were conducted under as similar conditions as possible. Both experiments were conducted when the two target animals were not able to see or hear one another (one was being processed on the deck of a boat during playback to the other; see Chapter 2). In all other cases, only one member of a pair was caught at a time, and no animal was held in the "DC" position unless it was a dependent calf of the target animal.

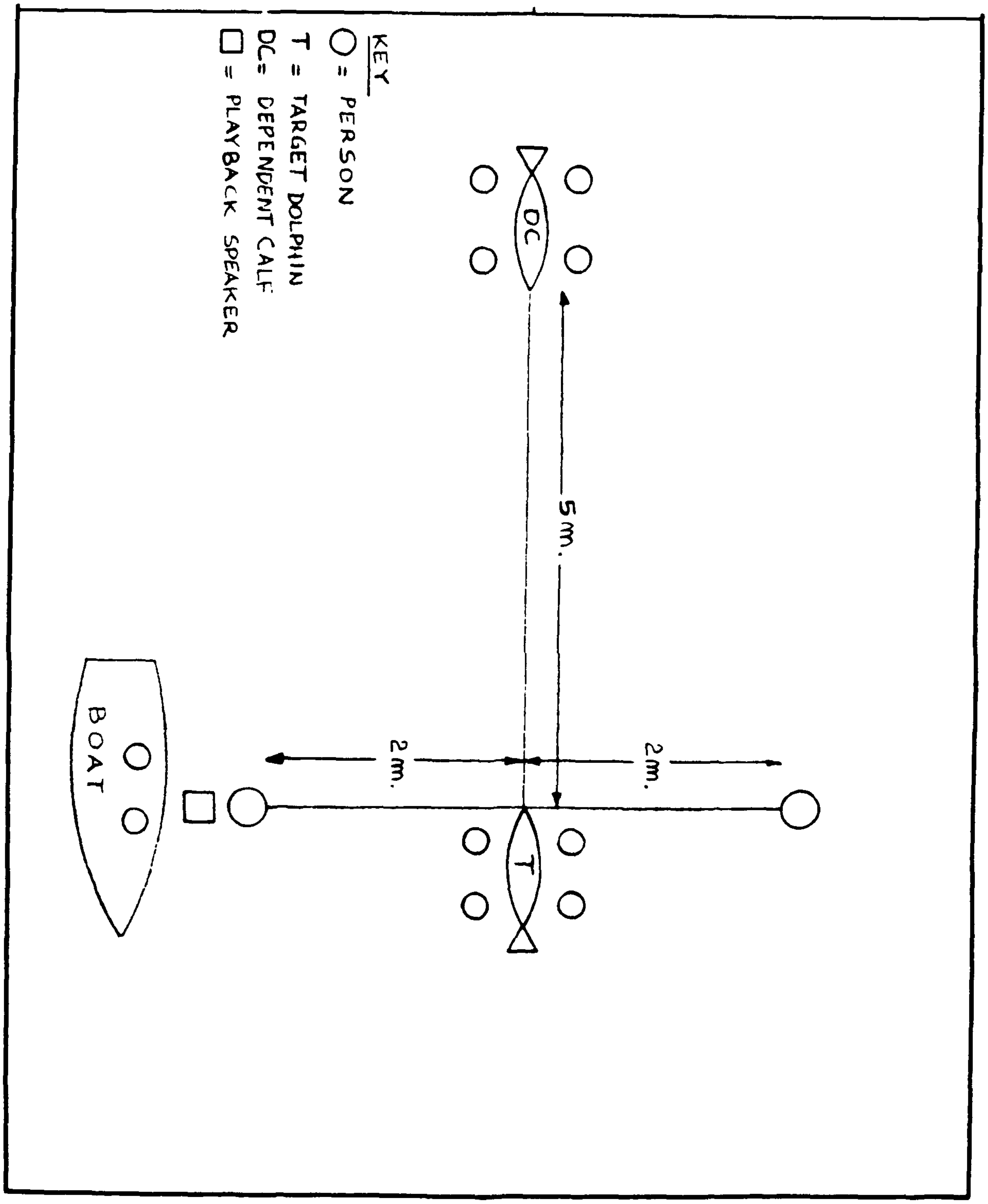

Figure 3.1. Schematic drawing of the layout for the playback experiments (not drawn to scale).

3.2.5 Analysis

Strength of the target animals' responses to playbacks were assessed through analyses of head turns toward the speaker and whistle production. These are described in detail below.

3.2.5.1 Head turns

Head turns toward the playback speaker primarily represent efforts by the target animal to echolocate on the source of the whistles,[5] and perhaps also to locate the source visually. Echolocation clicks were abundantly apparent in recordings of the target animals, and occurred almost without exception during head turns.[6] Thus, head turns were measured in order to determine whether target animals turned more in response to the predicted stimulus (e.g., did mothers/ independent offspring turn more in response to playback of their independent offspring/ mother, etc.).

a) Number of turns

Head movements toward or away from the playback speaker throughout the entire experiment were scored in three categories: a) greater than 20 but less than 45 degrees; b) between 45 and 90 degrees; c) greater

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[5] Since echolocation is highly directional (Norris et al. 1961), an animal must be oriented in the direction of an object of interest in order to effectively "visualize" it.

[6] During the experiments, target animals were prevented from echolocating directly onto the playback speaker by placing it behind a person's body.

than 90 degrees. Anything less than 20 degrees was not counted as a turn, since animals frequently move back and forth within a 20 degree turning radius. Turns 45 degrees or greater were considered strong turns.

Videotapes of four pairs of experiments completed between 1989 and 1991 were scored both by myself and by Janet McIntosh, a summer student fellow in the laboratory in 1990 and a research assistant in 1991. McIntosh was not familiar with any of the animals or their whistles, and she did not hear the whistles that were associated with the experiments while scoring head turns. She did not know in any case which stimulus was predicted to evoke the stronger response. In each case, her blind scores were remarkably consistent with my own. Out of 80 possible scores (8 experiments (4 pairs)), 5 "phases" each (pretrial, playback #1, etc.), and scores for turns toward or away from the speaker), 49% of ours were exact matches, and 89% differed by 2 or fewer turns. Since four additional pairs of experiments were completed in 1992 that were scored only by myself, I used only my scores for all eight pairs of experiments for the sake of consistency.

Head turns that occurred during the 30-second playback period were combined with those that occurred during the ensuing post-trial interval for analysis (the mean number of head turns toward the speaker during 30-second playback periods was only 2.8). Turns toward and away from the speaker in response to the two playback stimuli were compared within each pair to test the hypothesis that responses were greater to the predicted stimuli (against the null hypothesis that there were no differences in response). Data were analyzed with two-tailed chi-squared tests using 2 X 2 contingency tables. Fisher's method was used to combine the resulting P values, to test the null hypothesis of randomness in all m experiments, using the statistic:

$$S=-2\sum_{j=1}^{m} lnP_j$$

where P_j is the P value of the test in experiment j (j = 1...,m). This statistic has a chi-squared distribution with 2m degrees of freedom under the null hypothesis (e.g., Birnbaum 1954).

An additional indication of the salience of a particular playback stimulus is the occurrence of turns greater than 90 degrees (called "very strong turns"). These turns were relatively rare, resulting in sample sizes that were too small for the chi-squared test described above. Therefore, in order to test the hypothesis that very strong turns occurred more frequently in response to predicted stimuli (against the null hypothesis that they occurred equally in response to both stimuli), a binomial test was used.

b) Latency of turning response

In order to determine whether target animals responded more quickly to the predicted playback stimulus, latency (in seconds) to turn toward the speaker after the onset of the first stimulus whistle was calculated. A binomial test was used to test the hypothesis that shorter latencies occurred in response to the predicted stimuli, as opposed to the null hypothesis that they occurred at random.

3.2.5.2 Whistles

Bottlenose dolphins use whistles extensively in communication, and they engage in whistle exchanges in the Sarasota capture-release projects (Sayigh et al. 1990). Thus, whistle responses were measured in order to determine whether target animals whistled more in response to the predicted stimuli (e.g., did mothers/independent offspring whistle more in response to playback of their independent offspring/mother, etc.). Whistles produced by the target animals throughout the entire playback period were counted and classified as signature or variant (see Chapter 2).

a) Number and types of whistles produced

As described for head turns, whistles that occurred during the 30-second playback period were combined with those that occurred during the ensuing post-trial interval for analysis. Numbers of signature and variant whistles produced in response to the two playback stimuli were compared within each pair to test the hypothesis that more whistles were produced in response to the predicted stimuli (against the null hypothesis that there were no differences in response). Data were analyzed as described above for head turns.

b) Amount and latency of whistle response

The percentages of responses to whistles in each stimulus sequence were calculated in order to determine whether target animals were more likely to respond to the predicted stimuli. This differs from counting the total number of whistles produced during the 30-second playback trial and the ensuing 5 minute interval (section a above) in that it only quantifies actual responses. A whistle was classified as a response if it occurred within one second of the end of a stimulus whistle (or before the end). This measure should account for all responses, since Solow et al. (in press) found that most responses of one mother to the whistles of her calf occurred approximately one second after the start of a calf whistle. The number of whistles in a stimulus sequence ranged from 3 to 16, in accordance with the natural timing of whistle sequences of each stimulus animal.

Latency (in seconds) to respond to each whistle in a stimulus sequence was calculated in order to determine whether target animals responded more quickly to the predicted playback stimuli. This was accomplished by subtracting the start time of each stimulus whistle from the start time of each response. Solow et al. (submitted) found that start-to-start intervals were a better measure of response times than end-to-start intervals, because interruptions were common. Mean latencies were calculated for each playback. However, if individuals did wait until the end of a stimulus whistle to respond, the length of stimulus whistles could bias these results. For example, if an individual responded 0.1 seconds after the end of a stimulus whistle that was 1.0 seconds long, the start-to-start time would be 1.1 second. If the same individual responded 0.5 seconds after the end of a stimulus whistle that was 0.5 seconds long, the start-to-start time would be 1.0 seconds. Since average lengths of stimulus whistles were variable (Table 3.5), comparisons of mean start-to-start times between the two playbacks for a given individual are not as informative as comparisons of responses to the same stimulus by each member of the pair.

Table 3.5. Mean length (in seconds) of stimulus whistles used in 30-second stimulus presentations, for four paired trials. Standard deviations are in parentheses.

Target pair	Playback #1	Playback #2
Independent offspring		
1. #142 #144	0.87 (.18)	1.17 (0.19)
2. #148 #140	1.23 (.02)	0.99 (.05)
Mothers		
3. #22 #16	0.89 (.02)	0.75 (.17)
Other females		
4. #48 #23	1.00 (.38)	1.32 (.42)

3.3 RESULTS

3.3.1 Sample size

From 1989-1992, 31 playback experiments were completed, which included 17 playbacks to independent offspring, 9 playbacks to mothers, and 5 playbacks to females from different bands (hereafter called "other females"). However, the paired playback for 9 of these experiments could not be completed. Two target animals required to complete pairs died, and one target animal had a calf in 1991 (since calves are not caught until they are two years of age, this individual will not be caught again before 1993). Six trials were not completed because one of the stimulus animals died or disappeared; playback of whistles of dead animals might confound the results of the experiments. Of the 22 remaining experiments, 16 are completed paired trials, consisting of five pairs of independent offspring, two pairs of mothers, and one pair of other females (Table 3.6). The other six pairs may be completed in future capture-release sessions.

Table 3.6. Identification numbers (assigned by R. S. Wells) of target animals in each of eight completed paired playback trials. The year that each experiment was conducted is in parentheses.

Independent offspring

1. #142, #144 (1989, 1990)
2. #140, #148 (1991)
3. #160, #164 (1990, 1992)
4. #159, #144 (1991, 1992)
5. #3, #2 (1990, 1992)

Mothers

1. #16, #22 (1990, 1991)
2. #16, #32 (1989, 1992)

Other females

1. #48, #23 (1990, 1991)

3.3.2 Analysis of completed pairs

3.3.2.1 Head turns

a) Number of turns

Number of head turns toward the playback speaker was a strong indicator of response to the playbacks. Animals turned toward the speaker significantly more often during and after presentation of the predicted versus the non-predicted stimuli (p = .0002, Tables 3.7 and 3.8). In playbacks to independent offspring, mothers, and other females, stimuli predicted to evoke a stronger response were the mother, independent offspring, or female associate, respectively. Table 3.7 shows numbers of turns both toward and away from the speaker; all angles of turns were lumped for analysis, although numbers of strong turns are shown in parentheses. The data are condensed even further in Table 3.8, where only turns toward the speaker during the two playback periods are listed. There were no significant differences in turns away from the speaker ($p > 0.2$).

Very strong head turns occurred significantly more often in response to predicted stimuli (binomial test, $p < 0.0001$). Although these turns occurred only 17 times over all trials (with 5 out of 16 individuals producing at least one strong turn), 15 of these occurred in response to predicted stimuli.

Table 3.7. Total head turns toward and away from the playback speaker in eight paired playback trials. Turns during the playback were lumped with those produced in the following post-trial period. Numbers in parentheses indicate turns 45 degrees or greater.
In each case, * marks the stimulus predicted to evoke a higher response.

Target Pairs	Pretrial (125 seconds)	Playback #1 (335 seconds)	Playback #2 (335 seconds)
Independent offspring			
1. #14			
Toward	6 (4)	**12 (8)***	8 (3)
Away	5 (3)	**13 (9)**	13 (11)
#144			
Toward	1 (0)	1 (0)	**9 (1)***
Away	1 (1)	2 (1)	**1 (0)**
2. #148			
Toward	1 (0)	**6 (1)***	1 (0)
Away	4 (2)	**4 (0)**	2 (2)
#140			
Toward	12 (6)	43 (29)	**44 (25)***
Away	6 (5)	17 (9)	**15 (7)**
3. #164			
Toward	10 (5)	**21 (6)***	7 (3)
Away	5 (2)	**7 (2)**	8 (0)
#160			
Toward	4 (2)	22 (5)	**18 (5)***
Away	4 (2)	12 (6)	**9 (1)**
4. #2			
Toward	6 (1)	**14 (3)***	3 (0)
Away	1 (0)	**0**	1 (0)
#3			
Toward	12 (5)	31 (25)	**29 (14)***
Away	8 (6)	23 (21)	**23 (17)**
5. #144			
Toward	0	**3 (1)***	7 (2)
Away	0	**5 (1)**	5 (1)
#159			
Toward	1 (0)	3 (0)	**6 (1)***
Away	0	0	**2 (1)**

Target Pairs	**Pretrial (125 seconds)**	**Playback #1 (335 seconds)**	**Playback #2 (335 seconds)**
Mothers			
6. #22			
Toward	2 (0)	**18 (9)***	10 (1)
Away	4 (0)	**9 (0)**	7 (1)
#16			
Toward	10 (3)	22 (7)	**24 (11)***
Away	13 (4)	18 (6)	**24 (16)**
7. #32			
Toward	12 (6)	**32 (11)***	23 (10)
Away	9 (7)	**24 (18)***	15 (8)
#16			
Toward	11 (4)	29 (10)	**45 (35)***
Away	9 (3)	14 (7)	**10 (3)***
Other Females			
8. #48			
Toward	1 (0)	**3 (1)***	1 (1)
Away	0	**0**	0
#23			
Toward	8 (4)	9 (5)	**21 (17)***
Away	0	1 (0)	**0**

Table 3.8. 2 X 2 contingency table analysis (two-tailed) of total turns toward the speaker in response to the predicted versus the non-predicted ("other") stimulus in eight paired playback trials. Data are condensed from Table 3.7; again, numbers in parentheses refer to strong turns (45 degrees or greater).

Target Pair	Predicted stimulus	Other stimulus	p value
Independent offspring			
#142	12 (8)	8 (3)	**0.010**
#144	9 (1)	1 (0)	
#148	6 (1)	1 (0)	**0.059**
#140	44 (25)	43 (29)	
#164	21 (6)	7 (3)	**0.091**
#160	18 (5)	22 (5)	
#2	14 (3)	3 (0)	**0.022**
#3	29 (14)	31 (25)	
#144	3 (1)	7 (2)	**0.841**
#159	6 (1)	2 (1)	
Mothers			
#22	18 (9)	10 (1)	**0.163**
#16	24 (11)	22 (7)	
#32	32 (11)	23 (10)	**0.032**
#16	45 (35)	29 (10)	
Other females			
#48	3 (1)	1 (1)	**0.075**
#23	21 (17)	9 (5)	
Overall p value, using Fisher's method (see text):			**0.0002**

Head turns that occurred during the pretrial period were not factored into the analysis. These turns probably resulted from the animals scanning their new, unfamiliar surroundings. The playback design (Figure 3.1) required that the target animals be held with people stationed at various positions nearby. In seven of sixteen playbacks, the number of head turns declined between the first and second minutes of the pretrial period, indicating that the animals may have been acclimating to their surroundings. In three playbacks there was no change in number of turns between the first and second minute, and there were increases in the other six. Even if the animals were not yet acclimated to their surroundings, the paired design of these experiments would have corrected for any tendency of the animals to respond more strongly to the first stimulus. Within each pair, the order of stimulus presentations was the same, so the first stimulus was the one predicted to evoke a higher response for only one member of each pair. In this way, a tendency to respond more strongly to the first stimulus (a "surprise" effect) would have weakened the contrast between the two animals in each pair in the contingency table analysis.

b) Latency of turning response

In 10 of 16 playback trials, the target animal turned toward the speaker more quickly in response to the predicted stimulus. A binomial test yielded a p-value of 0.11, approaching significance. Latencies in response to the two playback stimuli were approximately the same in 2 trials, and there was a longer latency in response to the predicted stimulus in 4 trials.

3.3.2.2 Whistles

Whistle data were examined thoroughly for four paired playback trials that were completed between 1989 and 1991. No statistically significant trends were found in the numbers or types of whistles produced, the response latencies or the percentages of responses. Since whistles were not found to be a useful response category in analysis of the playbacks, they were not included in analysis of the four paired playback trials that were completed in June of 1992. Thus, data presented in this section are based solely on four paired playback trials; two with independent offspring, one with mothers, and one with other females.

a) Number and type of whistles

No significant differences ($p > 0.2$) were found in numbers of signature, variant, or total whistles produced in response to the two playback stimuli by either the mothers or the independent offspring (Table 3.9). There was a significant difference in signature whistle production in the playback experiment with females from different bands (Table 3.9). In this experiment, #23 produced a stereotyped, variant whistle that she had produced in previous capture sessions (Tyack 1991) in response to both playback stimuli. In the first post-trial period she produced a wide variety of variant whistles and no signature whistles. However, after the second playback, for which the source of the stimulus was a member of her female band, she produced many signature whistles, in marked contrast to her previous whistle production. Female #48 (with whom she was paired) did not respond in a parallel fashion, although she did produce more signature whistles (58 vs. 50) in the time period during and after playback of whistles of a member of her own matrilineal band. A 2 X 2 contingency table analysis (two-tailed) of number of signature whistles produced by the two females during the two playback intervals showed that there was a significant difference in their responses to the two playback stimuli ($p < .0001$, Table 3.9).

c) Amount and latency of whistle response

Only the female-female pair responded in the predicted direction in percentages of whistle responses to the two playback stimuli. Female #23 responded to 9/12, or 75% of the whistles of a member of her own female band, as opposed to 8/16, or 50% of the whistles of a (familiar) member of a different female band. The female with whom she was paired, #48, also responded in the predicted direction (Table 3.10, pair #4). In two of the remaining three pairs (pairs #1 and #3 in Table 3.10), one individual responded in the predicted direction (with a greater percentage of responses

Table 3.9. Numbers of signature and variant whistles produced in four paired playback trials. Whistles produced during the playback were lumped with those produced in the following post-trial period. P values correspond to 2 X 2 contingency tables (two-tailed) comparing the numbers of signature whistles in paired trials; all comparisons of variant whistles and total whistles were not significant. * indicates the stimulus predicted to evoke a higher response for each individual.

Target Pair	Pretrial (125 seconds)	Playback #1 (335 seconds)	Playback #2 (335 seconds)	P
Independent offspring				
1. #142				NS
Signature	8	14*	25	
Variant	28	37	30	
#144				
Signature	18	27	33*	
Variant	0	11	2	
2. #148				NS
Signature	14	33*	33	
Variant	3	5	6	
#140				
Signature	30	86	80*	
Variant	0	0	0	
Mothers				
3. #22				NS
Signature	12	56*	40	
Variant	4	4	5	
#16				
Signature	5	18	13*	
Variant	0	6	4	
Other females				
4. #48				< 0.0001
Signature	[illegible]	58*	50	
Variant	0	1	1	
#23				
Signature	3	0	40*	
Variant	4	58	22	

to the predicted stimulus), but the other individual showed the opposite of the predicted response. In the remaining pair (#2 in Table 3.10), one individual showed the same percentage of responses to both stimuli, and the other showed the opposite of the predicted response.

The mothers were the only pair which showed even weak whistle response latencies in the predicted direction (shorter in response to their own offspring; #3 in Table 3.10). However, the differences were very slight. In both pairs of independent offspring and in the pair of other females, one individual was quicker to respond to both stimuli than was the other individual. Results are summarized in Table 3.10.

3.4 DISCUSSION

The results of these playback experiments demonstrate that bottlenose dolphins are capable of discriminating between whistles of different familiar individuals, and strongly suggest that they recognize one another's signature whistles. Target animals in the experiments consistently showed a stronger response, in the form of head turns, to the predicted stimulus, which was either the mother, an independent offspring, or a close female associate. In addition, most occurrences of very strong head turns (> 90 degrees) were in response to predicted stimuli. All mothers used as targets and stimuli had had new calves since their association with

Table 3.10. Proportion of playback whistles to which the target animal responded (percentages are in parentheses), and average start-to-start time (in seconds) of these responses, for four paired trials.
* indicates the stimulus predicted to evoke a higher response for each individual.

Target pair	Playback #1	Playback #2
Independent offspring		
1. #14		
Responses	**2/10 (20)***	8/10 (80)
Avg. start-start	**1.86**	1.13
#144		
Responses	2/10 (20)	**9/10 (90)***
Avg. start-start	1.08	**1.12**
2. #148		
Responses	**6/7 (86)***	3/3 (100)
Avg. start-start	**0.99**	1.03
#140		
Responses	7/7 (100)	**3/3 (100)***
Avg. start-start	1.34	**1.43**
Mothers		
3. #22		
Responses	**4/5 (80)***	4/8 (50)
Avg. start-start	**1.01**	1.26
#16		
Responses	3/5 (60)	**2/8 (25)***
Avg. start-start	1.19	**0.96**
Other females		
4. #48		
Responses	**4/16 (25)***	1/12 (8)
Avg. start-start	**1.29**	1.61
#23		
Responses	8/16 (50)	**9/12 (75)***
Avg. start-start	0.74	**1.15**

the relevant stimulus or target offspring. Similarly, all offspring used as targets and stimuli had been independent for periods ranging from one to fourteen years and had formed close associations with other individuals. Since separation from their mothers, they showed low rates of association with their mothers and with the other adult females used in the experiments. Thus, it is highly unlikely that discriminations were based strictly on a familiar versus unfamiliar basis, wherein individuals simply habituate to frequently heard stimuli (e.g., see section 3.1.1).

In the female-female playbacks, both females whose whistles were used as stimuli associated with the target animals at similar rates. Both target animals had dependent offspring, yet both also responded preferentially to whistles of a member of their female band. These discriminations involve more than a simple, dichotomous (i.e., familiar versus unfamiliar) classification. Monogamous, territorial birds may also have to identify mate, offspring and neighbors simultaneously, although these discriminations are all strongly supported by locational cues. Mate and offspring are at the nest, neighbors are in a particular location (or they will be perceived as strangers). For dolphins living in a fluid, "fission-fusion" type society, locational cues are either nonexistent or unreliable. Problems could arise if, for example, an extremely vocal individual were a close associate of a mother-calf pair. If responses to whistles were based purely upon familiarity, this could cause confusion for a calf attempting to identify its mother.

Overall, these results indicate that dolphins recognize one another on a truly individual basis, as has been found for many primate species (section 3.1.3). Many primate social relationships are based upon knowledge of the histories of interactions among individuals in their social group (as discussed in section 3.1.2.3; see Essock-Vitale and Seyfarth 1986, Dasser 1985). The long-term, individually specific bonds that characterize the "fission-fusion" societies of bottlenose dolphins provide parallels with many primate societies (e.g., in alliance formations; see Connor et al. 1992). Dolphins interact repeatedly with many different individuals over periods of many years. It seems likely that recognition of individuals is important in maintaining these long-term associations, and that signature whistles function in effecting this recognition.

As in other studies of individual recognition (e.g., Cheney and Seyfarth, 1980), there was a considerable amount of inter-individual variation in responses. In the Sarasota capture-release projects, which typically take place once or twice per year (Chapters 1 and 2), inter-individual variability in vocal production can be obvious even to naive observers; certain animals are simply more or less vocal than others, year after year. For a given individual, variation in whistle production can also be seen in recordings from different years. This may relate to the immediate behavioral state of an animal (e.g., how recently it has fed, or had an aggressive encounter with another individual). Such factors could also have affected the strength of different individuals' responses to playbacks. Also, since both playback stimuli in every experiment were recorded from living animals present within the community, it seems possible that recent experiences (e.g., aggressive or affiliative interactions) involving the target and stimulus animals could also affect responses. If dominance relationships exist among free-ranging dolphins, this could also be a factor affecting strength of response. For example, an individual might respond more strongly to an individual other than its mother if that individual held high dominance status. Strength of response of a target animal could also be affected by knowledge of the location of a stimulus animal. For example, a greater response might be elicited if a target animal had recently associated with a stimulus animal in a distant portion of the home range.

Another factor that could increase inter-individual variability in responses to playbacks is the "surprise" effect, which could cause some animals to respond more strongly to the first of two playback stimuli because of its novelty. This "surprise" effect could explain why several individuals (#140, #160, #3 and #16 in trial #6, Table 3.7) responded more or less equally to the two stimuli; the first was salient because of its novelty, the second because of the identity of the vocalizer. Such cases still provide a strong control in this paired design: since response levels to the two stimuli were fairly equal, one stimulus is not simply more salient than the other. In all of these cases, the other individual in the pair responded strongly in the predicted direction, resulting in chi-square values that approached significance.

Intra-individual variation is also apparent in comparisons of responses of two individuals that were target animals in two different experiments in different years (Table 3.10: #144 in pairs #1 and #5; #16 in pairs #6 and #7). In 1990, #144 responded more strongly to whistles of her own mother than to those of the mother of #142. In 1992, however, she showed the opposite of the predicted response. This was the only one of the eight paired trials in which the p-value did not approach significance ($p = 0.841$). Any of the several factors discussed above could account for this difference. Another possibility is that the second stimulus used in the 1992 experiment may have been particularly salient for some reason. Also, in 1992 #144 had been a subject in an energetics study for which she remained in the net corral for 3 hours, substantially longer than usual (Chapter 2). The playback experiment was conducted at the end of this period, after the other animals with which she had been caught were released, so that it would be more comparable to the paired trial with #159, who was caught by herself. Perhaps the increased duration of time that she was held temporarily captive affected her response.

The other animal that was a target animal in two different experiments (#16) responded in the predicted direction in both trials, although in 1990 her responses were more equivocal, perhaps as a result of the "surprise" effect discussed above. Finally, the possibility can not be ruled out for either individual that a memory of the previous experiment somehow effected the intra-individual variability observed.

Whistle responses to playbacks in most cases did not conform to predictions. The lack of whistle responses by the target offspring (only 2 pairs were analyzed - see section 3.3.2.2) was perhaps not surprising in light of timing analyses of two mother-calf whistle exchanges (Solow et al., in press). The calf in this analysis showed no tendency to respond to his mother's whistles at either 18 months or 3 years of age. The mother showed a strong tendency to respond to her calf's whistles, but note that the calf in this analysis was dependent. Both target mothers whose whistles were analyzed (section 3.3.2.2) had dependent offspring with them during the experiments. So, if a primary function of signature whistles is for mothers to maintain contact with dependent calves, this may have prevented these mothers from responding vocally to the playback stimuli. Even so, the mothers were the only target pair which showed even a weak response latency in the predicted direction (Table 3.10).

Different uses of whistles outside of the context of a mother-calf contact call may be reflected by the significant differences in whistle production shown by the pair of females from different female bands. These females responded in the predicted direction to the playbacks both in the percentage of whistles to which they responded and in the overall numbers of signature whistles they produced. One of these females (#23) showed significant variability in both signature and variant whistle production in response to the two playback stimuli. If stereotyped whistle production is more important for maintaining contact with calves, variant whistles may occur more often in communication among adult animals. More playback experiments with females from different bands are needed before conclusions can be drawn from these results. Additional experiments have the potential to shed light on complexities of signature and variant whistle usage.

Future research on individual recognition in bottlenose dolphins could explore the extent to which individuals recognize relationships among other individuals. For example, as discussed earlier, Cheney and Seyfarth (1980) found that vervet monkey females not only recognized screams of their own offspring, but also that they were able to associate screams of particular juveniles with the appropriate mother. Playback experiments in which whistle exchanges between a mother-calf pair were contrasted with whistle exchanges between the same mother (or calf) and a different individual could perhaps begin to detect recognition of affiliations. However, it is not at all clear whether the "correct" or "incorrect" exchange would provoke a greater response. Even more telling might be playbacks conducted opportunistically in situations where relationships among individuals are changing, such as before and after a calf separates from its mother, or when males in a coalition shift affiliations (Connor et al. 1992). Such studies would need to take advantage of situations opportunistically, as they arose. However, the subtleties of individual relationships in bottlenose dolphins are only beginning to be explored, so these experiments could easily be confounded by unknown factors.

Even given such opportunities, these experiments would be challenging with free-ranging dolphins, given the constraints on visibility and opportunities to conduct experiments. They therefore might better be attempted with captive animals, where more subtle responses can be observed and trials can be repeated. Facilities with large captive breeding groups could provide a wide enough range of relationships among individuals to detect recognition of affiliations and changes among them. Östman (1991) and Samuels et al. (1991) have conducted detailed studies of dominance relationships among captive animals. However, differences in captive and wild environments necessitate that results obtained in captivity be validated in the wild.

As more knowledge accrues about the social behavior of bottlenose dolphins both in the wild and in captivity, we will be in a better position to begin studying the subtleties of their vocal communication. The results presented here provide a strong basis for integrating work on individually-specific social relationships and communication in these interesting mammals.

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CHAPTER 4: SEX DIFFERENCES IN SIGNATURE WHISTLE PRODUCTION

Portions of this chapter were published in Behavioral Ecology and Sociobiology (26:247-260) with P. L. Tyack, R. S. Wells, and M. D. Scott as coauthors.

4.1 INTRODUCTION

In analysis of signature whistle contours of individuals recorded during the Sarasota capture-release projects, I discovered sex differences in the tendency of calves to produce whistles similar or dissimilar to those of their mothers, and in their tendency to produce variant whistles (whistles other than the signature). These results and hypotheses as to why they occur will be discussed in the context of what is known about sex differences in vocalizations of other species.

Sex differences in animal vocalizations are widespread, and can occur in many different ways. As outlined by Green (1981), differences can arise when only one sex produces a particular sound, when the sexes differ in the usage of particular vocalizations, or when the acoustic structure of a particular sound or sounds differs between the sexes. Examples of sounds produced only by males are numerous; these tend to function for territory defense and mate attraction. Obvious examples include sounds produced by many species of frogs or toads (e.g., Davies and Halliday 1978, Davis 1987), songbirds (e.g., Baptista and Petrinovich 1986, Kroodsma 1982, Marler et al. 1988, Searcy and Brenowitz 1988), and primates (e.g., mangabey "whoopgobbles" (Waser 1977), "loud calls" of lion tailed macaques (Green 1981), long calls of orangutans (Galdikas and Insley 1988), and gorilla "roars" (Marler and Tenaza 1977)). Among marine mammals, male sperm whales (Weilgart and Whitehead 1988), humpback whales (Payne et al. 1983), northern elephant seal bulls (Shipley et al. 1986), and walruses (Stirling et al. 1987) produce distinctive, apparently sex-specific vocalizations.

Examples of sex differences in vocal usage include alarm calling in ground squirrels (Sherman 1977), where females produce a disproportionate amount of such calls. Females tend to be related to more group members than do males, so they stand to benefit more in terms of inclusive fitness (Hamilton 1964) by alarm calling. Cohesion calls of Roosevelt elk are produced more often by females than males (Bowyer and Kitchen 1987). Male rat pups produce more ultrasonic distress calls than females in mixed-sex litters (Naito and Tonoue 1987). Several examples of vocalizations of lion-tailed and Japanese macaques that differ in usage between the sexes are outlined by Green (1981). Finally, the verbal abilities of human girls develop faster than those of boys (Maccoby and Jacklin 1974).

Sex differences in acoustic structure of vocalizations can result from dimorphism in the size of the vocal tract (e.g., see Green 1981, Gould 1983, Murry and Singh 1980, Singh and Murry 1978). Marler and Hobbett (1975) stated that "there are ample cues available for a listening chimpanzee to establish the sex of distant pant-hooting...". Ultrasonic distress calls of female rat pups tend to be of shorter duration than those of males (Naito and Tonoue 1987). Sex differences in both of these examples could be a morphologically based. There are few examples in the literature of sex differences in acoustic structure of vocalizations that are not due to morphological differences. Gouzoules and Gouzoules (1989) found that young male pigtail macaques were less proficient than young females at both the production and proper contextual usage of calls used for recruitment of aid in agonistic encounters. These recruitment calls varied in acoustic structure according to the type of agonistic encounter in which an animal was engaged (e.g., contact aggression with a higher-ranking opponent, non-contact aggression with a lower-ranking opponent, etc., Gouzoules et al. 1985). Gouzoules and Gouzoules (1989) hypothesized that, since dominance rank is associated with matrilineal kinship in this species, and since females remain in their natal groups while males emigrate, recruitment screams may be less important for males than females as they grow older.

This chapter presents data documenting sex differences in whistle production among free-ranging bottlenose dolphins, *Tursiops truncatus*. First, male calves are more likely than female calves to produce individually distinctive signature whistles (Chapters 2, 3) very similar to those of their mothers. Female calves are more likely than male calves to produce signature whistles highly dissimilar to those of their mothers. Second, male calves apparently produce more whistles other than the signature whistle (termed "variant" whistles) than do females. As has been discussed previously, examples of such sex differences in usage of vocalizations are fairly widespread. However, the sex difference in the tendency to produce a signature whistle similar or dissimilar to that of the mother is a phenomenon for which there are no direct parallels available in the literature. The reason for this may be two-fold. First, many terrestrial animals rely on voice cues for individual recognition, because differences in vocal tract morphology provide ample information on individual identity (Tyack 1991, Chapter 3). Thus, species that have been the focus of most research to date simply do not produce the type of vocalization for which this sex difference was observed, i.e., individually distinctive vocalizations. Second, among free-ranging cetaceans (for which individually-distinctive vocalizations are fairly common (Chapter 3)), opportunites to record many individuals of known sex and maternity are extremely rare. Such an opportunity has been provided by the long-term research study of a resident community of bottlenose dolphins in waters near Sarasota, Florida (Wells et al. 1987, Chapters 1 and 2).

Signature whistles of 42 calves and their mothers were compared to look for similarities and differences. Similarity of dolphin whistles is difficult to quantify, since features such as absolute frequency and duration vary even among repetitions of one dolphin's signature whistle (Figure 4.1). Programs designed to assess similarity quantitatively (e.g., Clark et al. 1987 for bird song) do not allow for such variation. However, the human eye is quite good at judging overall shapes, such as those shown in Figure 4.1, as similar or different. Therefore, human judges were asked to rate the similarity of whistle contours of mothers and calves.

Methods and results are presented separately for comparisons of signature whistles of mothers and calves, which were the primary focus of this study, and for comparisons of variant whistle production between the sexes.

4.2 GENERAL METHODS

Background on the study site and the capture-release projects during which recordings were made, as well as details on recording techniques, are presented in Chapters 1 and 2.

4.3 MOTHER-CALF COMPARISONS

4.3.1 METHODS

4.3.1.1 Sample size

Between 1975 (when recordings were made by M. Scott and P. Graycar, see Chapter 2) and 1990, 42 calves, 21 male and 21 female, were recorded during temporary capture (Table 4.1). Calves were recorded from one to seven times while with their mothers (a period ranging from 3 to 10 years), and 18 calves were also recorded at periods ranging from one to over 10 years after separation from their mothers. Two mothers were recorded with four different calves over the years, 8 with two calves, and 18 with one, for a total of 28 different mothers (Table 4.1).

Figure 4.1. Spectrograms showing the range of variability in duration and frequency content of one female's signature whistle. All forms, as well as others, are common. They do not represent a progressive change in the whistle. Spectrograms were made on a Kay Elemetrics Corporation Sonograph Model 7029A Spectrum Analyzer with a narrow band (90 Hz) filter setting and a frequency range of 160-16000 Hz. Frequency (kHz) is on the y axis and time (sec) is on the x axis.

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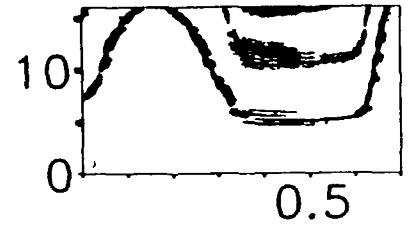
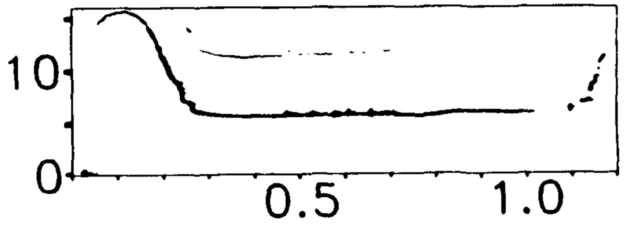
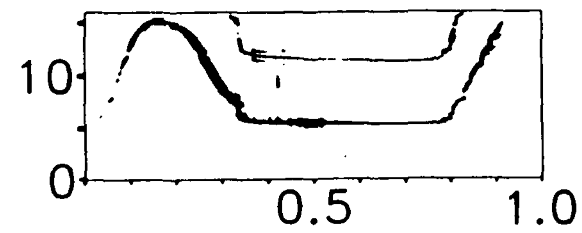






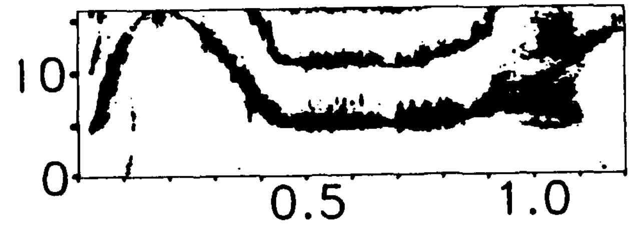


Table 4.1. Mother-calf pairs recorded during temporary capture between 1975 and 1990.

1975 - August-October
1976 - April-May
1984 - June-July
1985 - June-July
1986W - December 1986-January 1987
1986 - June
1987W - December 1987-January 1988
1987 - June
1988W - December 1988 - January 1989
1988 - June-July
1989 - June-July
1990 - June

Mother	Calf	Sex and (birth-date) of calf	Years recorded (* = calf only, + = temporary separation)
#5	#6	M(1980)	84, 86*, 87W*, 87*, 88W*
#5	#159	F(1986)	87, 88W, 88, 89W, 89
#9	#187	F(1988)	89
#23	#25	F(1981)	84, 86*
#23	#158	F(1986)	87, 88W
#22	#2	F(~1974)	76, 84*
#22	#148	F(1984)	85+, 86, 87W, 87, 88W, 88, 89W, 89
#151	#188	F(1988)	89
#8	#13	F(1980)	84, 87W*
#52	#164	F(1985)	88, 89
#32	#61	F(1983)	84, 85, 86*, 87*, 88*, 89W*
#32	#176	F(1988)	89W
#42	#67	M(1983)	87
#1	U	M(~1973)	75

Mother	**Calf**	**Sex and (birth-date) of calf**	**Years recorded (* = calf only, + = temporary separation)**
#1	#15	F(1982)	84, 85, 87*, 88W*, 89W, 89*, 90*
#48	#86	M(~1974)	76
#48	#170	F(1986)	89W, 89, 90
#2	#18	F(1982)	84
#10	#3	M(1973)	76, 84*, 87W*, 87*, 88*, 89*, 90*
#10	#17	M(1981)	85*, 88*
#10	#144	F(1984)	85, 87, 88W*, 88*, 89W*, 89*, 90*
#10	#166	M(1987)	88W, 89W, 89, 90
#28	#51	F(1983)	84, 85, 88*, 89
#7	#11	M(1974)	75, 84*, 87W*
#7	#12	M(1981)	84, 85*, 88*
#7	#142	M(1984)	85, 87W, 87, 88*, 89*
#7	#174	F(1988)	89
#35	#30	M(1975)	84, 87W*, 88*
#68	#147	F(1983)	85, 86
#16	#140	F(1984)	85, 86, 87, 88*, 89W*, 89*
#16	#177	M(1988)	89, 90
#4	#20	F(1982)	84, 85, 86, 87, 88W
#4	#173	M(1988)	88, 89, 90
#126	#129	M(~1974)	76
#79	#82	M(1979)	89W*
#182	#181	M(198?)	89W
#195	#194	F(198?)	89

Mother	**Calf**	**Sex and (birth-date) of calf**	**Years recorded (* = calf only, + = temporary separation)**
#50	#160	M(1985)	89, 90*
#215	#222	M(198?)	90
#216	#223	M(~1988)	90
#217	#226	M(1987)	90
#26	#33	M(1981)	89W*, 89*

4.3.1.2 Analysis techniques

At least one, and often two to three recording sessions of each mother-calf pair were monitored in order to determine the signature whistle of each animal. Most recording sessions of independent calves were also monitored. Before 1988, tapes were monitored by ear, and spectrograms were made on a Kay Elemetrics Corp. Sonograph Model 7029A Spectrum Analyzer with a narrow band (90 Hz) setting and a frequency range of 160-16000 Hz. Later analyses were performed on a Kay Elemetrics Corp. Model 5500 Digital Signal Processing System. With this system, tapes were also monitored by ear, but spectrograms of each whistle produced could also be viewed in real time.

4.3.1.3 Human judges' ratings of whistle similarity

Human judges were asked to make pairwise comparisons of signature whistles of mothers and calves, in order to assess similarity. An earlier sample (Sayigh et al.

1990) of 12 calves indicated that males tended to produce whistles similar to those of their mothers, and females tended to produce whistles highly distinct from those of their mothers. In order to quantify this trend, similarity was rated on a scale of one (not similar) to five (very similar). This numerical ranking system enabled calculation of reliability of judges' ratings, as described by Rosenthal (1982). This technique involved a two factor (mother-calf judgements and judges) analysis of variance of the similarity ratings. With the results of this analysis, estimates of R, the effective reliability of the ratings of all judges, and r, the reliability of a single average judge (p. 296, Rosenthal 1982) could be obtained using the following formulas:

$$R(est.) = \frac{MSjudgements - MSresidual}{MSjudgements}$$

$$r(est.) = \frac{MSjudgements - MSresidual}{MSjudgements + (n-1)MSresidual}$$

where n is the number of judges.

For the judges' ratings experiments, spectrograms were made of signature whistles (with good signal-to-noise ratios) of each of 42 calves and their mothers. These were then photocopied, without reduction and without frequency and time axes, onto 8½" x 14" paper (see Appendix I for a sample of one set of whistles used in the judgements). Calf whistles were divided into 5 groups of 10 each, so some calf whistles were judged by more than one group of judges. A total of 74 judges, divided into five groups containing from 13 to 18 judges each, rated the similarity of each of ten calf whistles to each of ten mother whistles, for a total of 100 judgements per judge (Appendix I).

Judges were instructed to focus on the overall shape, or contour, of the whistles rather than absolute frequencies or duration. They were also told to ignore harmonics and echolocation clicks on the spectrograms, and examples of these were shown. However, no examples of pairs of contours believed by the author to be similar or dissimilar were given. Finally, no information was available to the judges regarding the maternities of the calves.

Judges included undergraduates enrolled in a Boston University Marine Program course on marine mammals, marine mammal trainers at the New England Aquarium and the Brookfield Zoo, volunteer workers at the New England Aquarium, graduate students in the WHOI/MIT joint program, one research assistant, and staff and Earthwatch volunteers in Sarasota, Florida.

Each judge was first asked to rate the similarity of four calf whistles to four mother whistles (16 judgements) that were not included in their later judgements, in order to accomodate any learning curve that might be involved in the judgements. The remaining 100 judgements were made in a random order, so that each judgement was more or less independent of the others (i.e., so the judges were not able to compare the whistle of one calf to the whistles of all 10 mothers sequentially). The first 24 judges were instructed verbally as to the order in which to judge each pair of whistles (e.g., calf 2 to mother F, Appendix I). This order was randomized using a random number table prior to the judgement session. Judges were given 15 to 20 seconds for each comparison. This amount of time was a compromise between minimizing the overall amount of time needed to do the judgements, and allowing sufficient time to decide on a score.

For later judgement sessions (involving 50 judges), a different type of score sheet was used for two reasons. First, the earlier judges expressed dissatisfaction with the original score sheets, which were in the form of a grid (see Appendix I), because it was difficult to locate particular cells on the grid for writing their scores. Second, even though the order was randomized, all judges still did the judgements in the same order. So, if there was any learning curve in effect after the preliminary set of 16 judgements, this could potentially bias the results. So, on later score sheets the order in which the judges were to rate the various combinations was already printed out (e.g., C3, J7, etc., see Appendix I). These were randomized such that no two score sheets were the same. Judges were then given up to 30 minutes for all 100 judgements.

Judgement scores were entered into the spreadsheet program *Quattro Pro* (Borland Intl., Scotts Valley, CA), and reliabilities of the mean similarity scores were calculated as described above. Since the earlier sample of 12 calves (Sayigh et al. 1990) indicated that the whistles of females tended to be distinct from those of their mothers, and the whistles of males tended to be similar to those of their mothers, mean scores were divided into three equal categories: not similar (1.00 - 2.33), somewhat similar (2.34 - 3.66), and very similar (3.67 - 5.00). Nine pairs of whistles (5 male and 4 female) were rated somewhat similar; these whistles were neither obviously similar or different. Analysis focused on mean scores for the remaining 33 pairs, which fell into the not similar and very similar categories. Male and female calves were compared using a 2 X 2 contingency table and a chi-square test.

4.3.2 RESULTS

Mean judges' ratings of similarity between whistles of mothers and calves are shown in Figure 4.2. Effective reliabilities (R) of these mean scores ranged from .94 to .96 (mean .954), and reliabilities of a single average judge (r) ranged from .49 to .67 (mean .59). A 2 X 2 contingency table analysis of the not similar and very similar categories for males and females showed significant differences (chi square = 7.35, $p < .001$). 43% of males as opposed to 10% of females were rated very similar to their mothers, whereas 33% of males as opposed to 71% of females were rated not similar. Slightly more males than females were rated somewhat similar (24% versus

19%). Overall mean scores for males and females were 2.99 and 2.06 respectively. Examples of whistles rated 1.0 (female) and 5.0 (male) are shown in Figures 4.3 and 4.4. Further examples of whistles of several mothers and calves are shown in Figures 4.5-4.10 (female calves) and Figures 4.10-4.12 (male and female calves). These figures show spectrograms of whistles recorded from some animals in different years, to emphasize the stability of signature whistles (Chapter 2).

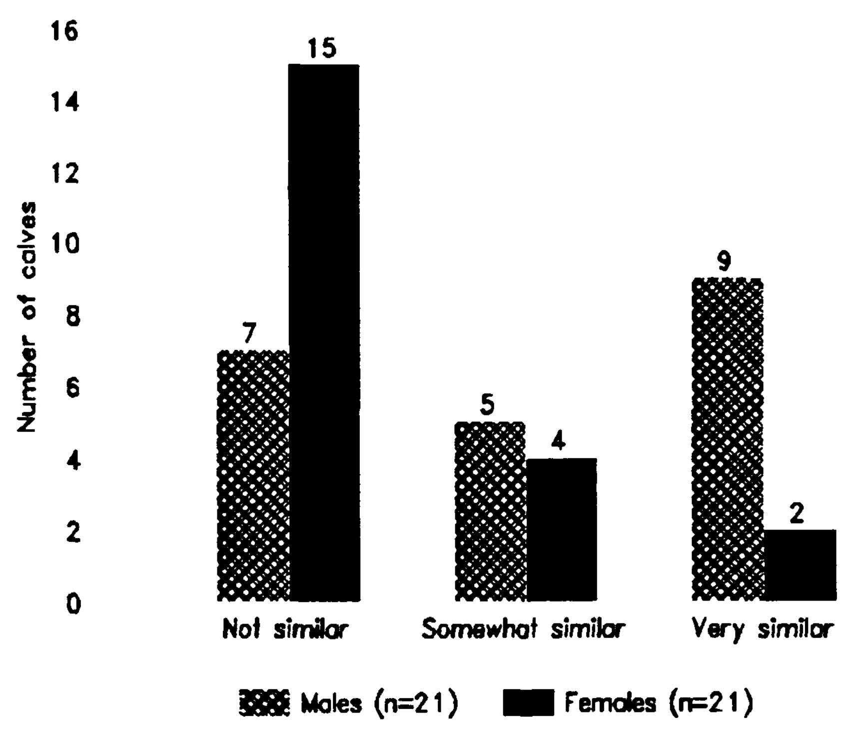


Figure 4.2. Judges ratings of whistle similarity between mothers and calves (see text for details on the rating system used).

Judges' similarity ratings for each mother-male calf pair are shown in Table 4.2, and for each mother-female calf pair in Table 4.3. The three male calves of each of two mothers (no. 7 and no. 10) clustered together with respect to the mean similarity of their whistles to those of their mothers' (Table 4.2). All of the whistles of no. 7's male calves were quite similar to their mother's (mean judges' score = 3.89, Figure 4.11), whereas all of the whistles of no. 10's male calves were quite different from their mother's (mean judges' score = 1.30, Figure 4.12). All of the other mothers were recorded with only one male calf each, so it was not possible to determine if this trend was widespread. Among female calves, a similar clustering was not evident, although the greatest number of female calves per mother was only two (see no. 23, no. 22, no. 32; Table 4.3). Mothers no. 7 and no. 10 were each recorded with a single female calf in addition to their three male calves (Table 4.3, Figures 4.11 and 4.12). The whistle of mother no. 7 was much less similar to that of her female calf, no. 174 (mean judges' score = 1.92), than to those of her male calves. The whistle of mother no. 10 was as dissimilar to that of her female calf, no. 144 (mean score = 1.20), as to those of her male calves.

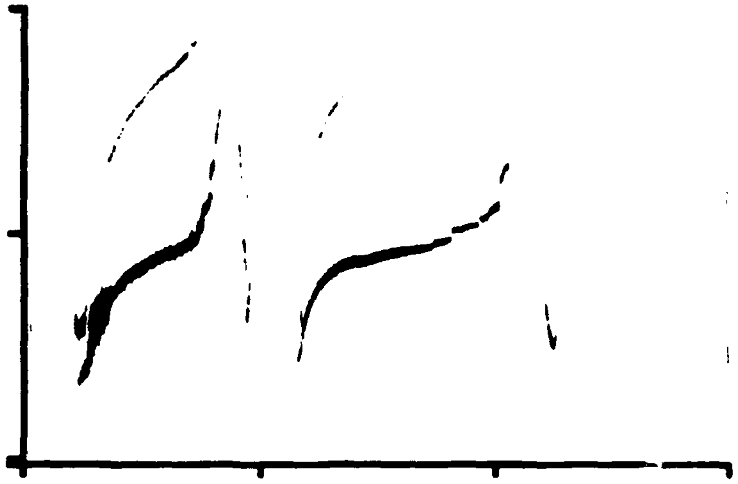
Table 4.2. Mean judges' ratings of similarity of whistles of mothers and male calves (in order of descending similarity, on a scale of 1 to 5).

Mothers	Male calves	Mean judges' rating
#50	#160	5.00
#26	#33	5.00
#215	#222	4.85
#126	#129	4.20
#216	#223	4.08
#217	#226	4.08
#7	#142	3.97
#7	#11	3.94
#7	#12	3.77
#1	U	3.39
#35	#30	3.00
#48	#86	2.57
#182	#181	2.47
#42	#67	2.33
#4	#173	1.98
#5	#6	1.67
#16	#177	1.54
#10	#3	1.39
#10	#17	1.31
#10	#166	1.20
#79	#82	1.00

Table 4.3. Mean judges' ratings of similarity of whistles of mothers and female calves (in order of descending similarity, on a scale of 1 to 5).

Mothers	Female calves	Mean judges' rating
#52	#164	4.20
#16	#140	3.80
#23	#158	3.31
#1	#15	2.92
#2	#18	2.77
#32	#176	2.73
#5	#159	2.31
#68	#147	2.17
#7	#174	1.92
#22	#2	1.72
#9	#187	1.67
#23	#25	1.67
#48	#170	1.67
#22	#148	1.60
#28	#51	1.53
#32	#61	1.39
#8	#13	1.28
#195	#194	1.27
#151	#188	1.20
#10	#144	1.20
#4	#20	1.00

Figure 4.3 (facing page). Spectrograms of whistles of mother no. 4 and her female calf, no. 20. These two whistles received a mean similarity score of 1.0 (least similar) from the judges. Spectrograms were made with a Kay Elemetrics Corporation Model 5500 Digital Signal Processing system, with a sample rate of 81,920 Hz, a 256 point FFT, and a Hamming window. Frequency (kHz) is on the y axis and time (sec) is on the x axis.


MOTHER NO. 4

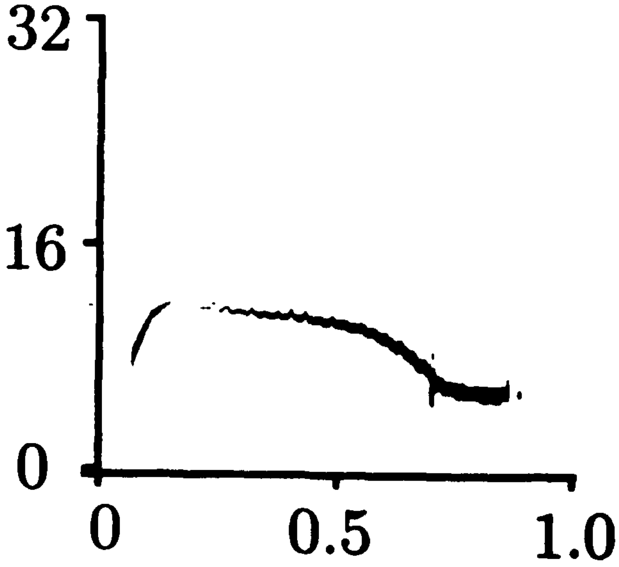
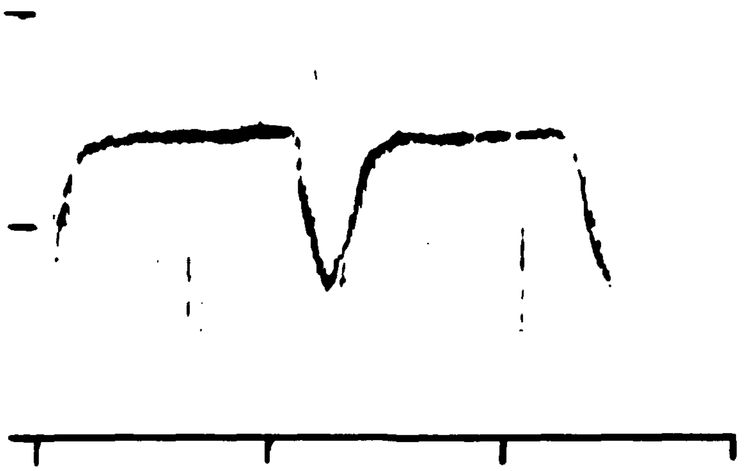

FEMALE CALF NO. 20
BORN 1982

Figure 4.4. Spectrograms of whistles of mother no. 26 and her male calf, no. 33. These two whistles received a mean similarity score of 5.0 (most similar) from the judges. Sample rate was 40,960 Hz; all other settings and axes are as in Figure 4.3.

MOTHER NO. 26



MALE CALF NO. 33
BORN 1981

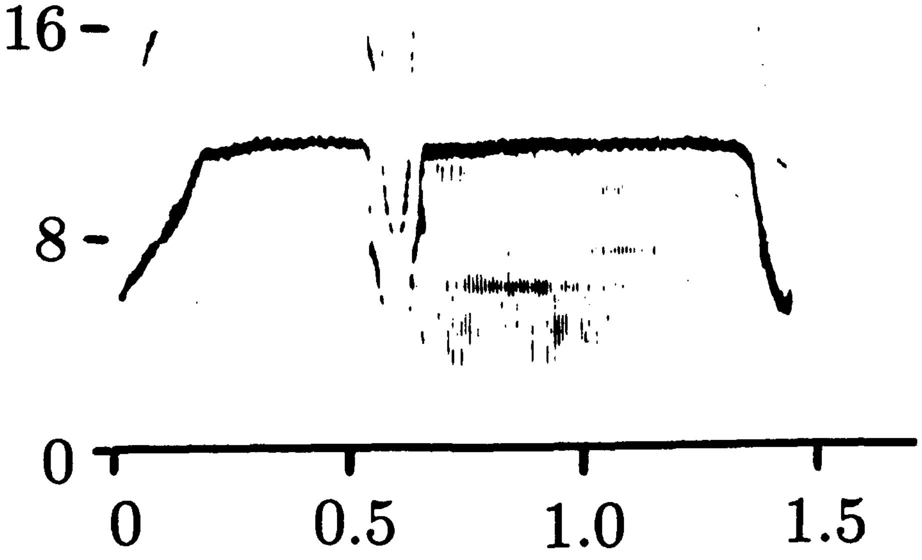


Figure 4.5. Spectrograms of signature whistles of mother no. 16 and female calf no. 140. The mean similarity rating of the whistles of this mother-calf pair was 3.80. A whistle of the mother recorded without a calf in 1976 is presented to illustrate whistle stability. Lines drawn between spectrograms of whistles of mother and calf in 1985 and 1987 indicate that they were caught together in these years and that the whistles were recorded during whistle exchanges between the pair. Axes and settings are as in Figure 4.1.

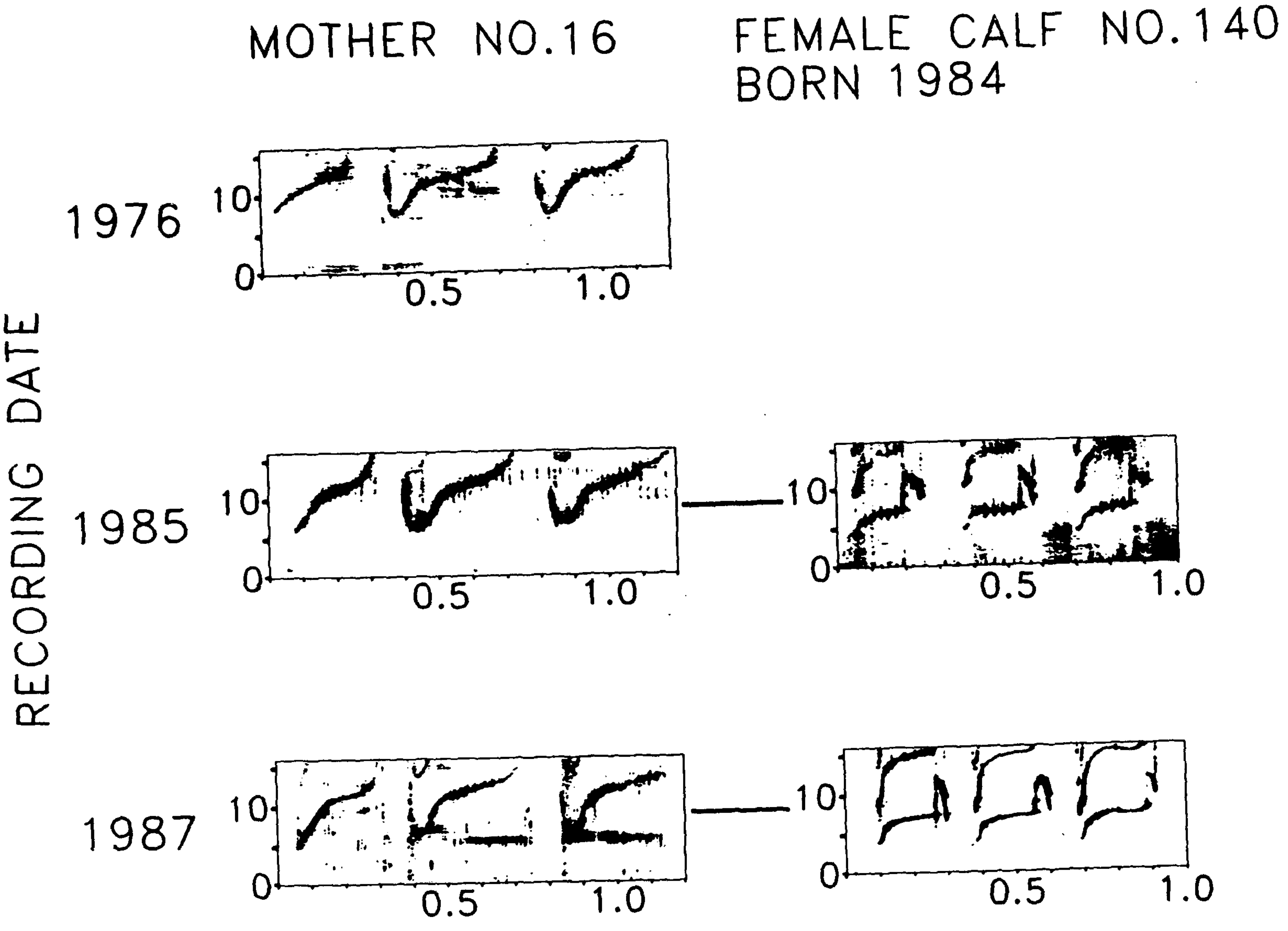

MOTHER NO.16
FEMALE CALF NO.140
BORN 1984
RECORDING DATE
1976
1985
1987
10
0
0.5
1.0

Figure 4.6. Spectrograms of signature whistles of mother no. 8 and female calf no. 13 recorded in 1984 and 1987. The mean similarity rating of the whistles of this mother-calf pair was 1.28. A whistle of the mother recorded without a calf in 1976 is presented to illustrate whistle stability. Lines drawn between spectrograms of whistles of mother and calf indicate that they were caught together. Axes and settings are as in Figure 4.1.

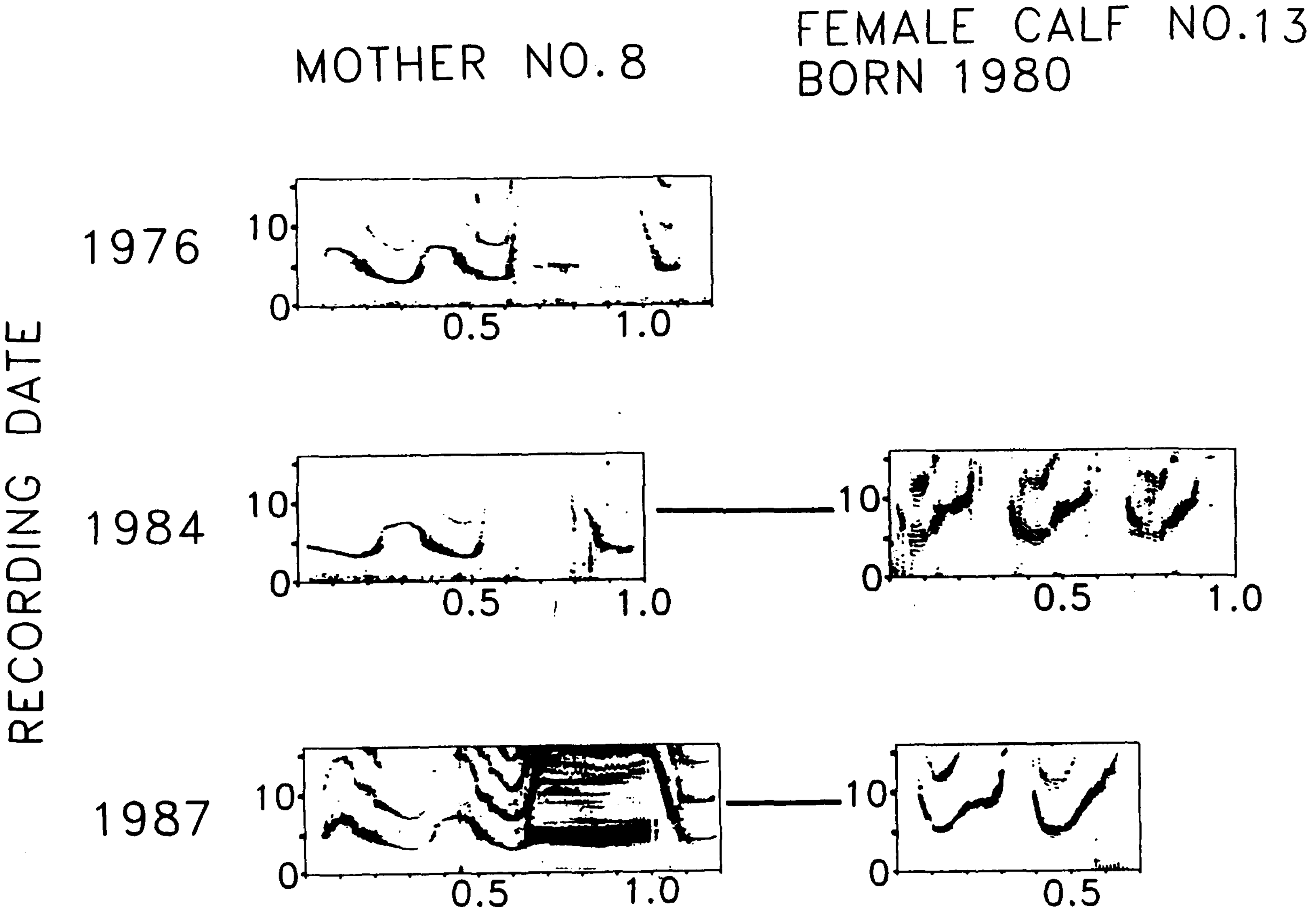

MOTHER NO.8
FEMALE CALF NO.13
BORN 1980
RECORDING DATE
1976
1984
1987
10
0
0.5
1.0

Figure 4.7. Spectrograms of signature whistles of mother no. 32 and female calf no. 61 recorded in 1984, 1985 and 1986. The mean similarity rating of the whistles of this mother-calf pair was 1.39. Lines drawn between spectrograms of whistles of mother and calf indicate that they were caught together. In 1986 mother and calf were caught separately. Axes and settings are as in Figure 4.1.

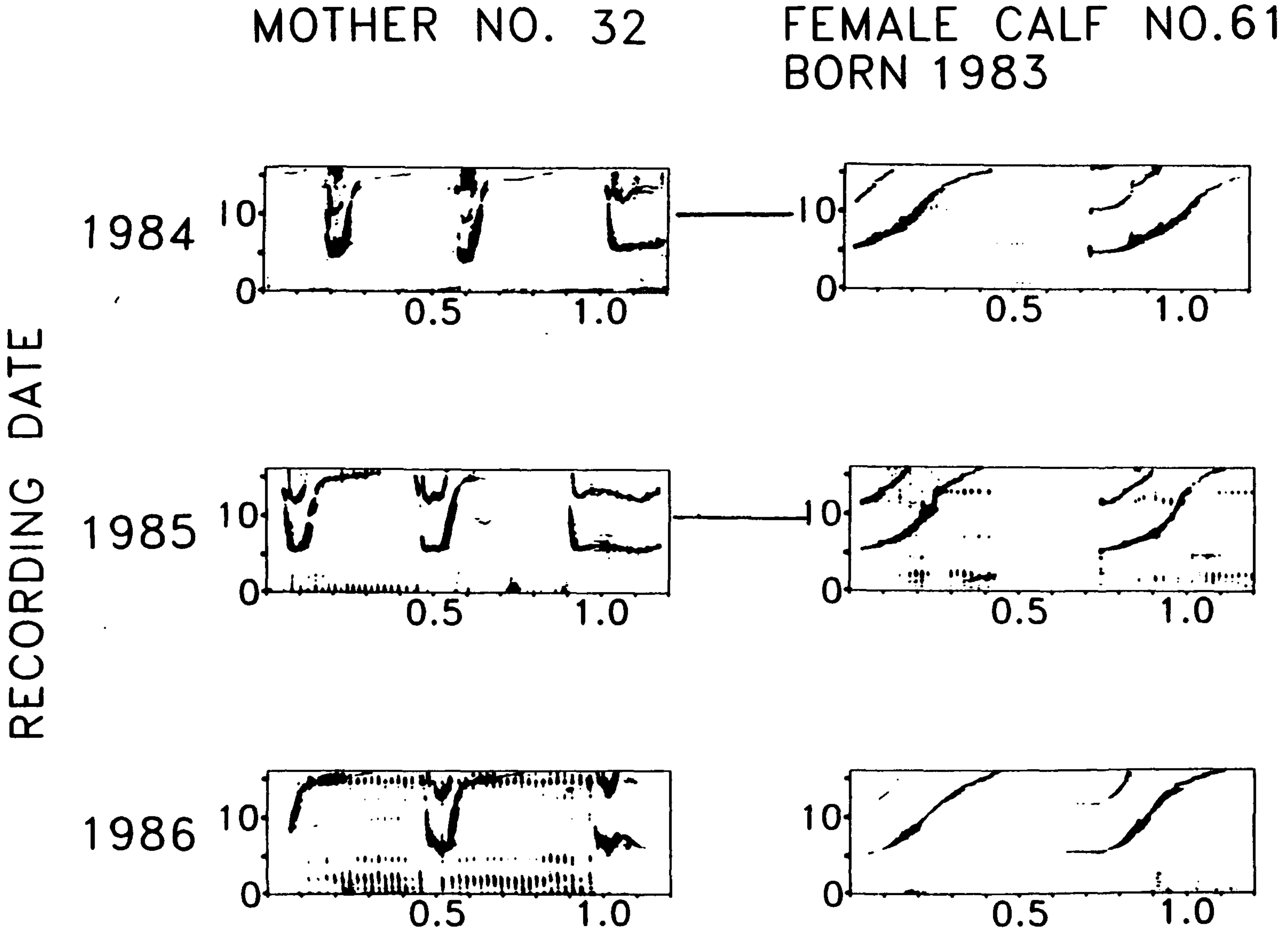

MOTHER NO. 32
FEMALE CALF NO.61
BORN 1983
RECORDING DATE
1984
1985
1986
10
0
0.5
1.0

Figure 4.8. Spectrograms of signature whistles of mother no. 68 and female calf no. 147 recorded in 1985 and 1986. The mean similarity rating of the whistles of this mother-calf pair was 2.17. Lines drawn between spectrograms of whistles of mother and calf indicate that they were caught together. In 1987 mother no. 68 was without a calf. Axes and settings are as in Figure 4.1.

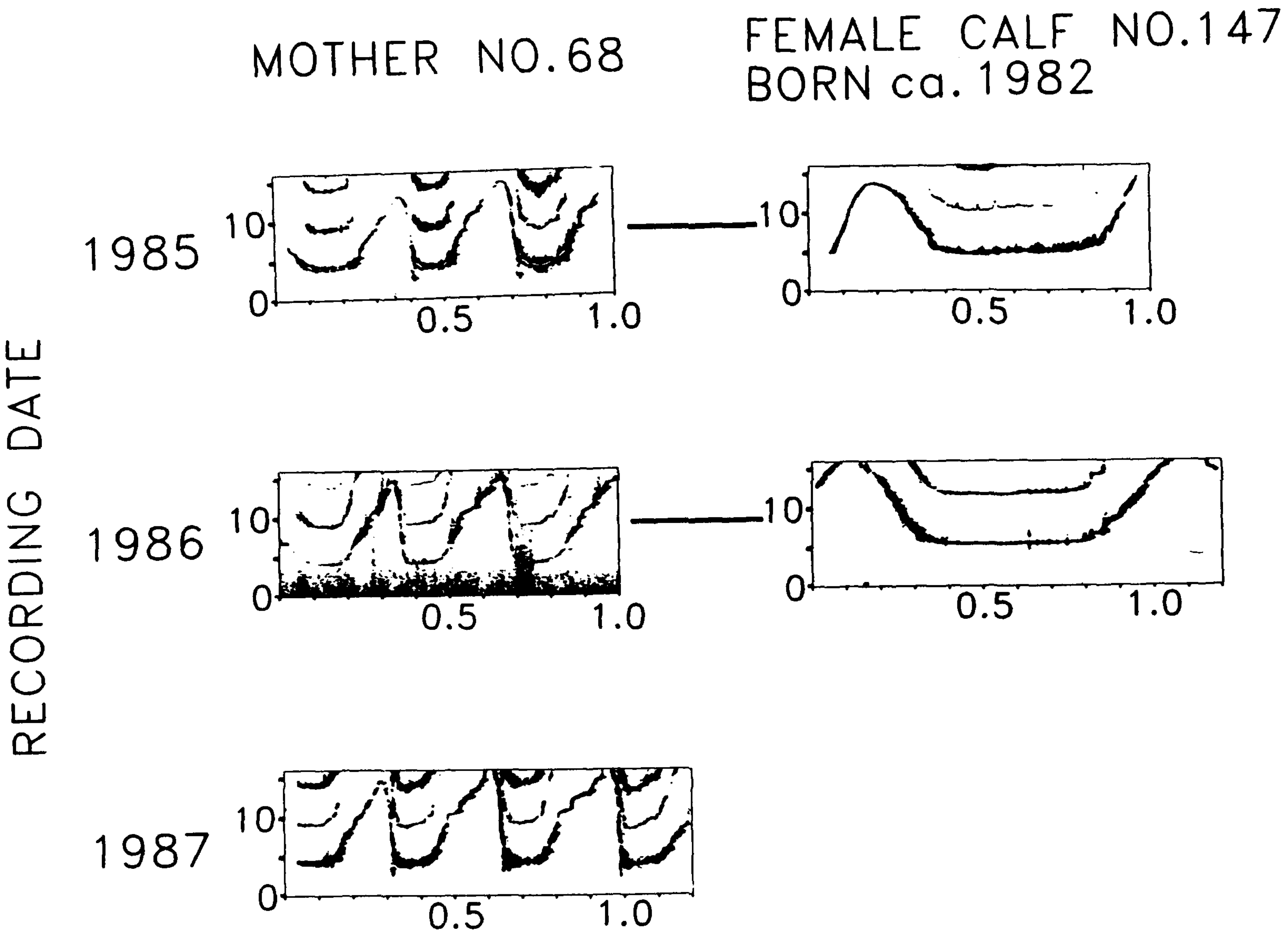

MOTHER NO.68
FEMALE CALF NO.147
BORN ca. 1982
RECORDING DATE
1985
1986
1987
0
10
0.5
1.0

Figure 4.9. Spectrograms of signature whistles of three generations of females, recorded in 1976, 1984 and 1987. Mean similarity ratings of whistles of these mother-calf pairs were: 1.72 for mother no. 22 and calf no. 2; 1.60 for mother no. 22 and calf no. 148; and 2.77 for mother no. 2 and calf no. 18. Lines drawn between spectrograms of whistles of a mother and calf indicate that they were caught together. In several cases, especially for recordings made in air in 1976, noise was whited over in the spectrograms in order to improve reproducibility. Frequency contours were not altered. Axes and settings are as in Figure 4.1.

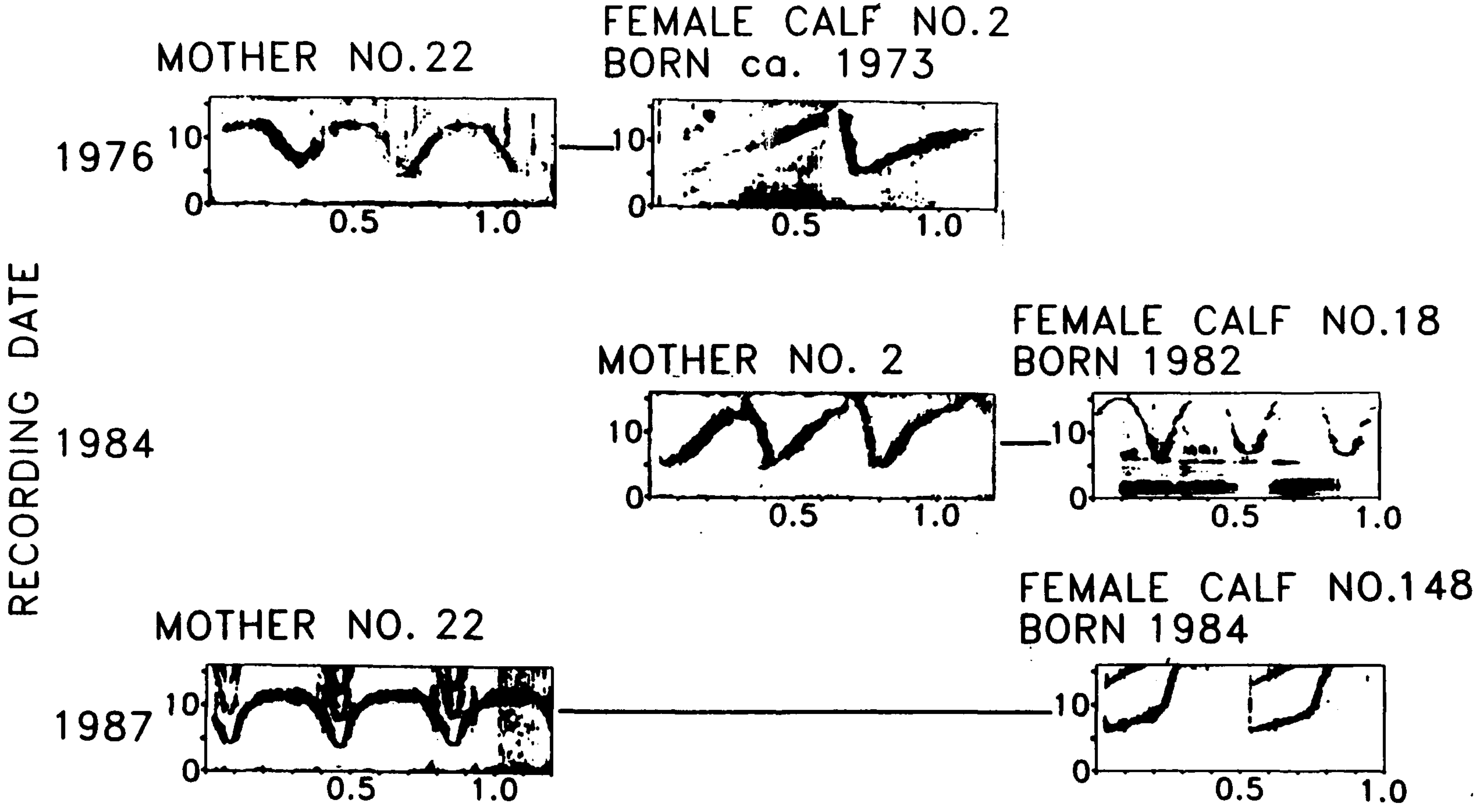

RECORDING DATE
1976
MOTHER NO.22
FEMALE CALF NO.2
BORN ca. 1973
1984
MOTHER NO. 2
FEMALE CALF NO.18
BORN 1982
1987
MOTHER NO. 22
FEMALE CALF NO.148
BORN 1984
10
0
0.5
1.0

Figure 4.10. Spectrograms of signature whistles of mother no. 1 with her male calf in 1975, with her female calf in 1984, and when separate from her female calf in 1987. Mean similarity ratings of whistles of this mother and her two calves were 3.39 for male calf "U" and 2.92 for female calf no. 15. Lines drawn between spectrograms of whistles of a mother and calf indicate that they were caught together. The whistle of mother no. 1 and that of her male calf are good examples of the loop structure, with an introductory loop, a variable number of central loops, and a terminal loop (Chapter 2). Introductory, central, and terminal loops are separated by vertical lines on the two upper spectrograms of this figure. The introductory loop in the first section of each of the upper spectrograms is marked with an "I". The central loop(s) are marked with a "C", and the terminal loop is marked with a "T". In these spectrograms, mother no. 1 produced two central loops while her male calf produced one central loop. In several cases, especially for recordings made in air in 1976, noise was whited over in the spectrograms in order to improve reproducibility. Frequency contours were not altered. Axes and settings are as in Figure 4.1.

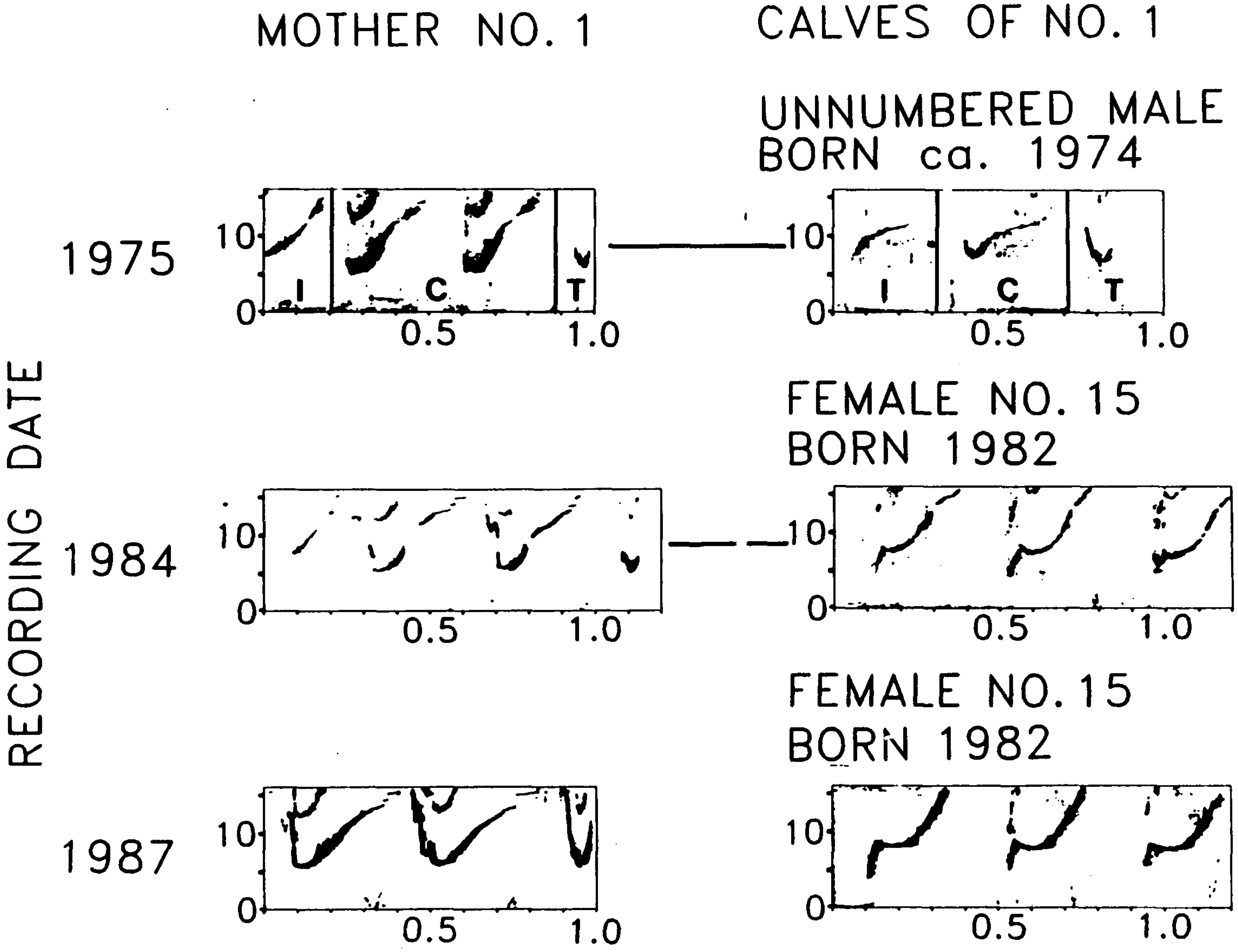

MOTHER NO. 1
CALVES OF NO. 1
UNNUMBERED MALE
BORN ca. 1974
FEMALE NO. 15
BORN 1982
FEMALE NO. 15
BORN 1982
RECORDING DATE
1975
1984
1987
I
C
T
I
C
T
0
10
0.5
1.0

Figure 4.11. Spectrograms of signature whistles of mother no. 7 with male calf no. 11 in 1975, with male calf no. 12 in 1984, with male calf no. 142 in 1987, and with female calf no. 174 in 1989. Mean similarity ratings of whistles of this mother and her four calves were as follows: male calf no. 11 - 3.94; male calf no. 12 - 3.77; male calf no. 142 - 3.97; female calf no. 174 - 1.92. Lines drawn between spectrograms of whistles of mother and calf indicate that they were caught together. Axes and settings are as in Figure 4.3.

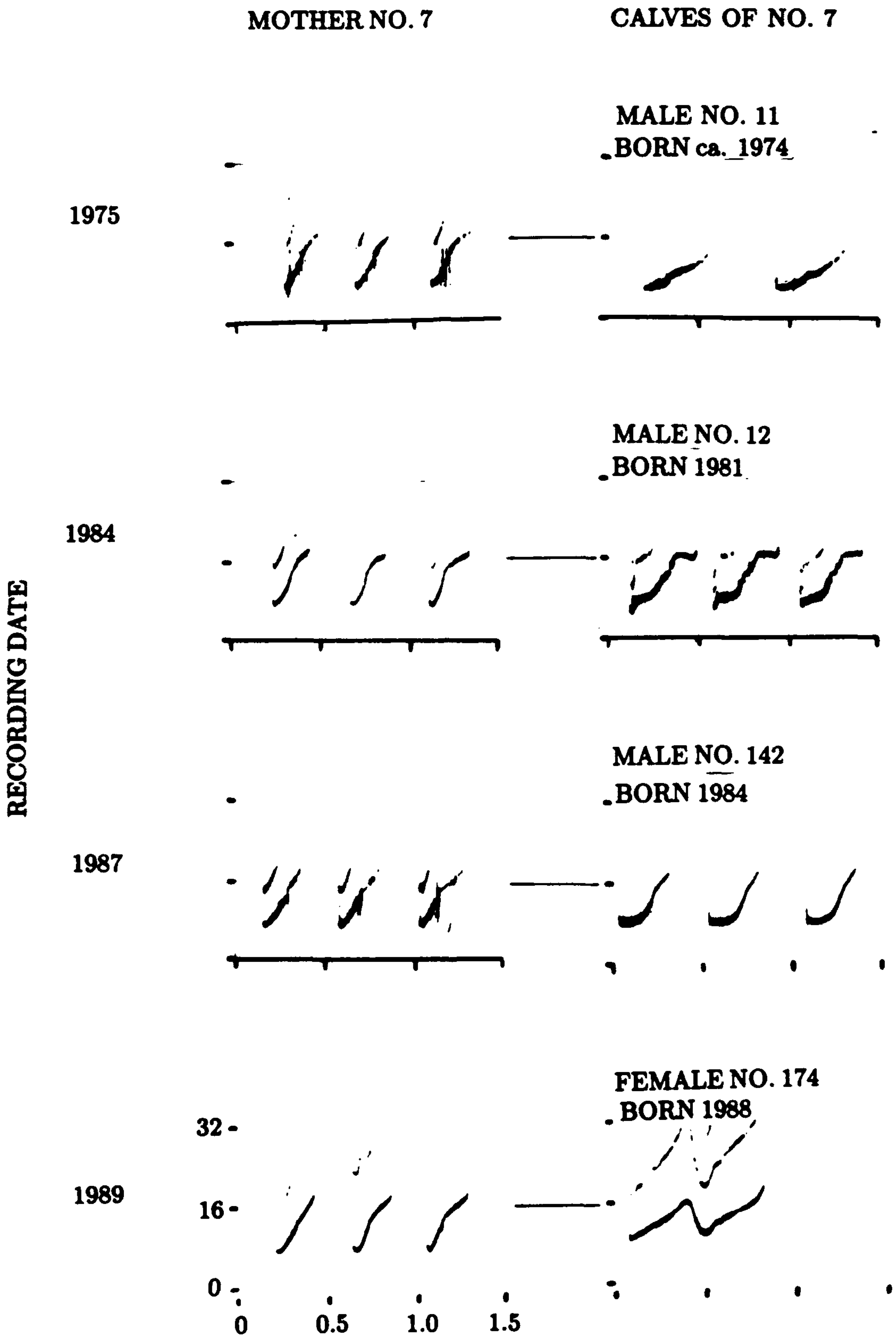
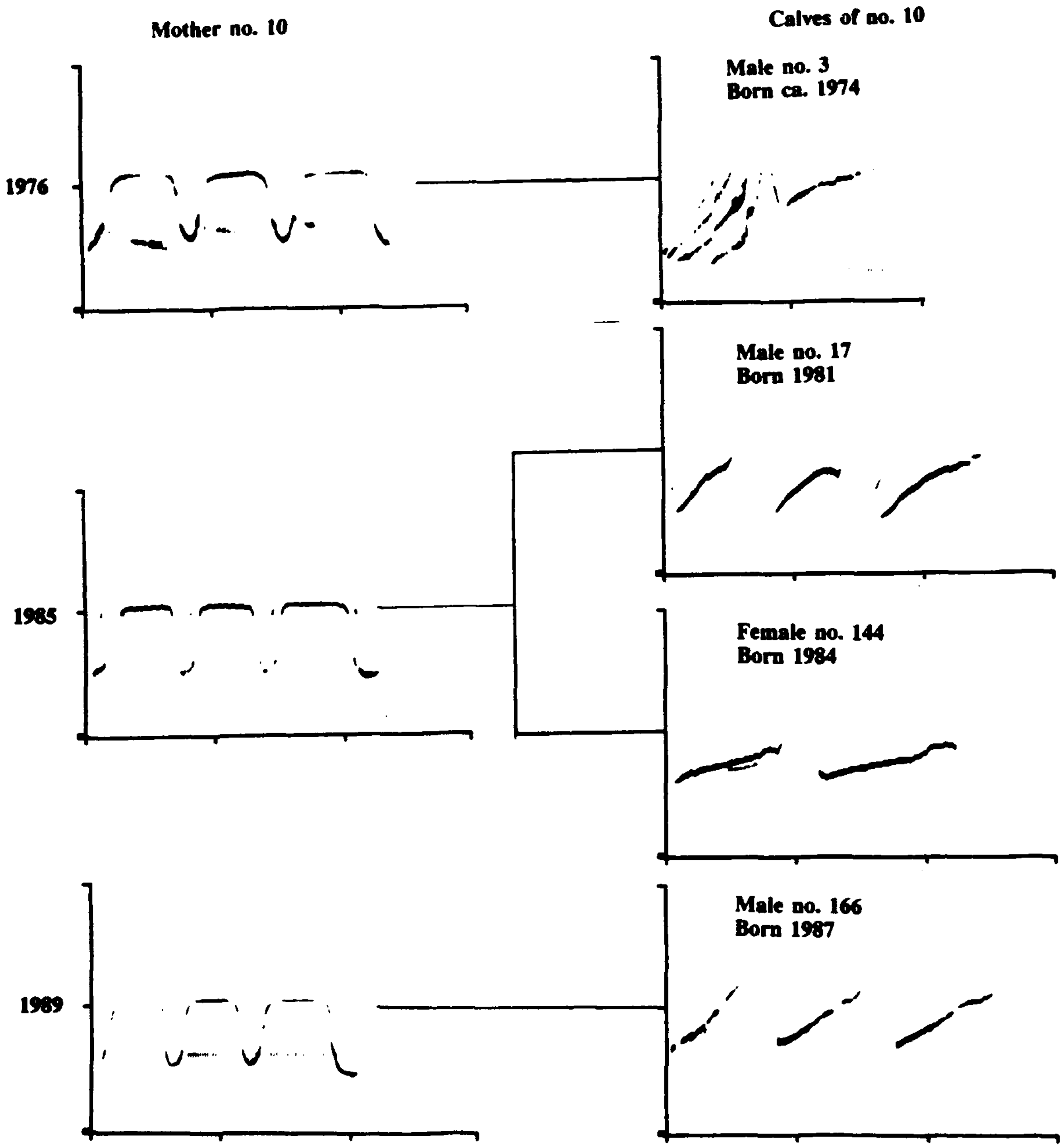

MOTHER NO. 7
CALVES OF NO. 7
MALE NO. 11
BORN ca. 1974
1975
MALE NO. 12
BORN 1981
1984
MALE NO. 142
BORN 1984
1987
FEMALE NO. 174
BORN 1988
1989
RECORDING DATE
32
16
0
0
0.5
1.0
1.5

Figure 4.12. Spectrograms of signature whistles of mother no. 10 with male calf no. 3 in 1975, with male calf no. 17 and female calf no. 144 in 1985, and with male calf no. 166 in 1989. Mean similarity ratings of whistles of this mother and her four calves were as follows: male calf no. 3 - 1.39; male calf no. 17 - 1.31; female calf no. 144 - 1.20; male calf no. 166 - 1.20. Lines drawn between spectrograms of whistles of mother and calf indicate that they were caught together. Axes and settings are as in Figure 4.3.


Mother no. 10
Calves of no. 10
1976
1985
1989
Male no. 3
Born ca. 1974
Male no. 17
Born 1981
Female no. 144
Born 1984
Male no. 166
Born 1987

4.4 VARIANT WHISTLES

4.4.1 METHODS

In an earlier subsample of 23 whistle exchanges from 12 different mother-calf pairs (Sayigh et al. 1990), spectrograms were made of at least 10 whistles for each animal from each capture session in which that animal was recorded (except for two sessions in which fewer than ten whistles were recorded). Whistles were qualitatively categorized as either the signature contour or as a variant (Chapter 2). In all cases, the signature whistle contour was estimated to comprise at least 80% of all whistles produced during the recording session. This analysis was performed on the Kay Elemetrics Corp. Sonograph Model 7029A Spectrum Analyzer (spectrograms were not displayed in real time). This resulted in a total of 829 spectrograms from 59 mother/calf recording sessions. The sampling of whistles, however, was not random. Because each animal typically emitted hundreds to thousands of whistles in a recording session, it was prohibitively time consuming to make a spectrogram of every whistle. At least 30-45 minutes of each recording session was monitored and signature whistles were chosen *ad lib* for spectrographic analysis. One criterion used for choosing signature whistles for spectrograms was the clarity of the signal. However, in most cases when a whistle was heard that sounded unlike the signature whistle of that animal (a variant), it was included in order to uncover the overall repertoire of whistles produced during each session. Variant whistles were subsampled when there were too many to analyze. This bias was believed to be consistent throughout and between sexes so some qualitative comparisons and observations were made from these data.

4.4.2 RESULTS

Male calves in this sample appeared to produce more variant whistles than did female calves. Table 4.4 shows the numbers of spectrograms made of signature and variant whistles for each animal in the early sample. Usually all of the small number of variant whistles produced by the females were sampled, and the larger number of variant whistles produced by the males was subsampled, because it was prohibitively time-consuming to make spectrograms of all of the male variant whistles. This sampling bias was likely to have worked against the direction of the results. Overall, 27% of the spectrograms made of whistles produced by the male calves were variants, as opposed to 8% produced by female calves (Table 4.5). All of the variant whistles produced by males for which spectrograms were made (38) were produced by three males with the same mother (Figure 4.11). The fourth male calf whose whistles were analyzed was recorded only once at approximately age one (Figure 4.10), and he produced no variant whistles at that time.

As young males matured, they appeared to produce a broader variety of whistle contours (Figures 4.13 - 4.14). In 1975, at age 1 year, male no. 11 produced only his signature whistle; in 1984 he was still producing the same signature whistle, as well as a suite of variant whistles (Figure 4.13). Male no. 12 was producing primarily his signature whistle in 1984 at age 3 years, whereas in 1985 he was producing a suite of variant whistles in addition to this signature whistle (Figure 4.14). The signature whistle of each of these two males was still produced more frequently than the variant whistles (Tables 4.4 - 4.5). Cases in which more spectrograms of variant than signature whistles were made (e.g. no. 12, 1985; no. 142, 1987), are the result of oversampling of variant whistles.

This sex difference in variant whistle production should be viewed as preliminary, however, both because whistles were not sampled randomly and because successive whistle types in a sequence are not independent of one another.[1] That is, an animal is more likely to produce a variant whistle if the preceding whistle was a variant than if it were a signature. Therefore, it would not be valid to use straight counts of different whistle types in statistical tests that require values to be independent of each other. Modelling of sequences of whistles for many different animals will be necessary before the sex difference reported here can be confirmed.

In some cases there was a high degree of similarity between a variant whistle of one animal and the presumed or known signature whistle of another animal. For example, Figure 4.15 shows a spectrogram of a variant whistle produced by male no. 11 (his signature whistle is shown in Figures 4.11 and 4.13) while he was being processed, which was immediately followed by a whistle of similar contour produced

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[1] This was determined by contingency table analysis of successive whistle types in several whistle sequences.

Table 4.4. Numbers of spectrograms of signature (S) and variant (V) whistles of male and female calves and their mothers in different sampling periods; sampling was non-random, and biased toward variant whistles.

	1975-6		1984		1985		1986		1986W		1987	
ID #	S	V	S	V	S	V	S	V	S	V	S	V
Male												
11	24	0	9	3[a]	-	-	-	-	11	4[a]	-	-
U	12	0	-	-	-	-	-	-	-	-	-	-
12	-	-	14	2	6	13[a]	-	-	-	-	-	-
142	-	-	-	-	12	0	-	-	10	9	4	7
Female												
2	14	0	14	2[a]	-	-	-	-	-	-	-	-
13	-	-	13	0	-	-	-	-	12	1	-	-
18	-	-	14	0	-	-	-	-	-	-	-	-
15	-	-	12	0	10	7	-	-	5	0	13	5[a]
147	-	-	-	-	10	1	13	1	-	-	-	-
61	-	-	15	0	11	0	12	0[a]	-	-	11	0[a]
140	-	-	-	-	14	0	12	0	-	-	13	2
148	-	-	-	-	11	5[b]	13	0	1	0	15	0
Mother												
1	17	1	12	0	10	7	-	-	11	0	11	0
7	20	0	11	4	11	1	-	-	12	6	5	5
8	13	1	11	0	-	-	-	-	11	0	-	-
16	12	0	-	-	16	0	11	0	-	-	12	3
22	4	0	16	0	-	-	15	1	11	0	14	1
32	-	-	13	0	12	4	10	3	-	-	-	-
68	-	-	-	-	22	0	19	2	-	-	15	2

[a] Calf had separated from mother

[b] Calf had separated accidentally from her mother; they later rejoined

by an animal in the net corral. In another case, each member of a closely bonded adult male pair (Wells et al. 1987, see Chapter 1) produced a variant whistle closely resembling the other's signature whistle during a capture-release session in 1986 (Figure 4.16).

Table 4.5. Percentages and numbers of spectrograms of signature and variant whistles stratified into the following classes: male calves, female calves, mothers and combined. N = # of individuals.

	Signature	Variant	Total	N
Male calves				4
Percent	72.9	27.1		
Number	102	38	140	
Female calves				8
Percent	92.0	8.0		
Number	253	22	275	
Mothers				7
Percent	89.6	10.4		
Number	371	43	414	
Combined				19
Percent	87.6	12.4		
Number	726	103	829	

Figure 4.13 (facing page). Spectrograms of signature whistles of male no. 11 recorded in 1975 and 1984 and of several variant whistles recorded in 1984. Note that the faint, steeper frequency upsweep in the 1975 spectrogram is the whistle of his mother (see Figure 4.11). Axes and settings are as in Figure 4.1.

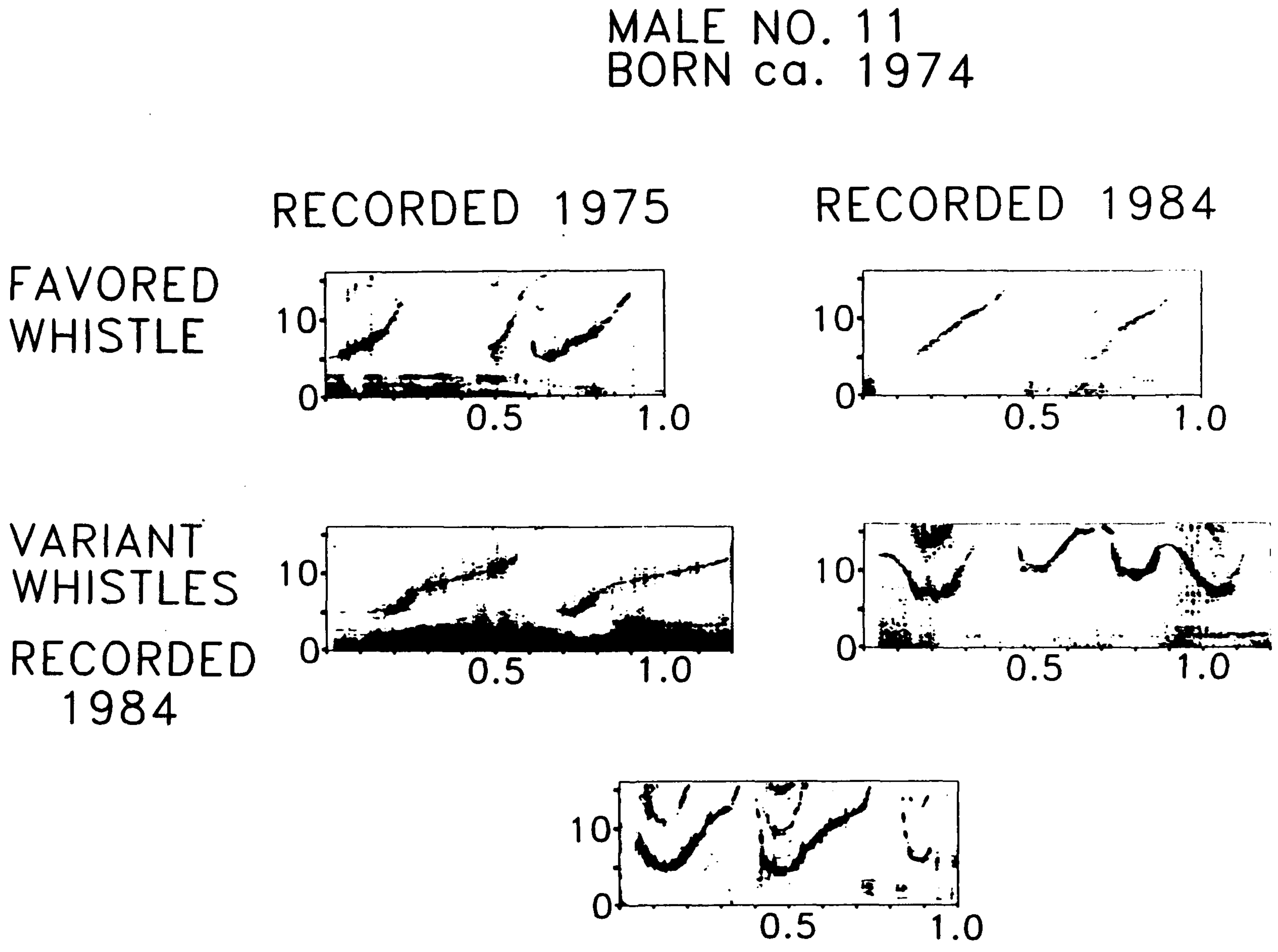

MALE NO. 11
BORN ca. 1974
RECORDED 1975
RECORDED 1984
FAVORED WHISTLE
VARIANT WHISTLES RECORDED 1984
10
0
0.5
1.0

Figure 4.14. Spectrograms of signature whistles of male no. 12 recorded in 1984 and 1985 and of several variant whistles recorded in 1985. Axes and settings are as in Figure 4.1.

MALE NO. 12
BORN 1981

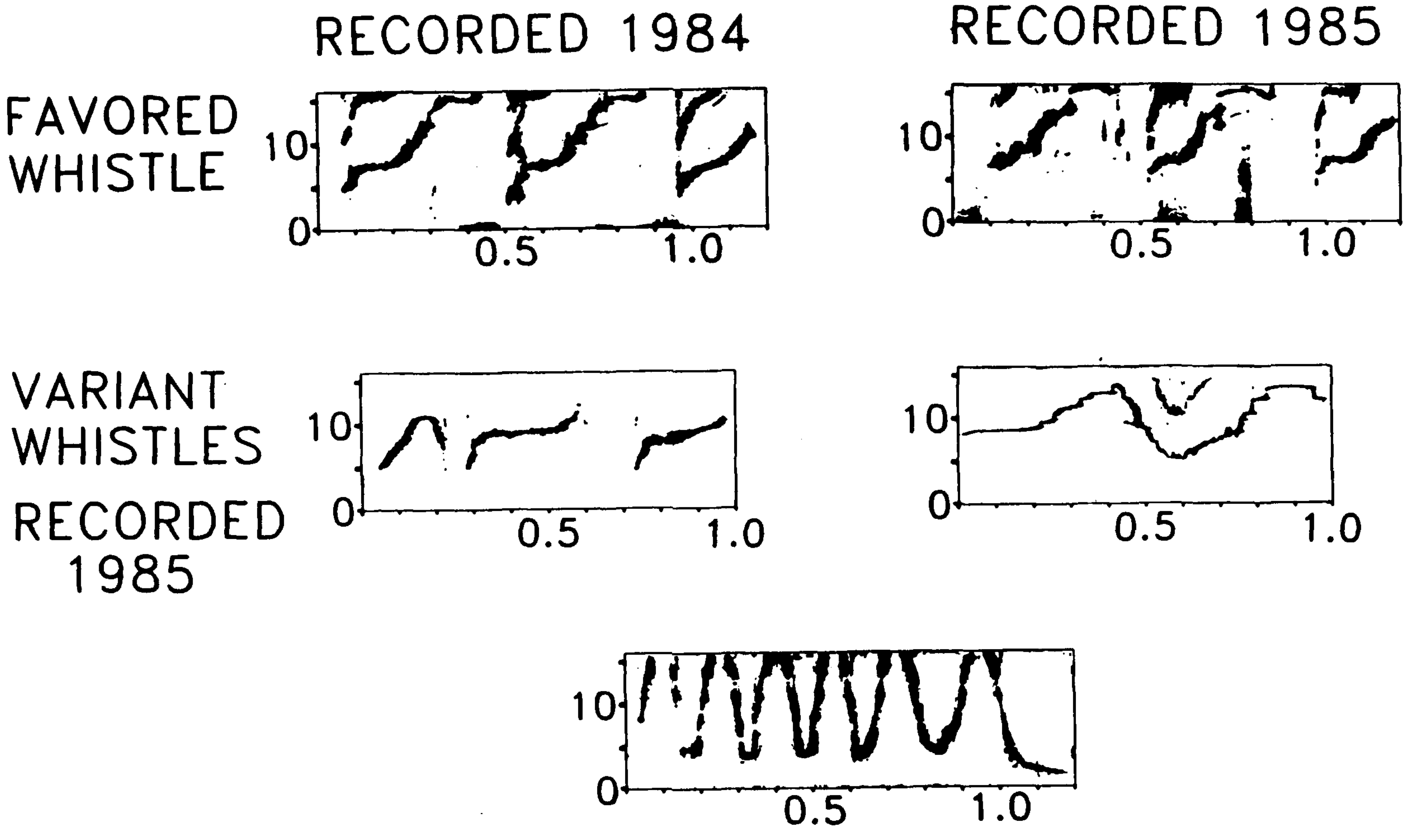
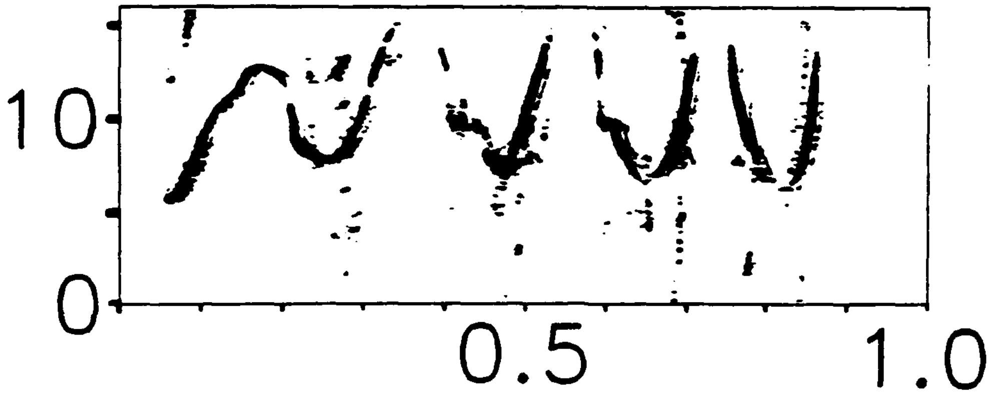


Figure 4.15. Spectrogram of a variant whistle produced by male no. 11 while he was being held in the raft. Immediately following this variant whistle, another whistle was produced as shown in the second spectrogram; it came from one of three males in the net corral. Axes and settings are as in Figure 4.1.

MALE NO. 11
VARIANT WHISTLE



UNIDENTIFIED MALE
IN NET CORRAL

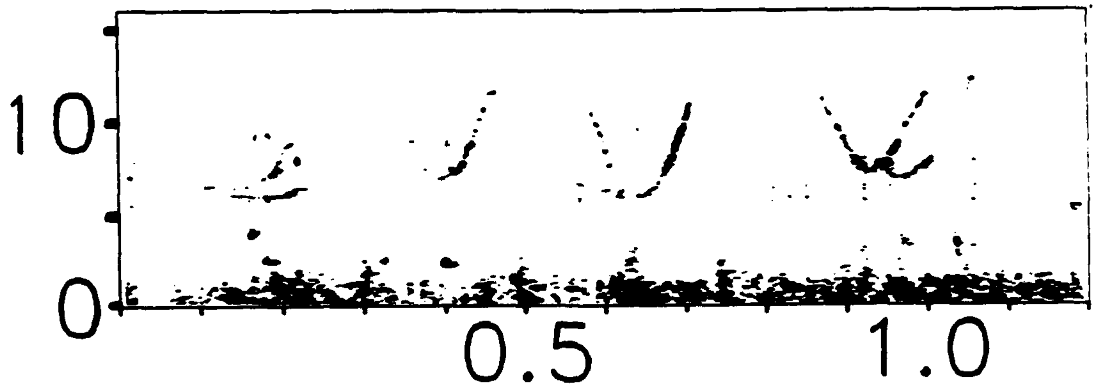
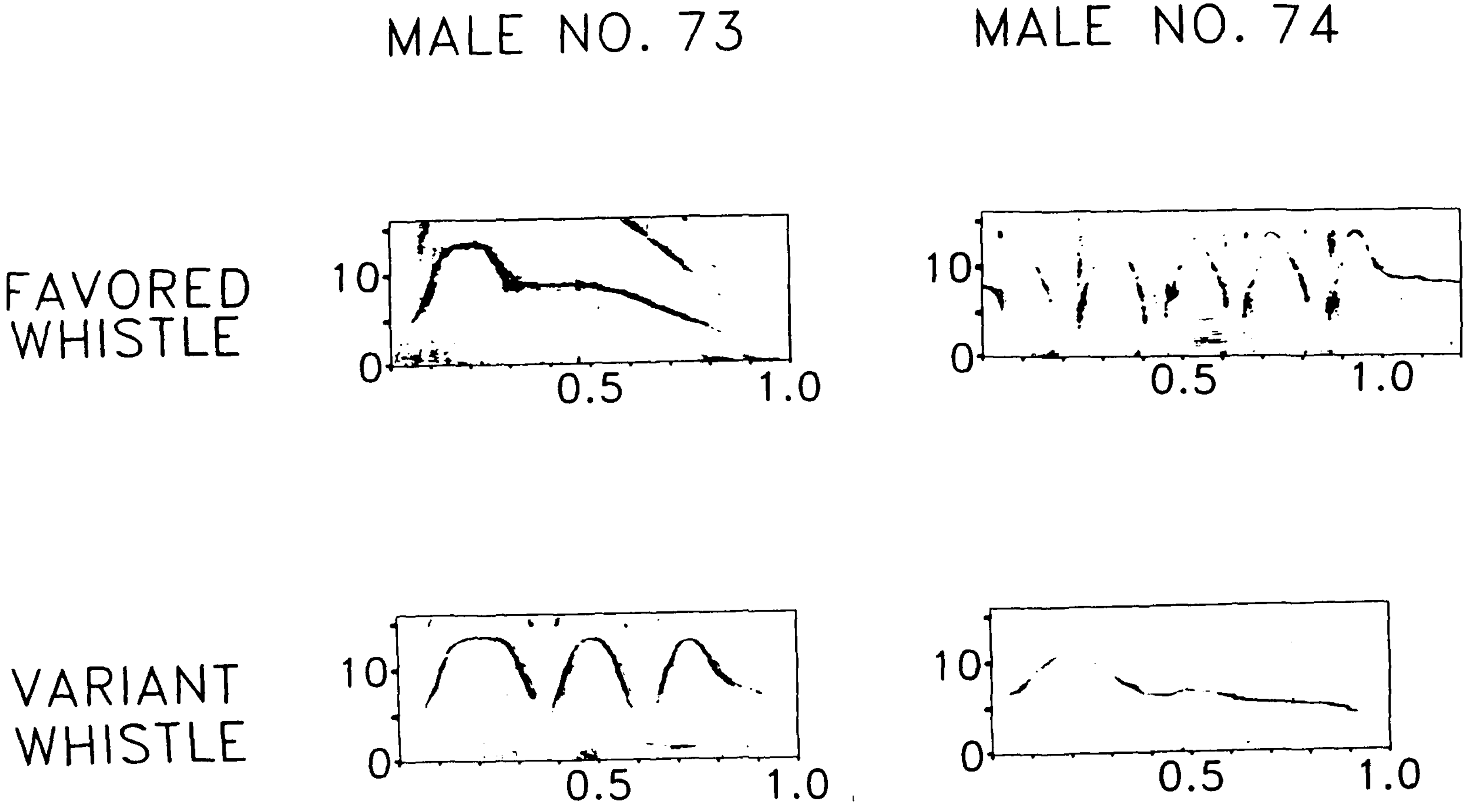


Figure 4.16. Spectrograms of signature and variant whistles produced by members of a closely bonded male pair. Note the similarity in contours of each variant to the other individual's signature whistle. Axes and settings are as in Figure 4.1.


MALE NO. 73
MALE NO. 74
FAVORED WHISTLE
VARIANT WHISTLE
10
0
0.5
1.0
10
0
0.5
1.0
10
0
0.5
1.0
10
0
0.5
1.0

4.5 DISCUSSION

4.5.1 MOTHER-CALF COMPARISONS

Male calves are more likely than female calves to produce a signature whistle very similar to that of their mother. Conversely, female calves are more likely than males to produce a whistle that is highly distinct from that of their mother. The obvious question of how this sex difference comes about, i.e., through what combination of genetic and learned components, will be addressed in Chapter 5 (Signature whistle development). This discussion focuses on the more speculative question of why such a sex difference might occur.

Sex differences in whistle production may reflect differences in the life histories of males versus females. Because signature whistle exchanges appear to help maintain contact between a mother and calf (McBride and Kritzler 1951), it could be difficult for a young calf to maintain contact with his or her mother if several females within a group had similar whistles. Since preliminary data suggest that adult females in Sarasota frequently associate with matrilineally related females (Wells et al. 1987), it may be of crucial importance for each female to develop a signature whistle distinctive from other females in her matriline. Greater selective pressures should act on females to produce vocalizations that aid in maternal care of offspring (Green 1981), especially in species where maternal investment is high. Such is certainly the case for bottlenose dolphins, where females remain in constant association with each offspring for an average of five years (Wells 1991). If difficulties could arise for young calves attempting to maintain contact with their mothers, or for mothers identifying which individual is her dependent offspring, then it is not difficult to envision strong selective forces for distinctive whistles among matrilineally related females.

Males, however, tend to disperse from the natal group while staying within the community (Wells et al. 1987). Because males do not preferentially associate with their mothers after dispersal, there may be no social pressures for males to develop a signature whistle distinctive from that of their mother. Indeed, it may be advantageous for males to retain some characteristics of their mother's whistle, either for avoidance of inbreeding or to maintain contact with and to recognize kin. In some primate species, matrilineal ties may influence dominance (Walters and Seyfarth 1986) and social alliances (Cheney and Seyfarth 1986). Dominance hierarchies have been reported for captive bottlenose dolphins (Shane et al. 1986), and alliances between males have been reported for wild dolphins (Wells et al. 1987, Connor et al. 1992). It may also be advantageous for dependent male calves to advertise their maternal lineage if matriline affects dominance or alliances in dolphins as it does in some primate species. This could explain why three male calves of one female all produced a whistle similar to their mother's, whereas three male calves of another female all produced whistles very different from their mother's. Mothers may be able to confer such an advantage more directly on female offspring by association, since females tend to remain in their natal groups.

This hypothesized explanation for the sex difference in signature whistle production contrasts with findings for pigtail macaques, a species which displays matrilineal dominance hierarchies. There is evidence that vocalizations in this species contain matrilineal signatures (Gouzoules and Gouzoules 1990). This level of variability is apparently present in conjunction with variability unique to each individual and to several distinct contexts. Similarly, individual chickadee calls converge on "flock specific" characteristics (Mammen and Nowicki 1981, Nowicki 1983). Killer whale "clans", which are presumed to be matrilineally based, also produce group-specific vocalizations (Ford 1991). Members of these clans associate together continuously for many years.

The group is a more stable unit in all of these species than in bottlenose dolphin societies, which are characterized by stable associations among individuals as well as more fluid patterns of association among many individuals (Wells et al. 1987). Individuals may interact repeatedly with one another over periods of many years. In this "fission-fusion" type society, individual recognition, rather than group recognition, should be at a premium (Chapter 3).

Overall, it is possible that a greater pressure on females to be distinctive is the driving force behind the observed sex difference. Males may be afforded greater flexibility, and thus may produce whistles similar to the mother in advantageous situations, or dissimilar otherwise. Another possibility is that the forces governing whistle development in males are more open (Mayr 1974), resulting in approximately equal numbers of males producing whistles not similar, somewhat similar, and very similar to the mother. The actual mechanisms governing the sex difference in signature whistle production are explored in Chapter 5.

It is not entirely clear to what extent the similarities that we perceive in the general characteristics of whistle contours are meaningful to the animals. Richards et al. (1984) found that captive *Tursiops* were extremely adept at mimicking various computer-generated frequency contours. Captive dolphins have also been found to spontaneously transpose frequency while mimicking a contour (Richards et al. 1984, Tyack 1986). Tyack (1986) found that two captive bottlenose dolphins could mimic the frequency contour of one another's signature whistles very precisely, although duration varied by as much as 30%. Overall, these studies indicated that frequency contours recognizable by visual inspection were also recognized by the animals. It is very difficult, however, to quantify whistle similarity when certain aspects of the whistle such as duration, highest and lowest frequency, and number of loops are not characteristics that are consistently conserved by the animals. This is the reason why human judges were used to assess whistle similarity, a technique which proved to be highly reliable. Future research should focus on experiments that test how similarity in whistle contours is perceived by dolphins.

4.5.2 VARIANT WHISTLES

Preliminary results from a sample of 8 female calves and 4 male calves (Sayigh et al. 1990) indicated that female calves appeared to produce fewer variant whistles than males. This sex difference is consistent with findings of Tyack (1986), who found that an adult female produced proportionately fewer variant whistles than an adult male in a study of two captive dolphins. In a study of 120 captive dolphins recorded over periods of many years, Caldwell et al. (1990) found that males tended to produce more variant whistles than females. This pattern too may reflect differences between males and females in the social structure of the community. If signature whistles are used by females for maintaining contact with calves, it may be particularly important for the whistle repertoire of a female to be especially stereotyped. It could be difficult for a calf to maintain contact with his or her mother if the mother is producing many different whistles. By contrast, when males disperse into the community after they leave their mother, it is likely that they broaden their social relationships (Wells et al. 1987). The number of variant whistles produced by two males (out of our earlier sample of four) increased at about the time they separated from their mother. Dispersal may put demands on males for an increased vocal repertoire.

In a study of two captive dolphins, Tyack (1986) found that each animal produced the signature whistle of his or her tank-mate more frequently than any other whistle, except their own signature whistle. An increased repertoire may be partially the result of vocal mimicry and thus may be serving a social function, such as a contact call. Examples of apparent signature whistle mimicry during the Sarasota captures provide additional support for this idea.

However, because the only three males for whom we have seen this increased repertoire so far are at least half-brothers, it may be that this is a characteristic unique to that one family. In addition, counts of variant whistles produced by males and females can not be compared statistically, due to serial dependence of whistle types in a sequence. Modelling of whistle sequences from many males and females at different ages should clarify this issue.

Only through the use of detailed behavioral observations with simultaneous acoustic recordings will it be possible to test hypotheses regarding the function of sex differences in bottlenose dolphin vocalizations. Quantification of dominance relationships, such as has been done in captivity by Östman (1991) and Samuels et al. (1991), should resolve whether any relationship exists between a male calf's whistle structure and his mother's dominance rank. The rare cases (10%) where female calves produce whistles similar to the mother may also prove illuminating. Variant whistle production in natural situations must also be quantified, in order to determine whether variant whistle usage differs between the sexes. This will require techniques to localize which animal is producing a sound, which are currently being developed (Freitag and Tyack, in prep.). The sex differences reported here provide a useful framework for further study of the social structure, behavior and communication of bottlenose dolphins.

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CHAPTER 5: SIGNATURE WHISTLE DEVELOPMENT

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5.1 INTRODUCTION

Although recent research on bottlenose dolphin signature whistles has begun to shed light on their social functions (e.g., Tyack 1986, Smolker et al. submitted, Chapter 3), there remains a paucity of information on the factors affecting signature whistle development. One study of captive calves (Caldwell and Caldwell 1979) focused on the time course of development, and did not address the relative roles of learning and inheritance. Another study of captive calves (Tyack et al. submitted) suggested that the acoustic environment of a young calf may affect signature whistle development. There is no information in the literature on signature whistle development in free-ranging dolphins. This chapter presents preliminary results from a study of whistle development of free-ranging calves from the Sarasota bottlenose dolphin community (Chapters 1-4).

A direct role of learning in vocal development, where vocalizations are matched to an external model, has been clearly documented for many species of songbirds (e.g., Kroodsma 1982, Marler and Peters 1981), and of course for humans. Buchwald and Shipley (1985) distinguish between two levels of vocal learning, stating that "[m]odulation of vocal behavior by mechanisms of auditory feedback exemplifies one level of vocal learning, whereas imitation and replication of externally generated auditory signals exemplify a second, more demanding level" (p.293). They report evidence for the first of these levels in domestic kittens. However, data documenting the second level of vocal learning in non-human mammals are sparse. Possible evidence is found in the lesser spear-nosed bat, *Phyllostomus discolor*, wherein young tend to develop individually distinctive calls with characteristics similar to those of their mothers (Esser and Schmidt 1989); however, it has not been ruled out that this is a genetically controlled maturational process. Masataka and Fujita (1989) claim to have found evidence for vocal matching of food calls in cross-fostered Japanese and rhesus macaques, but there are many problems with their study, as described by Owren et al (1992) and Snowdon (1990). In another study involving cross-fostered infant macaques, Owren and his colleagues not only did not find strong evidence for vocal learning (Owren et al. in prep.), but also did not find consistent species differences in acoustic structure of food calls of adult females (Owren et al. 1992). They concluded that food calls are not an appropriate vocalization upon which to base a study of vocal learning in these two macaque species. Overall, as stated by Snowdon (1990, p. 226):

> The net result of work on ontogeny of vocal structure in monkeys is predominantly in favor of vocal structures being fixed and relatively unmodifiable in development. There is little conclusive evidence for vocal learning in any species of non-human primate.

Given the importance of vocal learning for humans, the lack of evidence in other mammals is surprising.[1] Are most non-human mammalian vocalizations not modifiable by experience? Or has not enough attention been given to this question in the study of non-human mammals?

The question of the relative contributions of genetic and environmental factors to development of traits, including vocal patterns, is a matter of considerable controversy. Johnston (1988) argued that it is meaningless to label any trait, such as bird song, as innate or genetically determined, but that an interactionist approach (as espoused by Lehrman 1970) must be used. As evidenced by the extensive commentary following Johnston's article (e.g., Alcock 1988, Bekoff 1988, Slater 1988, Steklis 1988) it appears that few researchers would argue with the need for an interactionist approach; this is primarily an argument over semantics. Obviously behaviors themselves are not innate; genes specify processes that interact within the developing organism, leading to varying outcomes depending upon the extent to which environmental factors influence development. Mayr's (1974) concept of open and closed "genetic programs" provides a useful framework here. Some developmental processes will take place regardless of the rearing conditions of the individual, unless terminated by death. Others require environmental input for the behavior to develop typically. To use examples from the birdsong literature

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[1] Note that this discussion has focused only on vocal production; there is substantial evidence for a role for learning in the development of appropriate contextual usage of and responses to vocalizations in primates (see Snowdon 1990 for a review).

described by Johnston (1988), some species of birds develop normal, species-specific repertoires in the absence of auditory stimuli (e.g., Kroodsma 1984), some develop normally in isolation with only auditory input (e.g., Marler 1970), and others require more complex combinations of social and auditory stimuli (e.g., Baptista and Petrinovich 1986, Clayton 1989).

Johnston (1988) argues that "non-obvious" stimuli such as non-vocal social stimulation from conspecifics may affect vocal development in many species, but very little research has been done in this area. For example, brown headed cowbird (*Molothrus ater*) males produce a wide variety of sounds early in life, and modify sound production as a result of reinforcement by females, which perform a particular display for preferred sounds (West and King 1988). This emphasizes the point that atypical development of vocalizations in isolated birds does not necessarily imply that auditory experience is involved in vocal development. However, normal development of vocalizations in the absence of auditory input does not leave much room for learning to play a role in vocal development. Such situations represent "closed genetic programs" (Mayr 1974), and appear to account for development of the vast majority of non-human mammalian vocalizations.

Evidence for vocal learning among marine mammals is stronger than for most other mammalian groups. Hoover, a harbor seal at the New England Aquarium in Boston, imitated human speech with a regional accent (Ralls et al. 1985). Humpback whales learn complex songs that change progressively (Payne et al. 1983). Bottlenose dolphins are highly skilled at imitating manmade sounds (Caldwell and Caldwell 1972, Richards et al. 1984) and imitation of signature whistles appears to play an important role in the natural communication system of this species (Tyack 1986, see also Chapter 4).

Without experimental manipulations it is difficult to differentiate between consequences of learning and maturation, especially if all members of a population or species develop similar vocalizations. For example, Seyfarth and Cheney (1986) found that young vervet monkeys (*Cercopithecus aethiops*) produce calls with a higher fundamental frequency than the species-typical calls of adults. As they grow older, these sounds become more similar to those of the adults. This may be a result of growth of the vocal tract, rather than of learning (Seyfarth and Cheney 1986). It would be easier to test for vocal learning in a species where different individuals produce different naturally occurring repertoires. Dolphin whistles are particularly promising signals for the study of vocal learning because each animals develops an individually distinctive signature whistle (Chapters 1 and 2).

To date, there have been two studies of whistle development in captive bottlenose dolphins (Caldwell and Caldwell 1979, Tyack et al. submitted). Caldwell and Caldwell (1979) reported that calves produced unstereotyped whistles at birth, and gradually developed individually distinctive whistles, generally by 1½ to 4 months of age. Tyack et al. (submitted) found more rapid whistle development, occurring primarily in the first month of life. One individual produced whistles approximating her signature contour within days of birth. The Caldwells provided little information about the acoustic environments of the calves in their study, although they did note a similarity between whistles of one calf and those of his mother. They also noted a similarity between whistles of another *Tursiops* calf and a highly vocal Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) with which the calf and his mother were housed. Tyack et al. (submitted) found that three captive calves at the Miami Seaquarium apparently copied sounds present in their acoustic environment in developing their own signature whistles. One calf's whistle strongly resembled the whistle used by trainers to reinforce behaviors. The other two calves' whistles resembled those of other individuals in the tank (not their mothers).

In free-ranging Sarasota calves, males are more likely than females to produce a whistle similar to their mothers', whereas females are more likely than males to produce a whistle distinct from their mothers' (Chapter 4, Sayigh et al. 1990). Nothing is known about the time course of whistle development in the wild, or about the mechanism by which the sex difference arises.

This sex difference provides a unique control for study of the factors affecting whistle development in bottlenose dolphins, and allows the formation of testable predictions about whistle development based on differing contributions of genetic and environmental factors. For example, if the acoustic structure of the signature whistle were somehow genetically coded, comparisons with parental whistles should reveal predictable patterns. In crickets (Hoy 1974), frogs (Gerhardt 1974), squirrel monkeys (Newman and Symmes 1982) and gibbons (Brockelman and Schilling 1984), offspring of two individuals with different call types produce hybrid call types. A similar genetic model for dolphins would need to incorporate sex linkage in order to explain the observed sex difference. For example, a simple model would predict that genes necessary for coding whistle structure were present on the X chromosome. Since males possess only one X chromosome, which is inherited from the mother, this would result in a male calf producing whistles like those of its mother. Females inherit one X chromosome from the mother and one from the father, with the result that their signature whistles might contain features of either or both whistles depending upon potential dominance effects.[2]

If learning contributes to signature whistle development, differences in experiential factors may contribute to the sex difference in whistle production. For example, a mother may produce her whistle more frequently in the company of a male calf, or she may limit the calf's contact with other individuals (and thus other whistles). On the other hand, a mother may increase the rate at which she produces whistles other than her signature whistle after having a female calf, producing

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[2] Dominance effects are unlikely; they imply that some females would produce whistles similar to their mothers' and some similar to their fathers' whistles. This would not fit the data at hand, where most females are known to produce whistles highly distinct from those of their mothers (Chapter 4).

different acoustic models for the daughter to copy. Alternatively, she may allow daughters relatively more contact with other individuals.

Two different lines of research were undertaken to specify the potential roles of genetic and learned factors in signature whistle development. First, whistles from free-ranging Sarasota calves and from captive calves at the Miami Seaquarium were compared to those of their parents to look for similarities. Second, detailed focal observations and acoustic recordings of Sarasota calves were made during the period of whistle development. The major goals of the focal observations and recordings of mother-calf pairs were as follows: 1) to study whether the early social environment influences signature whistle development (by looking at the strength of the association between a calf and its mother and with other individuals); 2) to track the whistle repertoire of calves during the first year of life; 3) to quantify the overall acoustic environment of developing calves; and 4) to determine general behavioral correlates of whistle production.

If whistle development is affected by the acoustic environment of a young calf, then the time course and the eventual outcome of development could vary considerably among different calves. As discussed above, three captive calves at the Miami Seaquarium apparently incorporated sounds present in their acoustic environment in the rapid development of their own signature whistles (Tyack et al.

submitted). These calves were exposed to continuous high whistle rates (appr. 7.4 per minute (Tyack et al. submitted) in their tank (versus less than 1 per minute for free-ranging calves (section 5.3.2.2.1)). For free-ranging calves, there is much greater potential for variability in the acoustic environment of a developing calf, as well as potential for the mother to control what the calf hears. Factors such as the abundance and diversity of whistles heard by a calf, and the strength of a calf's association with its mother and with other individuals, could affect both how quickly the whistle develops and the contour eventually adopted by a calf. For example, studies of vocal development in birds have found that a variety of factors can affect which song a young bird eventually adopts. Zebra finches may not simply adopt the song that is heard most frequently, but may instead selectively copy a song similar to that of the father, or to that of an individual with which it interacted most aggressively (Clayton 1987). Indigo buntings may copy songs of an individual of high dominance rank (Payne 1983). Although in most cases it is not possible to observe these types of subtle interactions in free-ranging bottlenose dolphins, it is possible to observe general association patterns and to quantify the overall acoustic environment. Differences in these parameters may then be related to differences in the time course of whistle development or in the tendency of a calf to develop a whistle similar to the mother or to another individual.

The remainder of this chapter is divided into two major sections:

1) comparisons of whistles of parents and offspring (both wild and captive);

2) examination of effects of the early social and auditory environment on whistle development, using focal observations and recordings of undisturbed free-ranging mother-calf pairs.

5.2 COMPARISONS BETWEEN PARENTS AND OFFSPRING

5.2.1 METHODS

To determine whether the acoustic structure of signature whistles may be inherited from the parents, whistle contours of calves were visually compared with those of their parents. The extent to which similarities and differences conformed to the predictions of a simple genetic model was evaluated.

5.2.1.1 Wild dolphins

5.2.1.1.1 Mother-offspring comparisons

Similarity between whistle contours of 42 Sarasota mothers and calves were rated by judges using methods described in Chapter 4. (Background on recording and analysis techniques used for the Sarasota animals was described in Chapter 2.)

5.2.1.1.2 Father-offspring comparisons

Work is in progress (by Debbie Duffield at Portland State University) to determine paternities of the Sarasota calves. Duffield and Wells (1991) described the techniques that are being employed to achieve this end, including protein electrophoresis, chromosome banding, and DNA fingerprinting. So far, twelve known mother-calf pairs have been tested against nine possible fathers present in the Sarasota community using various combinations of these techniques. Of the twelve calves, four did not match any of the potential fathers. For the remaining eight calves, all but one potential father was excluded for seven (five males and two females), and all but two potential fathers were excluded for one female calf. Four of the nine possible fathers tested did not match any of the twelve calves. These data are summarized in Table 5.1. Further analyses may still eliminate some of the potential fathers that were included in this analysis. This would indicate that the actual father was not included in the pool of 9 possible fathers, and that other males must be investigated.

Table 5.1. Summary of paternity data for Sarasota calves

Identification	numbers
Male calves	**Possible father(s)**
17	74
166	58
11	34*
12	78
142	78
Female calves	
144	41*
159	41*
61	41*, 74

* Signature whistle not known

Of the five males that were included as possible fathers in this analysis, one (no. 34) was recorded only once, and he produced no whistles at that time (1985). Another of the five (no. 41, unfortunately a candidate to be the father of all three female calves) was recorded during six different capture sessions since 1985, but in over 8 hours of recordings only ten whistles were heard, and they were not all the same contour. Six whistles were classified as chirps, which are short, unstereotyped frequency upsweeps that are produced frequently by most animals. Three whistles were longer, more gradual upsweeps, and one was a multilooped contour (Chapter 2). Thus, no one contour was dominant, and I was not able confidently to attribute a signature whistle to this male. The remaining three males produced enough stereotyped whistles (at least 10) to allow confident attribution of a signature whistle contour. Whistles of these three possible fathers were compared to those of five calves, four male and one female.[3]

5.2.1.2 Captive dolphins

Whistles of nine bottlenose dolphins born in captivity and of their parents were recorded at the Miami Seaquarium over a period of two weeks in December of 1988 and two days in December of 1990. The father of two of these calves, Dawn

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[3] I qualitatively judged as similar or not similar the whistle contours of fathers and calves, as well as of captive parents and offspring discussed in the next section. I feel that these judgements are reliable, since my judgements of whistle similarity among the Sarasota mothers and calves closely matched those made by the independent judges (Chapter 4). I judged the whistles of 42 mother-calf pairs as not similar, somewhat similar, or very similar, and 95% of my judgements agreed with those of the judges. In only 2 cases (5%) did my judgements place whistles in an adjacent similarity category (e.g., somewhat similar as opposed to not similar) to that decided upon by the judges.

and Dancer, was no longer alive at the time these recordings were made; thus only seven father-offspring comparisons were possible. Recording equipment included a Marantz PMD-430 stereo cassette deck and a hydrophone designed by Peter Tyack. Recordings were analyzed on a Kay Elemetrics Corp. Model 5500 Digital Signal Processing system, and spectrograms of whistles of parents and offspring were visually compared.

5.2.2 RESULTS

5.2.2.1 Wild dolphins

5.2.2.1.1 Mother-offspring comparisons

To summarize results presented in Chapter 4, 9 of 21 males versus 2 of 21 females produced signature whistles very similar to those of their mothers (Figures 4.4, 4.10-4.11). 15 of 21 females, versus 7 of 21 males, produced signature whistles very different from those of their mothers (Figures 4.3, 4.5-4.10). The remaining 5 males and 4 females produced whistles that were somewhat similar to those of their mothers.

5.2.2.1.2 Father-offspring comparisons

Visual comparisons of whistle contours of five calves, four male and one female, to whistles of their potential fathers did not reveal any obvious similarities (Figures 5.1-5.3). The whistles of males no. 17 and no. 166, their mother, no. 10, and their potential fathers, no. 74 and no. 58, respectively, are shown in Figure 5.1. The whistle contours of these two males do not resemble those of either parent (the whistle of male no. 166 is discussed in more detail in section 5.1.3). Figure 5.2 shows the whistles of female no. 61, her mother, and one of her potential fathers, no. 74. (A signature whistle was not determined for her other potential father, no. 41, as discussed in section 5.2.1.1.2.) Again, no similarities are evident. Although this is the only female whose whistle could be compared to both that of her mother and that of her possible father, this comparison provides no support for the idea that whistle structure is genetically determined. Her whistle does not share any obvious features with the whistles of either parent.

The last two males for which the paternity analysis indicated a possible father are no. 12 and no. 142, both of which apparently have the same mother and father (shown in Figure 5.3). These are two of the males that were found to produce a whistle similar to that of their mother (Chapter 4, section 5.2.2.1.1); neither calf's whistle appears to share features with their father's whistle.

Figure 5.1 (facing page). Whistles of two Sarasota male calves, no. 17 and no. 166, their mother, no. 10, and possible fathers, no. 74 and no. 58 respectively. Note the lack of similarity between whistles of parents and offspring. Spectrograms were made with a Kay Elemetrics Corporation Model 5500 Digital Signal Processing system, with a sample rate of 81,920 Hz, a 256 point FFT, and a Hamming window.

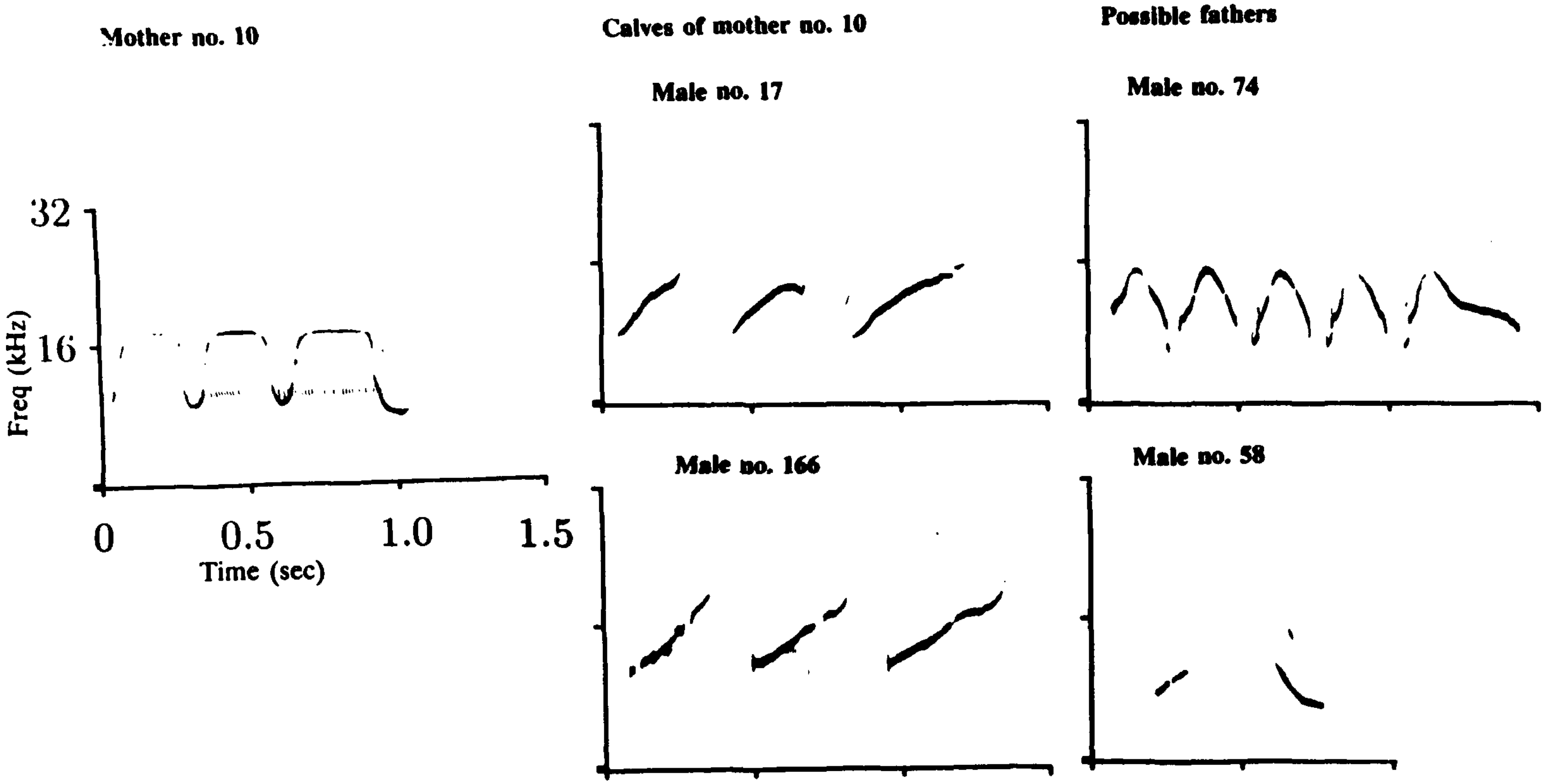

Mother no. 10
Calves of mother no. 10
Possible fathers
Male no. 17
Male no. 74
Male no. 166
Male no. 58
32
16
Freq (kHz)
0
0.5
1.0
1.5
Time (sec)

Figure 5.2 Whistles of Sarasota female calf no. 61, her mother (no. 32), and one of two possible fathers (no. 74). (No signature whistle was attributed to her other possible father, no. 41). Note the lack of similarity between whistles of parents and offspring. Settings are as in Figure 5.1.

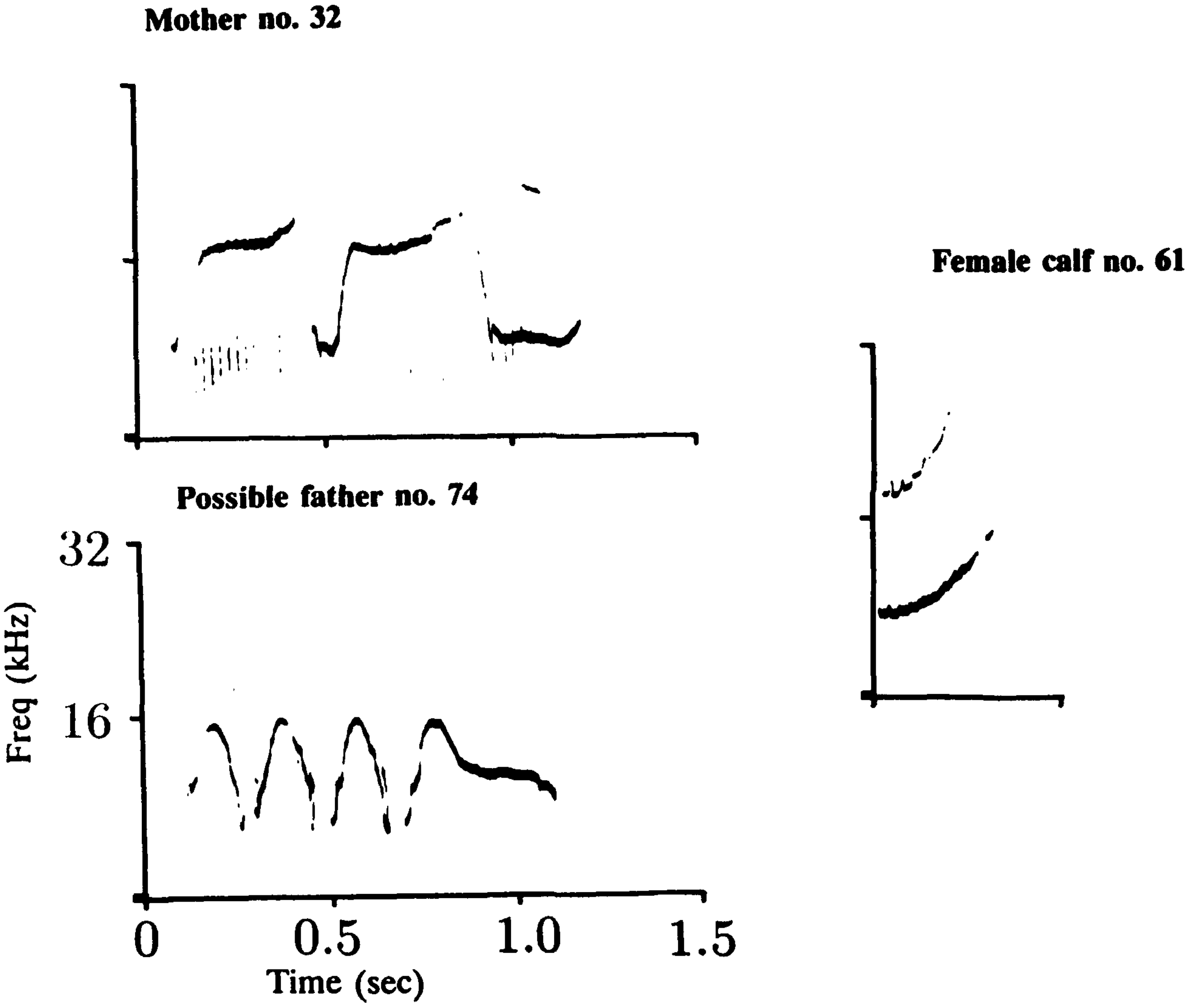
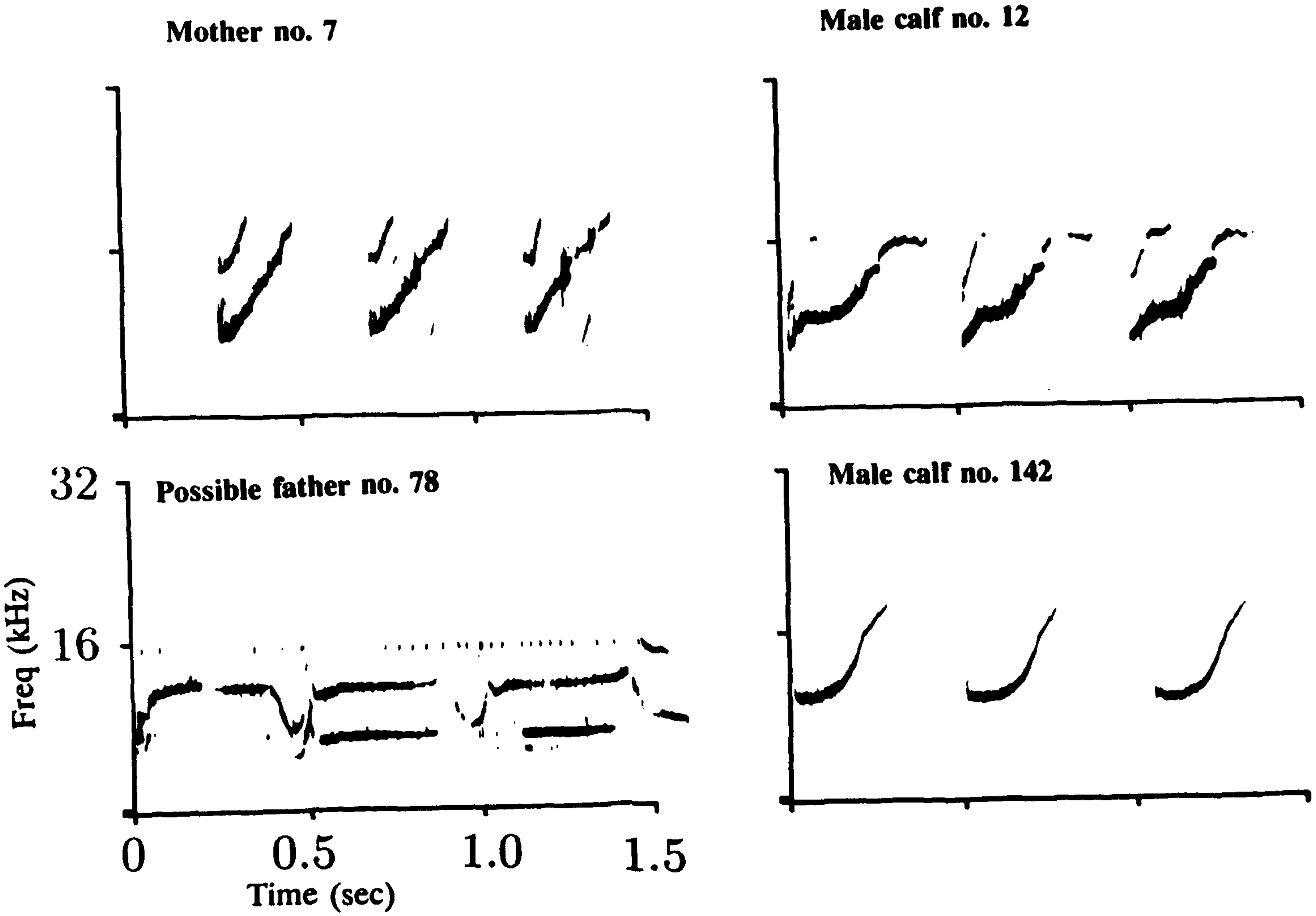

Mother no. 32
Female calf no. 61
Possible father no. 74
32
16
Freq (kHz)
0
0.5
1.0
1.5
Time (sec)

Figure 5.3 Whistles of Sarasota male calves no. 12 and no. 142, their mother, no. 7, and their possible father, no. 78. Note the similarity between the whistles of the mother and her calves, and the lack of similarity between whistles of the calves and their possible father. Settings are as in Figure 5.1.


Mother no. 7
Male calf no. 12
Possible father no. 78
Male calf no. 142
32
16
Freq (kHz)
0
0.5
1.0
1.5
Time (sec)

5.2.2.2 Captive dolphins

Data from nine captive calves recorded at the Miami Seaquarium do not show the same pattern of sex differences found in Sarasota. Of five male and four female calves, only one female, Dancer, produced a whistle somewhat similar to that of her mother. None of the five male calves recorded at the Miami Seaquarium produced a whistle similar to that of their mother (Figures 5.4 - 5.6).

Papi, the father of seven of the calves whose whistles are shown in Figures 5.4 - 5.6 (Ivan, Shadow, Samantha, Noel, Tori, Sundance, and PJ), produced the whistle shown in Figure 5.7. Although there is some similarity between Ivan and Papi's whistles, there are no obvious similarities between his whistle and those of his other six offspring.

Figure 5.4 (facing page). Whistles of one mother (Cathy) and her three calves; one male (Ivan) and two female (Samantha and Tori), recorded at the Miami Seaquarium. Note the lack of similarity between the whistles of these calves and their mother. Settings are as in Figure 5.1.

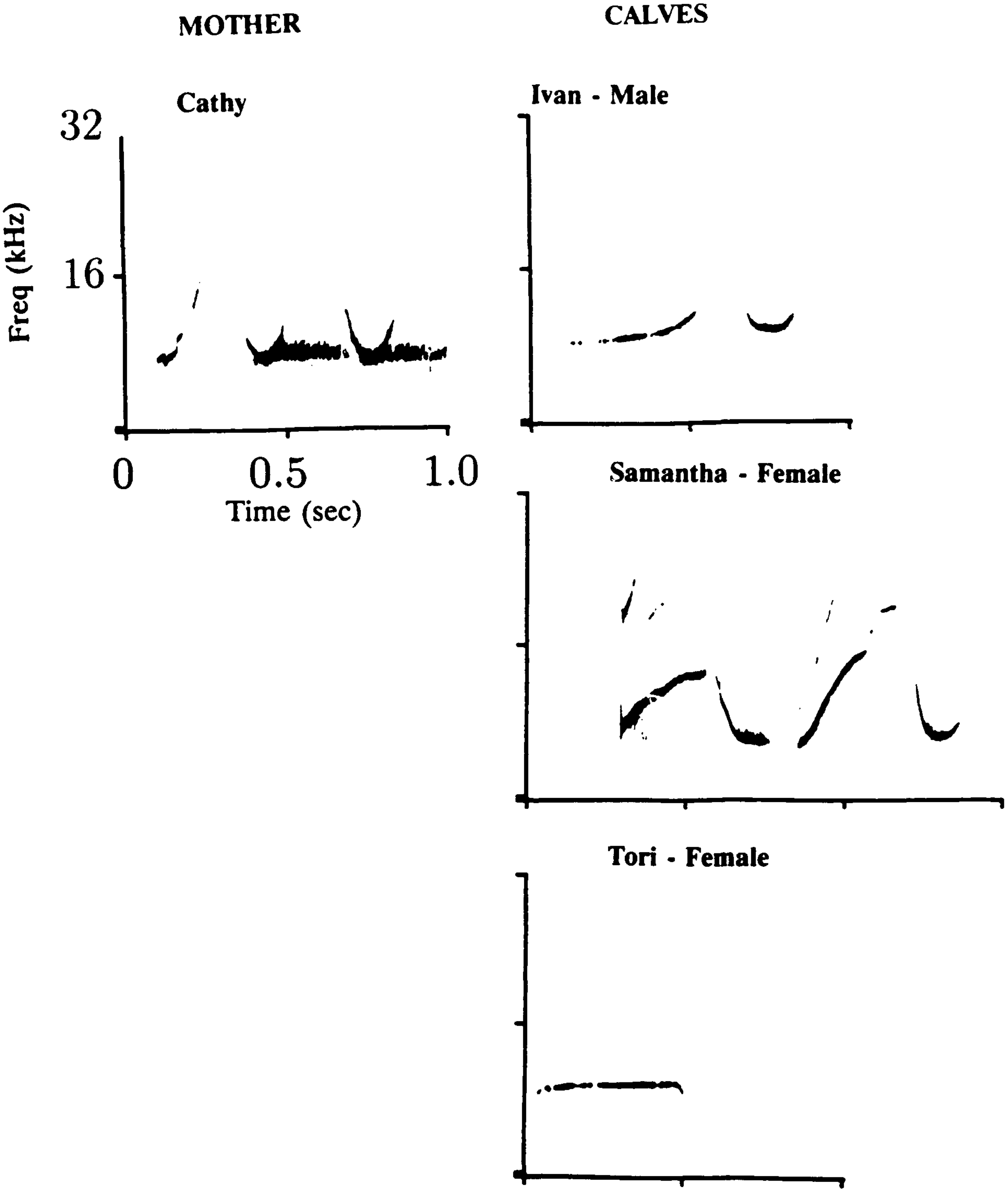

MOTHER
CALVES
Cathy
Ivan - Male
Samantha - Female
Tori - Female
32
16
Freq (kHz)
0
0.5
1.0
Time (sec)

Figure 5.5 Whistles of two mothers (April and Bebe) and their male (Noel and Sundance) and female (Dawn and Dancer) calves, recorded at the Miami Seaquarium. Note the similarity between whistles of Dancer and her mother, and the lack of similarity in the remaining mother-offspring comparisons. Settings are as in Figure 5.1.

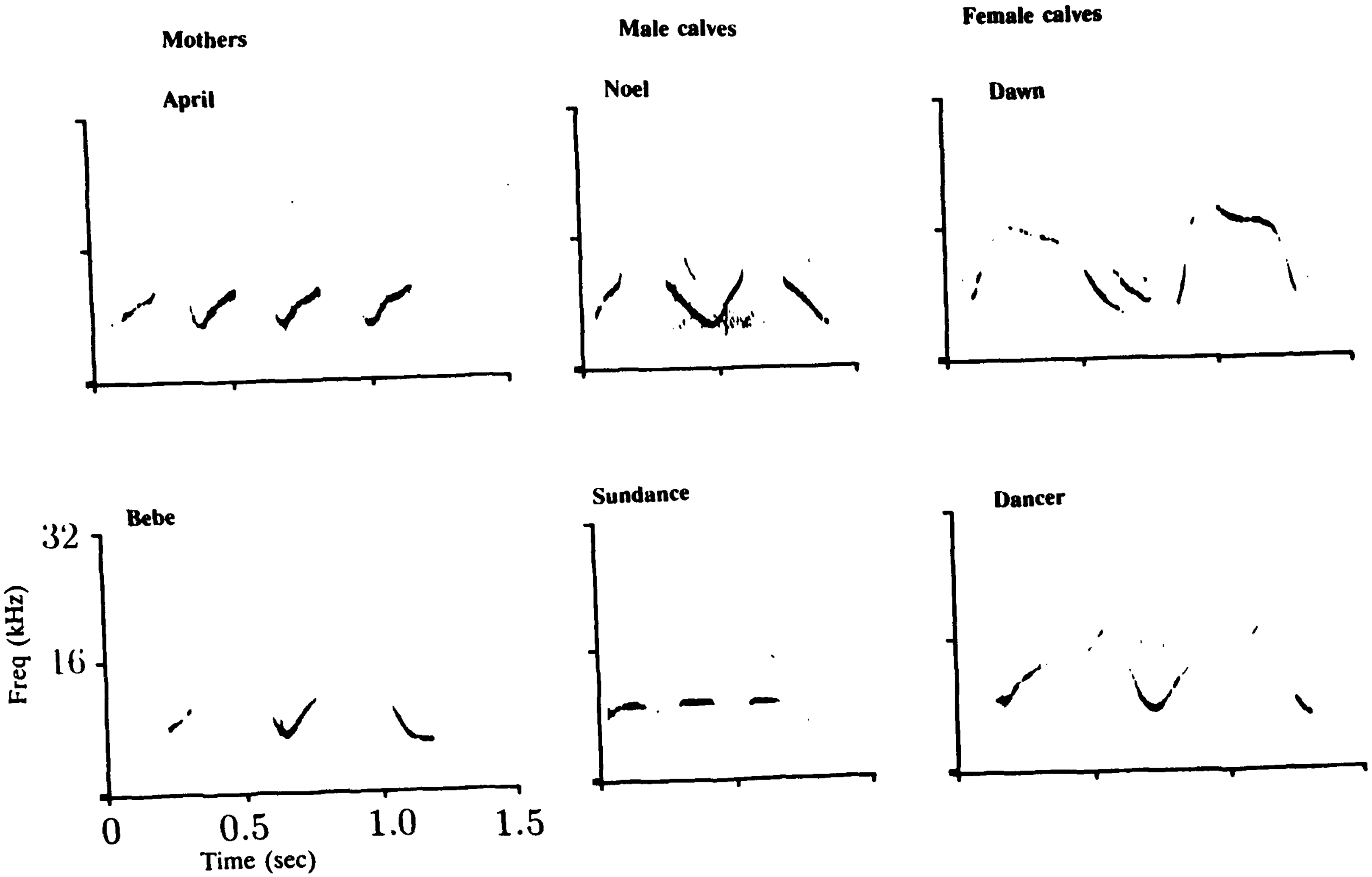
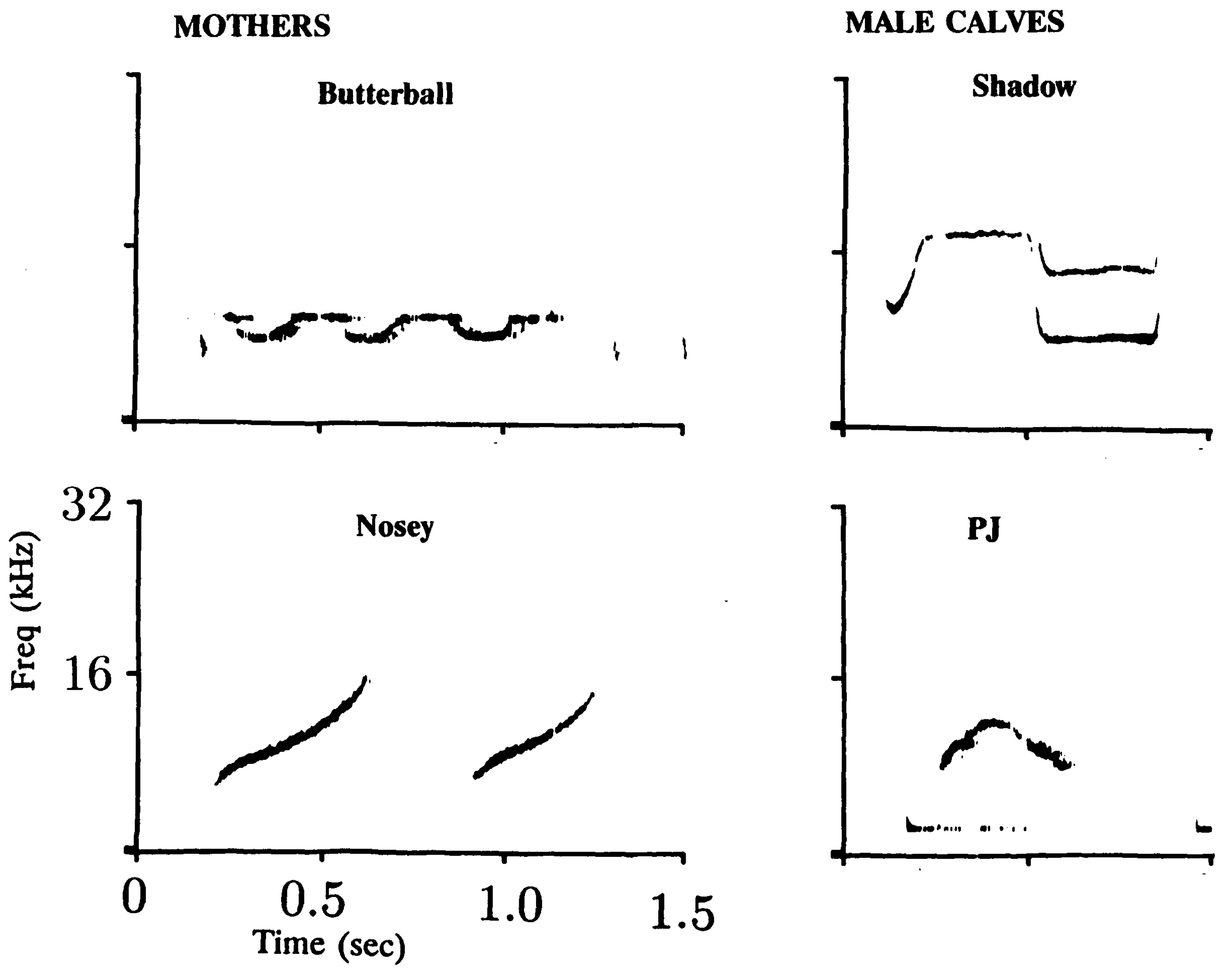

Mothers
April
Bebe
Male calves
Noel
Sundance
Female calves
Dawn
Dancer
32
16
Freq (kHz)
0
0.5
1.0
1.5
Time (sec)

Figure 5.6. Whistles of two mothers (Butterball and Nosey) and their male calves (Shadow and PJ). Note the lack of similarity between whistle contours of the mothers and calves. Settings are as in Figure 5.1.


MOTHERS
MALE CALVES
Butterball
Shadow
Nosey
PJ
Freq (kHz)
32
16
0
0.5
1.0
1.5
Time (sec)

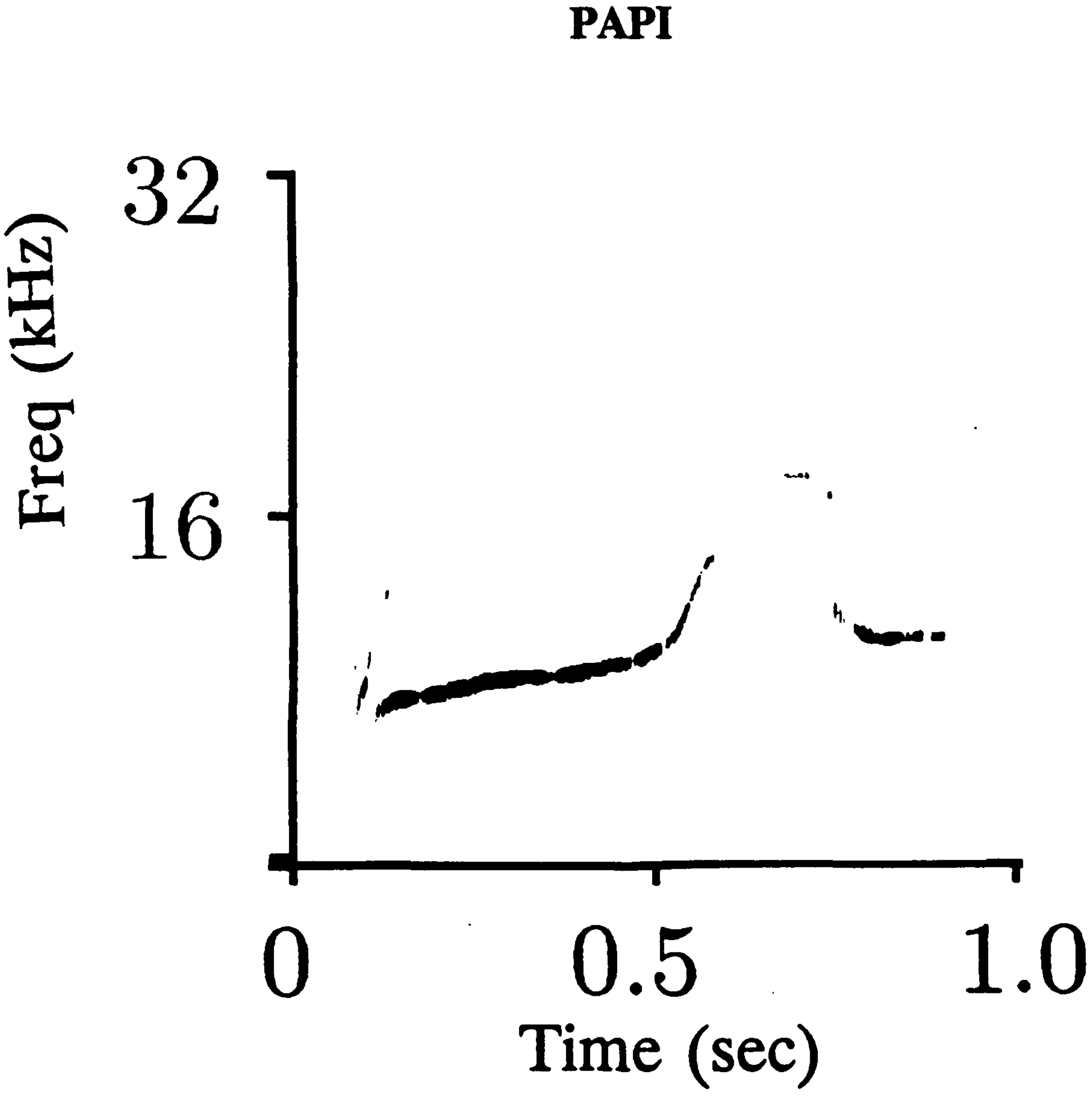


Figure 5.7 Whistle of Papi, the father of seven of the calves shown in Figures 5.4 - 5.6 (Ivan, Samantha, Tori, Noel, Sundance, Shadow, and PJ). Note the similarity between Papi's whistle and that of Ivan (Figure 5.4), and the lack of similarity to all others. Settings are as in Figure 5.1.

5.2.3 DISCUSSION

Comparisons among whistles of parents and offspring, both in the wild and in captivity, do not support the idea that signature whistle structure is exclusively genetically determined. A simple genetic model, incorporating sex-linkage of genes affecting whistle structure to account for the sex difference observed in Sarasota, predicts that 1) males would produce signature whistles similar to those of their mothers, and that 2) females would produce whistles that shared features with the whistles of both their mothers and fathers. However, the sex difference is statistical, with slightly fewer than half of all Sarasota males producing whistles similar to their mothers' (Chapter 4). In addition, the whistles of Sarasota females tend to be highly distinct from their mothers' whistles (Chapter 4, section 5.2.2.1.1). Four Sarasota male calves and one female calf also did not produce whistles that resembled those of their possible fathers.

Data from captivity provide further evidence against strict genetic determination of whistle structure. Of nine calves, only one female produced a whistle similar to that of her mother and one male produced a whistle similar to that of his father. No other similarities between parents and offspring were observed. These data contrast with the pattern found in Sarasota, where the whistles of more males than females are similar to those of their mothers, the whistles of females tend to be very different from those of their mothers', and no obvious similarities between whistles of possible fathers and offspring were observed.

Therefore, the simple genetic model for determination of whistle structure is inadequate to account for the data. Either a more complicated genetic model is required, or learning may be the primary means by which a bottlenose dolphin calf acquires his or her signature whistle. Two studies of whistle development in captive calves have already provided evidence for learning (Caldwell and Caldwell 1979, Tyack et al. submitted). Differences between the Sarasota and Seaquarium calves could have arisen from vast differences in the acoustic environments of captive and wild calves. The acoustic environment of a captive calf is limited to the sounds present in its tank, where the whistles of a very vocal individual could dominate. In the wild, the mother's whistle is probably a dominant component of a calf's acoustic environment, but there is a much greater potential for variability. A mother may influence the acoustic environment of her calf both through her own whistle production and through control of associations with other individuals.

Recordings made during a capture-release session (Chapters 1 and 2) in 1989 provide anecdotal evidence indicating that a calf's whistle structure may have been affected by his acoustic environment (Sayigh and Tyack 1990). Male no. 166 was recorded exchanging whistles back and forth with female no. 14, in a manner similar to that observed for many mother-calf pairs (Sayigh et al. 1990, also Solow et al. in press). At this time, male no. 166 was 1½ years old, and female no. 14 had been one of his 5 closest associates over his lifetime (R. Wells, pers. comm.). He produced a signature contour strikingly similar to that of female no. 14, and quite distinct from that of his mother (Figure 5.8). This observation lends credence to the idea that young calves may be influenced by their acoustic environment in developing a signature whistle. This possibility will be explored in more detail in the next section.

5.3 EFFECTS OF THE EARLY SOCIAL AND AUDITORY ENVIRONMENT ON SIGNATURE WHISTLE DEVELOPMENT

5.3.1 METHODS

5.3.1.1 Focal observations

The method of examining effects of the early social and auditory environment on signature whistle development involved focal observations (Altmann 1974) of calves[4] with simultaneous acoustic recordings during the first year of life (hereafter called "follows"). Older mother-calf pairs were also followed to look for sex differences in mother-calf association patterns and whistle (signature and variant) usage. Background work in a variety of areas was necessary before I was able to collect and analyze data from follows systematically. Table 5.2 outlines the time periods spent doing field work that related to aspects of this project.

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[4] In this chapter, individuals are called "calves" from the time of birth until they become independent from their mothers. Other studies (Caldwell and Caldwell 1979, Smolker et al. submitted) have used the term "infant".

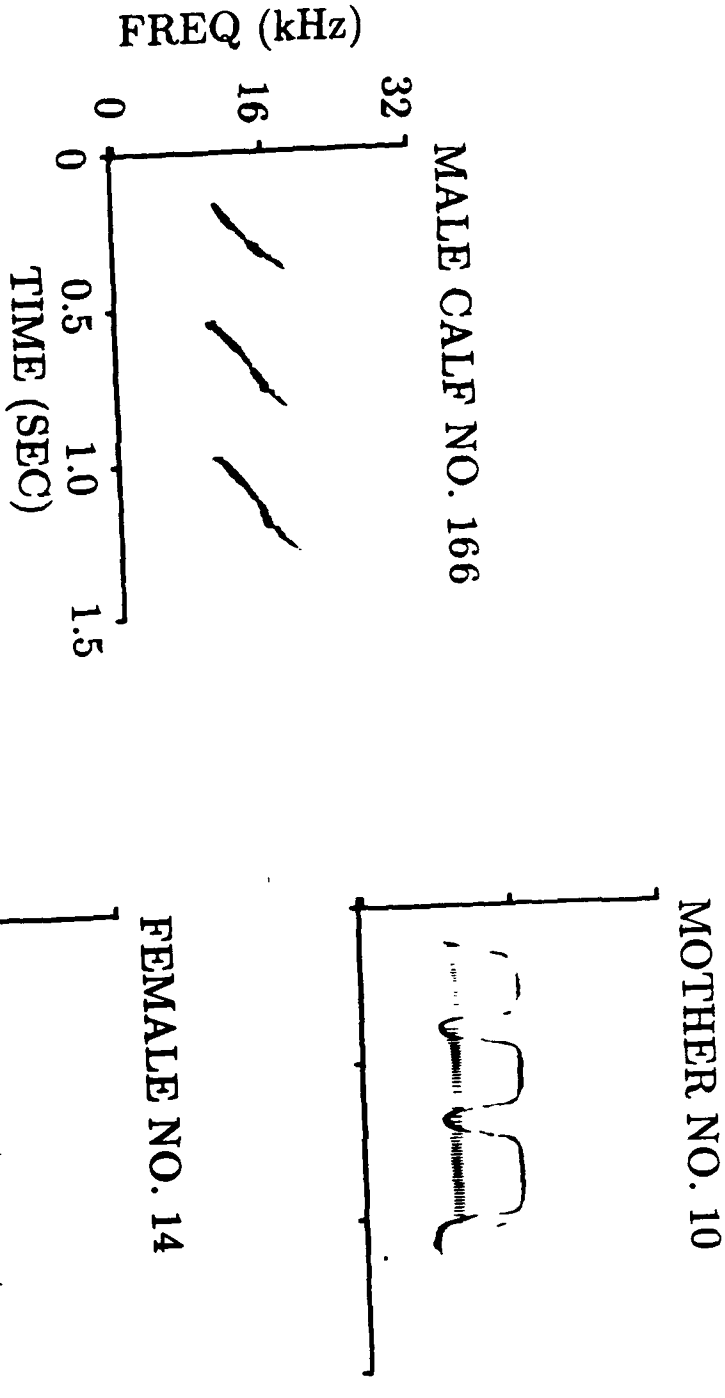

Figure 5.8. Signature whistles of male calf no. 166, his mother (no. 10), and a close female associate (no. 14). The similarity in whistle contours between no. 166 and no. 14 suggests that no. 166 may have learned his whistle from no. 14. Settings are as in Figure 5.1.

Table 5.2. Time spent in the field from 1986-1992

Activity	**Focus**	**Years**	**# days**
Sarasota capture-release projects	Learning individual whistles and fins	1986-1992	138
Sarasota follows	Devising recording protocol, learning dorsal fins and boat handling	1988	23
Shark Bay visit	Learning focal-animal observation techniques	1988	20
Sarasota follows	Devising observation protocol, learning dorsal fins and boat handling	1989	49
Sarasota follows	Collecting focal-animal observation data and recordings	1990-1991	128
TOTAL FIELD	DAYS		358

Sarasota capture sessions were devoted to recording signature whistles from as many known individuals as possible (background and methods are in Chapter 2). I became familiar with the signature whistles of most individuals in the Sarasota community after listening to many capture tapes and studying spectrograms of whistles. This knowledge proved essential to meaningful analysis of recordings of undisturbed animals. Though I was seldom able to identify which individual was vocalizing, I could at least associate particular contours with particular individuals present in the group. In most cases, there was close agreement between the dominant signature contours heard and my visual identifications of individuals present in the group. Thus, if one unknown contour appeared time after time in groups of known animals, I was able to attribute it to the focal calf with some degree of confidence. Details on criteria used in attributing whistles to the focal calves are provided in section 5.3.1.2 (Analysis). When contours of individuals not known to be present appeared, these individuals were usually visually identified in the area soon after. In a few cases, contours of individuals not known to be present were not correlated with visual identifications. These rare events may have been due to: 1) oversights in visual identifications; 2) the individuals in question being too far away to identify; or 3) imitations by group members of signature whistles of individuals not present.

The captures and early follow sessions also provided me with opportunities to learn the distinctive markings on the dorsal fins of many individuals. This skill was essential for effective focal observations of specific individuals. In addition to identifying the various focal mother-calf pairs, it was also important to identify their associates, as these individuals contributed to the acoustic environments of the developing calves. Through field observations with the help of Randy Wells, and through studying photographs of dorsal fins of known individuals, I was able to learn most of the individuals that were encountered frequently. I attempted to photograph all of the individuals present during focal observations, and the photos in most cases corroborated my real-time identifications. In the few cases where I was not able to photograph all individuals that were encountered during a follow (due to a shortage of field assistants), my visual identifications were used. A great effort was made to photograph unfamiliar individuals.

Starting in 1988, Randy Wells and I began observations of mother-calf pairs. At this time, a standard protocol had not been worked out, and observations were made on an *ad libitum* basis. Much of the emphasis in this first season was on learning dorsal fins and boat handling skills, and on developing a satisfactory method for recording dolphin sounds throughout the observation sessions while underway in the boat. Ironing out this method required a considerable time investment. The final recording technique is described in detail in Sayigh et al. (in press), which is included as Appendix II.

In 1989, with substantial help from Amy Samuels, I devised a standard protocol for collecting behavioral data. During this period, data collection was fine-tuned to focus on specific measures that might differ between male and female calves and that might plausibly affect whistle development. The protocol was ultimately a compromise between desired information and information that could reasonably be collected continuously and consistently under frequently adverse sighting conditions. Murky water, heavy recreational boat traffic, and windy conditions often caused us to lose focal animals, or allowed us to observe only gross features such as group size and activity, rather than fine scale behavioral interactions. However, data on mother-calf distance, calf nearest neighbors, mother-calf and group synchrony, the composition, size and spread of the group, and various specified behaviors pertaining to the level of association between the calf and its mother or other individuals (see below), were collected fairly consistently. All of this information, as well as the location and activity of the focal animals and any other animals in the area, their distance and direction from the boat (for sound localization, see Appendix II), and the occurrence of whistles, was recorded verbally on tape as well as on check sheets at five minute intervals. This sampling regime is called "instantaneous", "scan", or "point" sampling (Altmann 1974, Cheney et al. 1987), and has been used successfully in observations of free-ranging dolphins (e.g., Mann and Smuts 1991, Shane 1990, Smolker et al. submitted). A detailed outline of the final protocol and a sample check sheet is included in Appendix III. The first year in which the protocol was used consistently in its final form was 1990.

Observation sessions in 1988 and 1989 helped to define behaviors that pertained to the strength of the mother-calf association and the calf's association with other individuals. These were noted continuously throughout the observation sessions, both verbally and on check sheets (Appendix III). For example, mothers and calves spent a majority of time at a distance of less than 1 m from each other (see section 5.3.2.1.1). When the calf surfaced alongside but slightly behind and touching or almost touching the mother, it was called "baby position".[5] Since a calf spends a large proportion of time in baby position or less than 1 m from the mother, any separation of greater than 1 m was noted as a behavior relevant to the strength of the mother-calf association. The following distance categories were used to specify

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[5] The tendency for calves to stay in physical contact with the mother has been noted by other researchers (e.g., Smolker et al. (submitted): *Tursiops*; Taber and Thomas 1982: right whales). It was hypothesized by Norris and Dohl (1980) that calves may get a "free ride" from the mother's movement.

mother-calf distance, calf's nearest neighbor(s), and overall group spread: BP - baby position; 0 - less than 1 m; 1 - between 1 and 3 m (within approximately 1 adult dolphin length); 2 - greater than 3 and less than 10 m; 3 - between 10 and 50 meters. For the purposes of these observations, animals greater than 50 m away were no longer considered part of the group, as it was too difficult to keep track of them at this distance. Such individuals were noted in the "Other Animals" category (Appendix III).

Synchrony of surfacings can also provide an indication of the closeness of a bond between individuals (Connor et al. 1992). I defined synchrony broadly, encompassing any overlap at all in the surfacings of two or more individuals. Asynchronous mother-calf surfacings and synchronous surfacings of calves with individuals other than the mother were noted as relevant behaviors. Any occurrences of an individual other than the mother being the calf's nearest neighbor were also noted.

As group size increased, the level of obtainable detail often decreased. If only 2 or 3 individuals were present, it was rarely difficult to identify the nearest neighbor of the calf. If a large number of animals were present, and a surfacing did not provide a good view of their dorsal fins, it could be extremely difficult to identify each individual. However, every effort was made to ascertain at least whether or not the mother and calf surfaced synchronously, how far apart they were, and whether or not other individuals surfaced near to the calf.

Table 5.3 summarizes the follows conducted using the final protocol. Approximately 130 additional hours of follows were conducted in 1988 and 1989 before the final protocol was established. For the purposes of this chapter, I have focused exclusively on the follows listed in Table 5.4. Three of these calves (#210, #212, and #209) were followed extensively over their first 7-16 months of life. Calf #203 was also followed extensively over his first 5 months of life[6] in 1989, and although the final protocol was not employed, much comparable information was obtained. This is because calf #203 spent a majority of time with only his mother or with few other individuals (see section 5.3.2.1.4), making it easier to ascertain mother-calf distance and the calf's nearest neighbor.

Throughout this chapter, calves will be referred to by the identification numbers assigned to them by Randy Wells, as part of the Sarasota database. For clarity of presentation, the identification numbers of the mothers of these calves will not be used; they will be referred to in connection with the identification numbers of their respective calves (e.g., "M-#210", "M-#203").

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[6] With a great deal of assistance from R. Wells, A. Samuels and others.

Table 5.3. Summary of follows conducted using the final protocol.

Calf ID #	**# follows**	**# hours (appr.)**	**age of calf**
#210	17	42	0-12 months
#212*	16	33	0-16 months
#209	12	20	0-7 months
#205	7	17	9-12 months
#224	6	5	0-1 month
#211	4	3	1-3 months
#166	3	9	3 years
#159	3	3	4 years
#250	2	2	1-3 months
#980	1	1	4 months
#173	1	1	2 years
#177	1	1	2 years
#170	1	1	4 years

* Calf orphaned at 15 months

Table 5.4. Follows used in analysis

Calf ID#	**# follows**	**# hours (appr.)**	**age of calf**
#210	17	42	0-12 months
#212*	16	33	0-16 months
#209	12	20	0-7 months
#203+	17	35	0-5 months

* Calf orphaned at 15 months

+ Follows conducted in 1989; final protocol not used

The sexes of only two of these four calves are known at the time of this writing. Calf #203 suffered a shark attack at 5 months of age, and his carcass was recovered by Mote Marine Laboratory in Sarasota; a rather unfortunate means of determining his sex (male). The sex of calf #210 (female) was determined during temporary capture in June of 1992 when she was 2 years old. Calf #212 was orphaned in September, 1991 at 15 months of age (its mother was apparently killed by human intervention). Although sightings indicate that it may be still alive, it was not found during the June 1992 capture session, so its sex remains unknown. Calf #209 disappeared at approximately 7 months of age and no carcass was recovered, so its sex is unlikely to be known.

5.3.1.2 Analysis

Each tape was monitored, both to verify verbal comments that had been written onto check sheets, and to note the contours of all whistles produced and any information available regarding the identity of the vocalizers or the context of vocalizations. Depending upon the number of whistles, a two-hour video tape took between 4 and 12 hours to analyze. Information about the tapes were entered into the lab's tape database (Watkins et al. 1991), and hundreds of vocalizations were digitized and incorporated into the lab's sound database.

Whistles from each follow were tallied according to whether they were the signature contour of the mother or other known individuals present. Characteristic unstereotyped whistles occurred consistently when young calves were present in the group. These were frequently faint and/or "quavery" (a term used by Caldwell and Caldwell 1979), with little frequency modulation or erratic patterns of modulation. Such whistles were attributed to the focal calves in situations where few individuals were present, when the calf was very close to the boat, when whistle exchanges with the mother occurred, and when there was overlap with known contours of individuals with which the calf was interacting. The same criteria were used in determining the crystallized signature contours of the calves.[7] Once these were established, occurrences of the calves' signature contours were counted as whistles produced by the calves.

These judgements were made very conservatively, and all other whistles were lumped into one "other" category. If whistles were faint, partially obscured by engine noise, or resembled the contour of the signature whistle of an animal not known to be present at the time (a relatively rare event; discussed in section 5.3.1.1), they were included in the "other" category. This comprised a large portion of all whistles recorded. Counting whistles is to some extent a subjective process; for signature whistles with which I am familiar, I count a standard number of repetitions of a loop

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[7] The time period of whistle crystallization was defined as when one stereotyped contour was repeatedly attributed to the calf.

(Chapter 2) as one whistle. For faint or unfamiliar whistles, I attempted to judge repetitions as single or multiple whistles, but in some cases I may have underestimated the actual number of whistles produced. In addition, there were many instances where noise from our own engine (moving quickly) or from passing boats was likely to have obscured whistles. Thus, whistle counts represent minimum estimates.

A calf's first year life was divided into 4 periods: early (0-3 months), middle (4-6 months), late (7-9 months) and yearling (10-12 months). The number of follows in each category for each of the four calves is listed in Table 5.5. Figure 5.9 shows the numbers of completed 5 minute point samples for each of the four calves during early, middle, late, and yearling periods. Statistical analyses to look for individual or age differences were not possible, since two calves were not sampled in all four stages. Thus, results of this preliminary study are more descriptive than quantitative.

Table 5.5. Number of follows of each calf at early, middle, late, and yearling stages.

Calf	**Early**	**Middle**	**Late**	**Yearling**
#210	3	6	6	2
#212*	4	3	4	2
#209	5	6	1	0
#203	9	8	0	0

* Follows conducted after calf was orphaned are not included

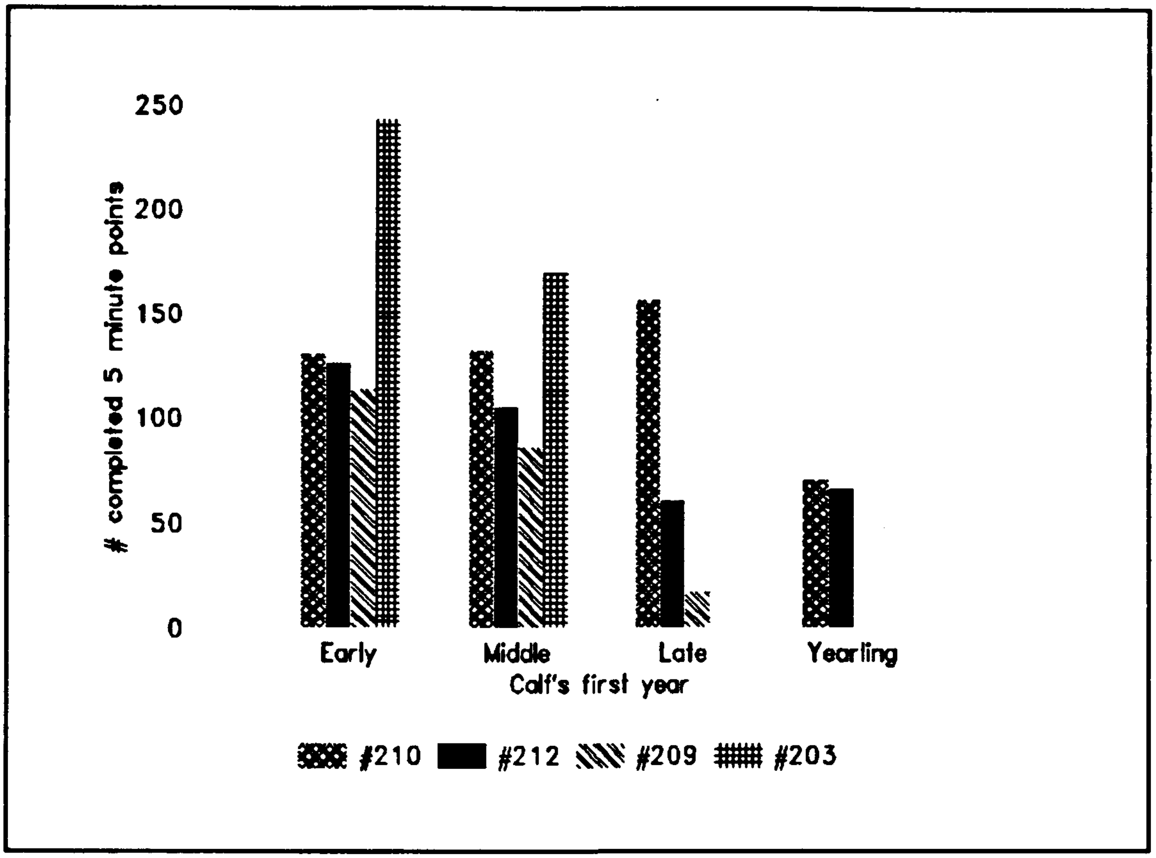


Figure 5.9. Number of completed 5 minute point samples for each of the four focal calves during early, middle, late, and yearling sampling periods.

Data from the five-minute intervals recorded onto check sheets (see Appendix III) were entered into the relational database program *PARADOX* (Borland International, Scotts Valley CA). The following categories were entered: group composition, group size (minimum and maximum estimates) and overall group spread, mother-calf distance, calf's nearest neighbor, mother-calf and group synchrony, activity, whether other animals were present, and whether whistles occurred. Data from the continuous behavior record were not included in this analysis. The database was then queried for information regarding the relation between calf age and factors such as mother-calf distance, mother-calf synchrony, and group size. Calculations were normalized according to the number of 5 minute point samples in which the variable of interest was observed, rather than on the total number of 5 minute samples. Thus, these totals vary for different variables; some were more difficult to observe consistently than others.

5.3.2 RESULTS

Analyses of focal observations and recordings of four mother-calf pairs during the calves' first year of life focused on patterns of similarities or differences among the calves that may have related to signature whistle development. With only two calves of known sex, it is not possible to generalize about sex differences. However, it is still possible to examine how the early experiences of these calves may have affected their signature whistle development.

Results of these analyses are divided into two major sections. First, data from the five-minute point samples are discussed, including mother-calf distance; mother-calf synchrony; calves' nearest neighbors; overall number of associates and persistence of associates; percentage of time spent with associates; and maximum group size. Second, whistles recorded during the mother-calf follows are discussed, including total numbers of whistles produced; breakdowns of different whistle contours; detailed descriptions of the whistle development process for each of the four calves; and characterization of general behavioral correlates of whistle production.

5.3.2.1 Analyses of 5-minute point samples

Analyses of focal data show some consistencies among the calves, but also highlight the large amount of individual variability in each calf's association with its mother and with other individuals. Data on mother-calf distance, synchrony, calves' nearest neighbors, and overall association patterns will be presented.

5.3.2.1.1 Mother-calf distance

The percentage of time spent in close proximity is a basic measure of the strength of the mother-calf association. This is measured as the percentage of time that the calf spent in baby position (BP) or less than 1 meter from its mother (Figure 5.10). In general, this percentage is quite high (ranging from 87% to 97%) in the early and middle periods for all four calves. Calf #209 is the exception (62%) in the middle period, but during its excursions away from the mother it was frequently accompanied by its older sister, who was the most persistent associate of any of the four focal calves (section 5.3.2.1.4). The overall trend is for calves to spend more time further away from their mother as they get older; the late data point for calf #209 should be viewed with caution as it is based on only one follow (Table 5.5).

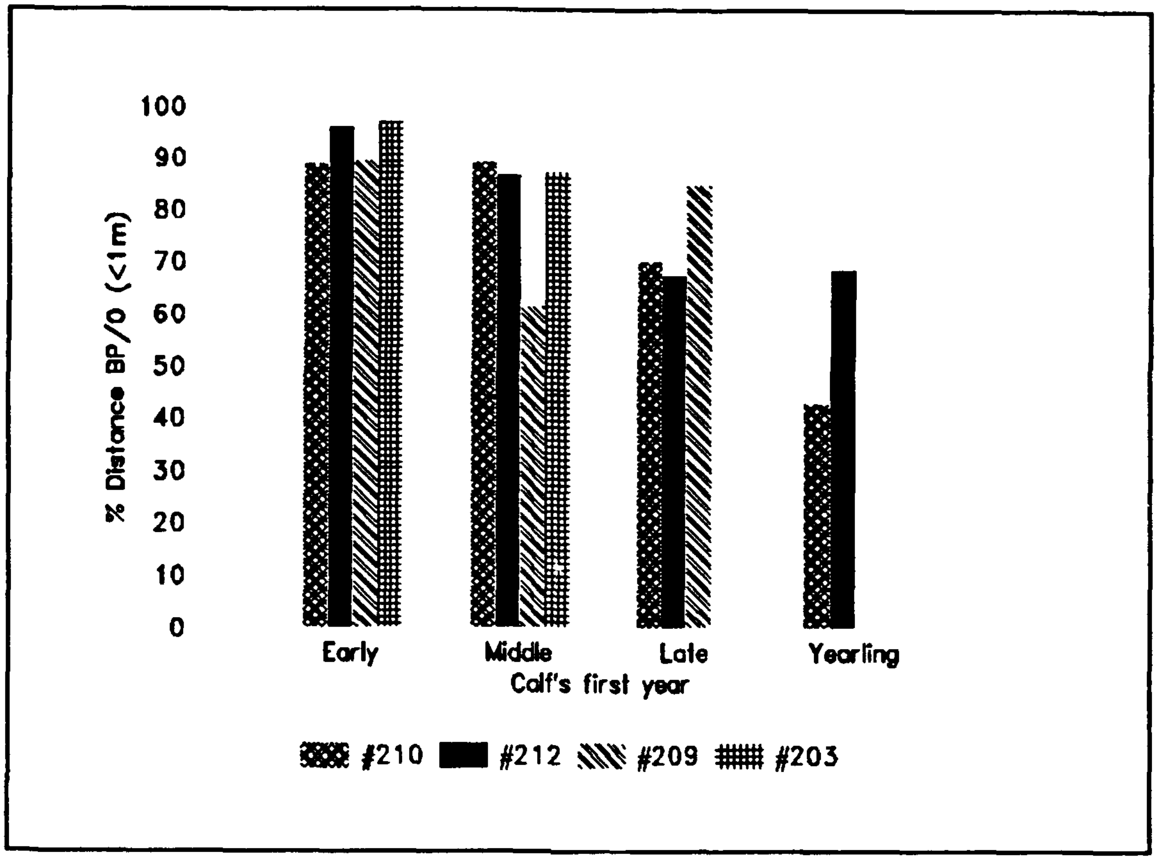


Figure 5.10. Percentage of 5-minute point samples during which the calf was either in baby position (BP) or less than 1 meter from its mother for each of four focal calves during early, middle, late and yearling stages.

Mother-calf distance was related to activity, with traveling pairs tending to stay closer together. Activity at each 5-minute point sample was noted as either travel, mill (non-directed movements), rest, socialize, feed, or some combination of these activities (more precise definitions are given in Appendix III). The overall percentage of 5-minute intervals during which the focal mother-calf pairs were at least partially engaged in an activity other than travel ranged from 32% to 71% for the four pairs (Figure 5.11). However, between 53% and 91% of their time was spent engaged in non-travel activities when mother-calf distance was 1 meter or more (Figure 5.11).

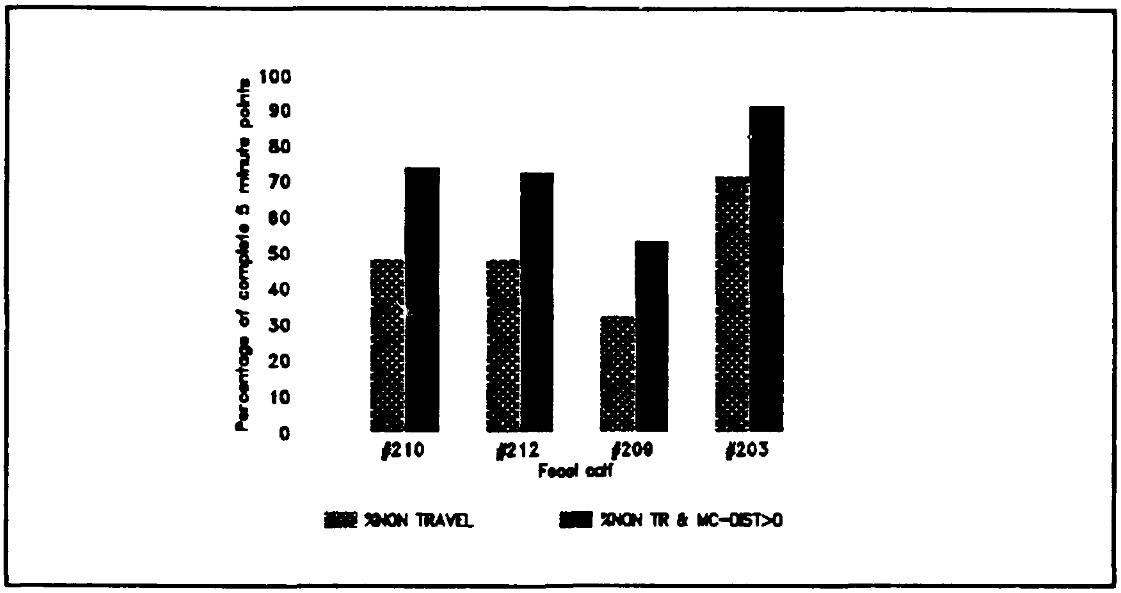


Figure 5.11. Relationship between activity and mother-calf distance: overall percentage of 5-minute point samples spent at least partially engaged in non-travel activities such as mill, rest, socialize and feed (%NON TRAVEL) as compared to the percentage of time spent engaged in these activities while mother-calf distance was 1 meter or more (%NON TR & MC-DIST>0).

5.3.2.1.2 Mother-calf synchrony

Figure 5.12 shows the percentage of 5-minute point samples during which the mother and calf surfaced asynchronously, which includes surfacings of the calf by itself and synchronous surfacings of the calf with another individual. The overall trend among the four calves was an increasing tendency to surface asynchronously from the mother with age. By the time she was a yearling, calf #210 surfaced asynchronously the majority (57%) of the time. However, each calf showed a different pattern. Calf #203 maintained a constant low level (7%) of asynchronous surfacings throughout the early and middle periods (after which he died). Calf #209 showed a peak in asynchronous surfacings in the middle period (39%), which corresponded with a lower percentage of time spent less than 1 meter from the mother (Figure 5.10; but note that the percentage for the late period is based on only one follow). Calf #212 showed a low level of asynchronous surfacings in the early period, followed by increases in the middle and late periods, and a decline as a yearling. Calf #210 showed a fairly steady level of asynchronous surfacings throughout the early, middle and late periods (18%-29%), and an increase as a yearling. Of the four calves, #210 showed the highest level of asynchrony (23%) in the early period (23%), and #203 and #212 showed the lowest (7% and 8%).

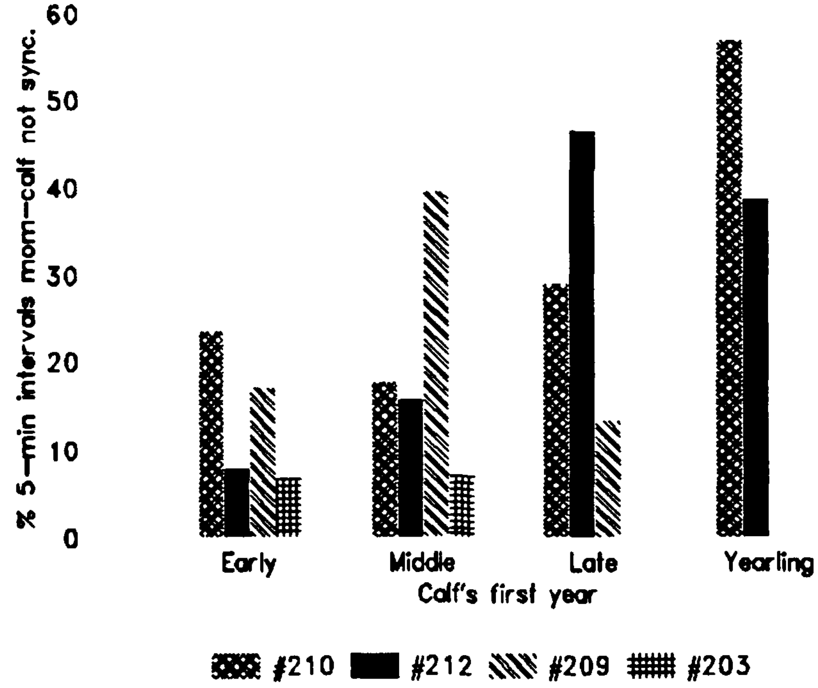


Figure 5.12. Percentage of 5-minute point samples during which the mother and calf surfaced asynchronously, including surfacings of the calf with another individual, for each of four focal calves during early, middle, late, and yearling stages.

5.3.2.1.3 Calves' nearest neighbors

The tendency for a calf to surface with an individual other than the mother as the nearest neighbor or with no nearest neighbor (when all others are too far away to judge which is closest) also varied considerably among the four calves (Figure 5.13). It is not surprising that this measure would be allied to some extent with the percentage of surfacings that were not synchronous with the mother (Figure 5.12), for in most cases when the calf surfaced synchronously with someone other than the mother, this individual was also its nearest neighbor. Accordingly, the trends are the same as those seen for synchrony. The overall levels are lower, however, because a large proportion of asynchronous surfacings occurred when the calf surfaced alone, with no obvious nearest neighbor.

No consistent pattern emerged among the four calves, except for a general increase in this variable as calves got older. The most striking difference is that calf #203 showed only 0.3% of surfacings with a nearest neighbor other than the mother over all follows (which were conducted exclusively in the early and middle periods). This is largely because calf #203 spent a greater percentage of time with only his mother than did the other three calves, thereby constraining his nearest neighbor to be his mother, no matter what her distance. This will be explored in more detail in the next section, where data on group size, diversity, and the patterns of association with other individuals will be discussed.

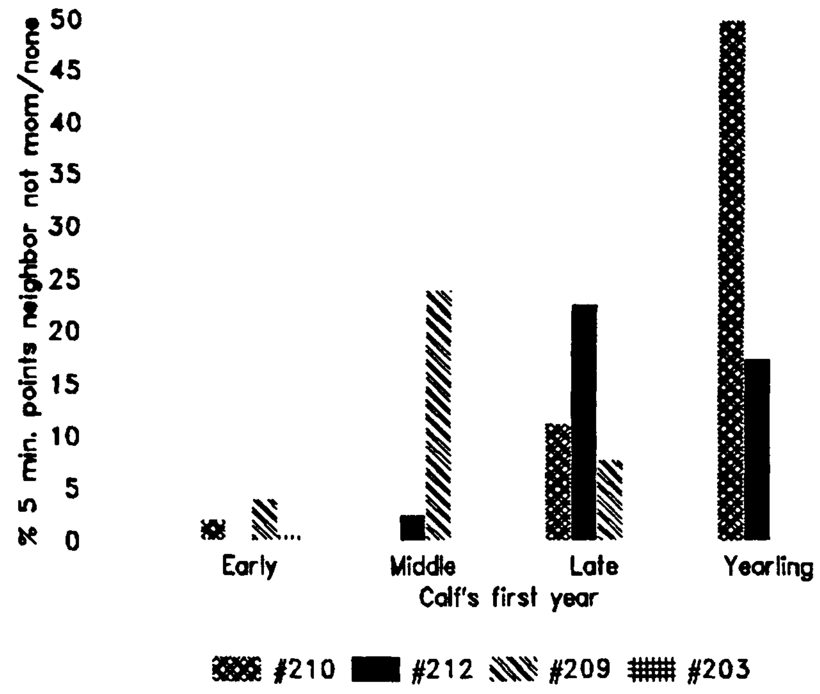


Figure 5.13. Percentage of 5-minute point samples where the calf had a nearest neighbor other than the mother or no neighbor within 50 m, for each of four focal calves during early, middle, late, and yearling stages.

5.3.2.1.4 Associations with other individuals

Total number of different associates in all follows of each of the four focal calves is shown in Figure 5.14. The only obvious difference among the calves is that #203 had fewer overall associates than did the other three calves. Figure 5.15 tallies the number of follows in which each associate of the four calves was sighted. The majority of individuals were present in only one or two follows, although one associate of calf #210 was present in 12 different follows.

In 46% of all follows, unidentified individuals were present. These could have been individuals that were present for too short of a time to see or photograph, or they may have been individuals that I was simply unable to identify. In the latter case, unknown individuals were unlikely to have been present in more than one follow, because I would have had the opportunity to become familiar with them over the course of several follows. Thus, counts of individuals present in 3 or more follows are fairly accurate estimates; counts of individuals present in only 1 or 2 follows are underestimates (Figure 5.15).

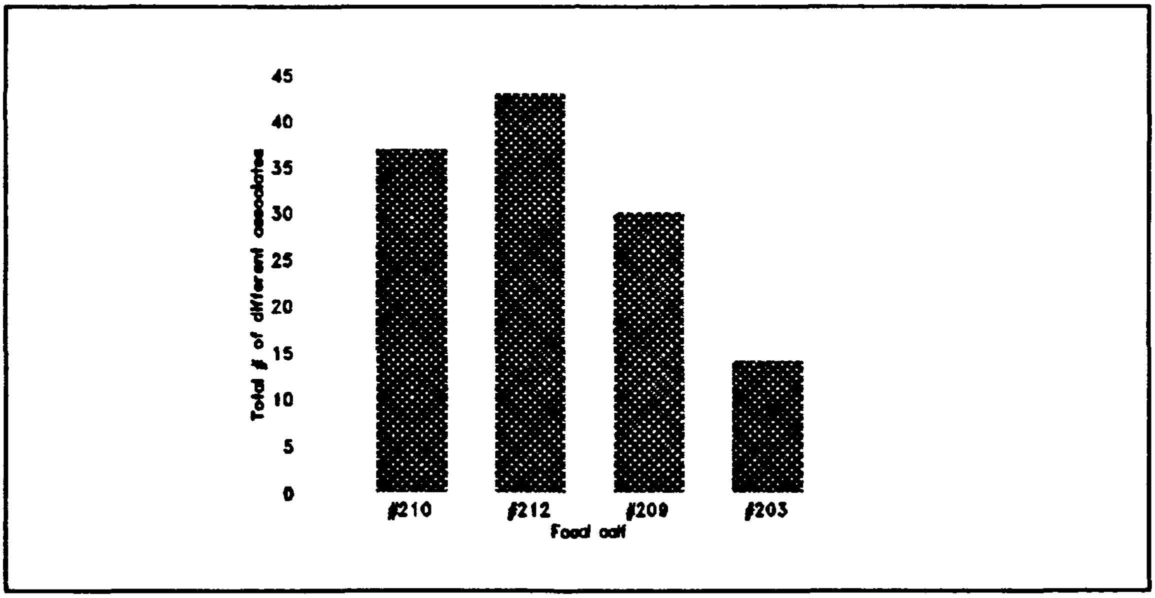


Figure 5.14. Total number of different associates present in all follows of 4 calves.

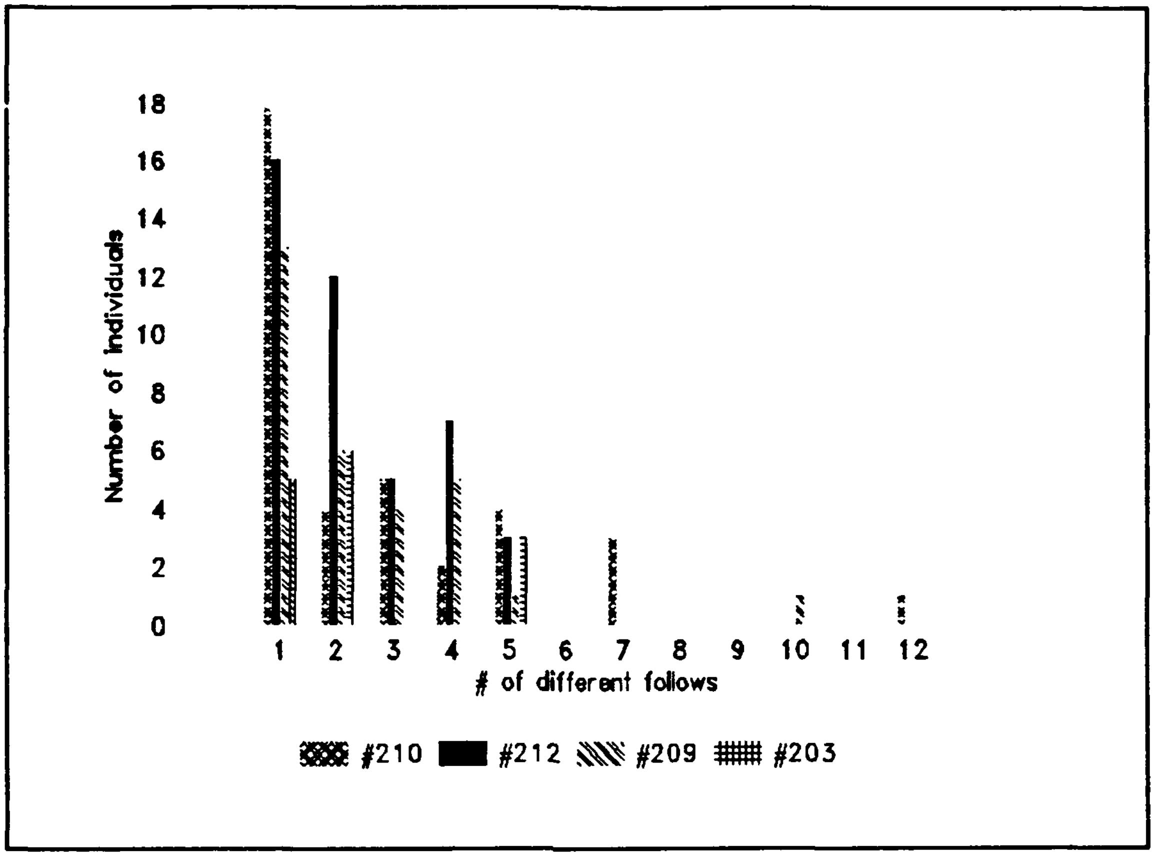


Figure 5.15. Tallies of the number of different follows in which each associate of the four calves was present; this ranged from one follow up to a maximum of 12 follows.

The same data expressed as percentages of the total numbers of associates are shown in Figure 5.16. Even though the numbers are underestimated, the associates present in one and two follows still account for a majority. Associates that were present in more than 2 follows are called "persistent" associates. The overall (maximum) percentages of persistent associates are shown for each focal calf in Figure 5.17. Note that calf #203 not only had the fewest overall associates of all of the calves (Figure 5.14), but also a smaller percentage of these were persistent associates (21%).

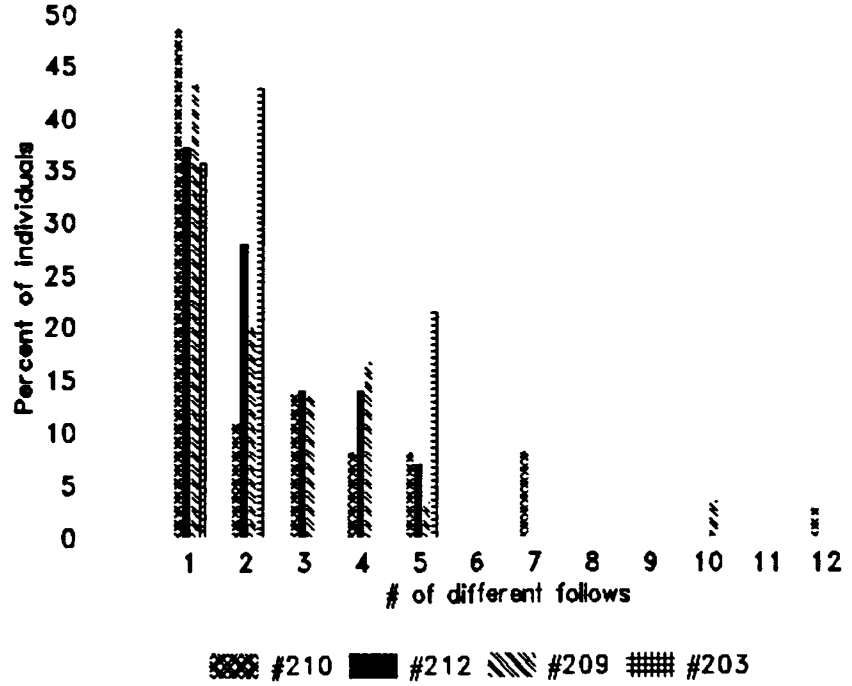


Figure 5.16. Data from Figure 5.15 (tallies of the numbers of different follows in which each associate of the four calves was present) expressed as percentages of total associates.

Numbers of persistent associates and the average percentage of time each one spent with a particular focal calf (averaged over all follows) are shown in Figure 5.18. Calf #203 had the fewest persistent associates (only 3), and each one was present for between 15% and 17% of the time. Calf #209 had 11 persistent associates, of which 10 were present for between 5% and 13% of the total time that this calf was followed, and the 11th was present for 74% of the total time. This individual was an older female offspring of M-#209, and she was the most persistent associate of any

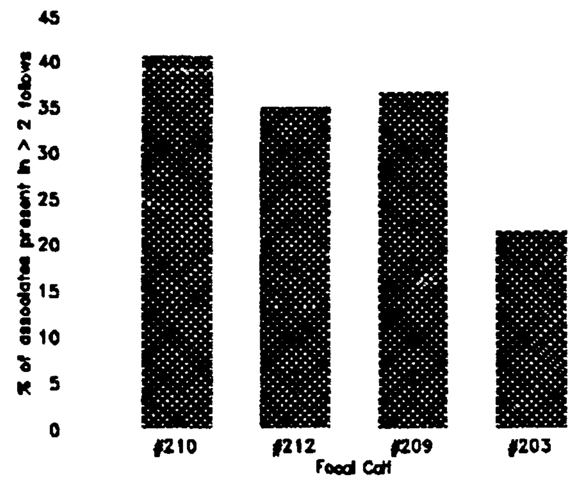


Figure 5.17. Overall percentages of persistent associates (defined as associates present in 3 or more follows) for each of four focal calves.

of the four focal calves. As noted in the section on mother-calf distance (5.3.2.1.1), this sibling frequently accompanied calf #209 during mother-calf separations. The second most persistent associate observed in these follows was also a female sibling, who was present with calf #210 for 38% of the time. Calves #210 and #212 showed somewhat similar patterns of association; each had 15 persistent associates and each associated with the majority of these for less than 20% of the time. However, there were four associates (including the sibling mentioned above) of calf #210 that were present for greater than 27% of the time. None of the persistent associates of calf #212 were present for greater than 23% of the time. This may have been because #212 was the first surviving offspring of M-#212; the two most persistent associates of the other focal calves were both older siblings.

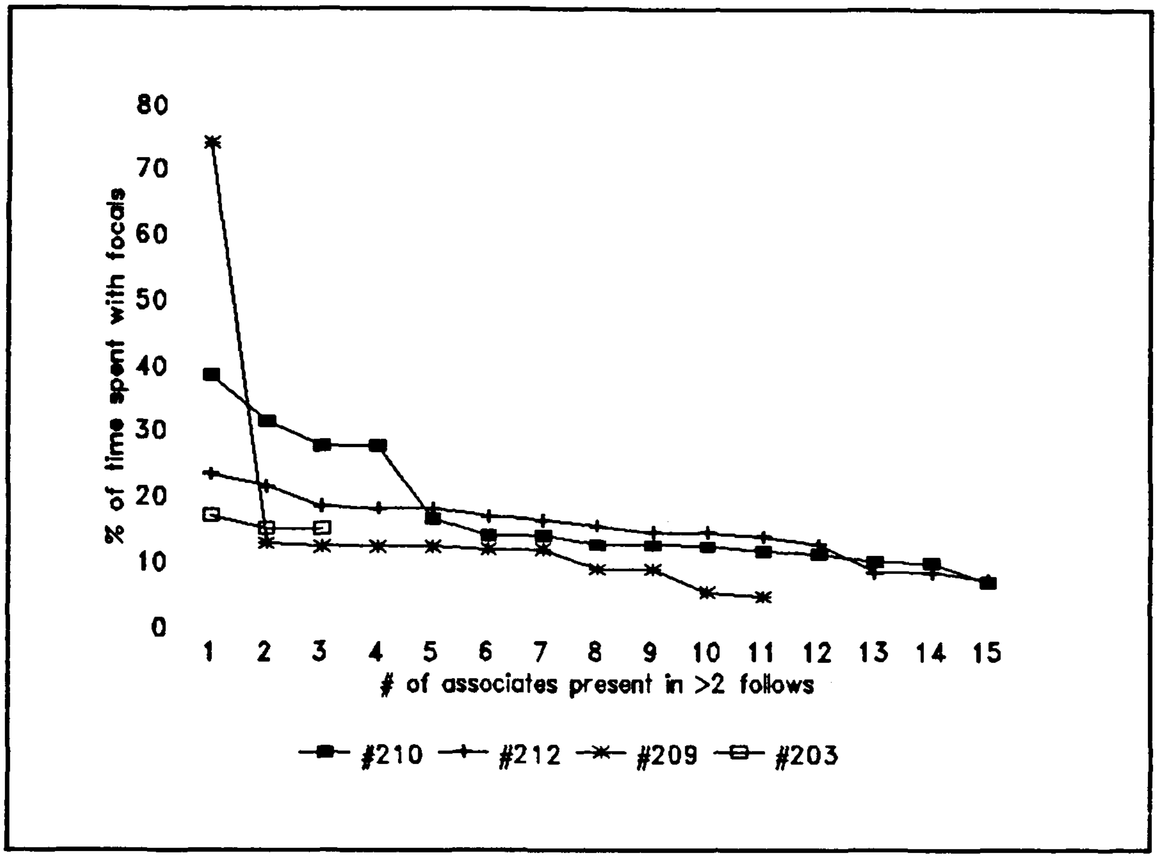


Figure 5.18. Number of persistent associates of each of the four focal calves, and the amount of time each spent with the focal calves expressed as a percentage of the total time followed.

The percentage of time that each calf spent alone with its mother was calculated conservatively, as a percentage of 5-minute point samples during which the maximum group size estimate was two animals. Of the four calves, calf #203 spent the greatest overall percentage of time alone with his mother (Figure 5.19, average = 63%). Calves #210, #212, and #203 showed a peak in the percentage of time spent alone with their mother in the middle period. This was followed by a decline in calves #210 and #212 (no late or yearling samples were obtained for calf #203).

Calf #209 spent an overall low percentage of time alone with its mother (average = 7.5%); 74% of its time was spent with its older sibling (Figure 5.18).

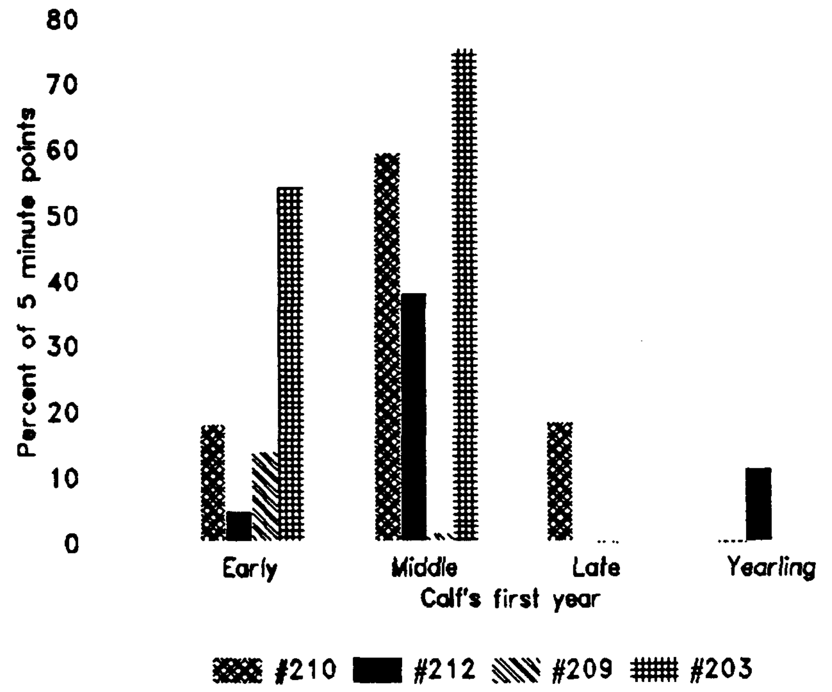


Figure 5.19. Percentage of 5-minute point samples during which the calf was alone with the mother for each of four focal calves during early, middle, late, and yearling stages.

Averages of the maximum group size reached during each follow for each calf over the early, middle, late and yearling periods are shown in Figure 5.20. Calf #203's average maximum group size was generally smaller than that of the other three calves.

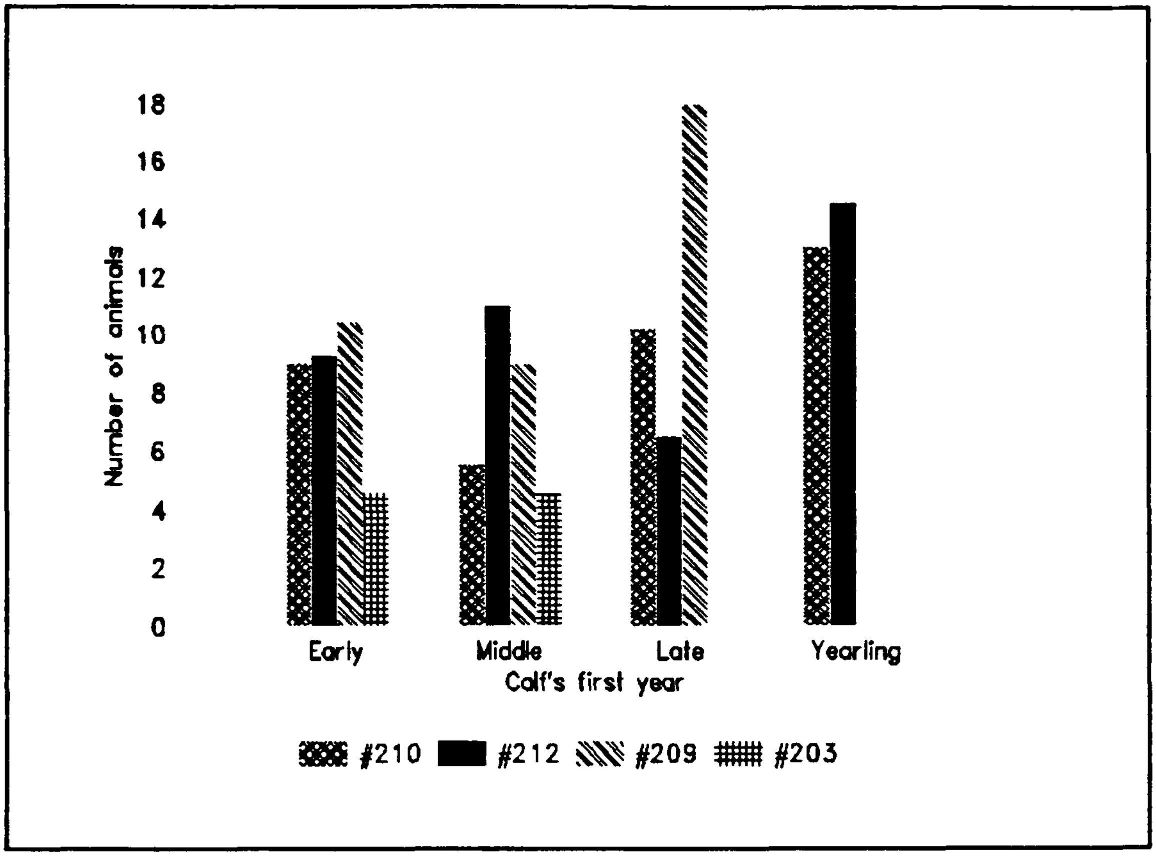


Figure 5.20. Average maximum group size for each of four focal calves in early, middle, late, and yearling stages.

Group size was correlated with the occurrence of whistles. Since average group size for all four focal calves ranged from 3 to 7 individuals, groups containing more than 7 individuals were considered to be larger than average. Whistles occurred in 42% of all 5-minute point samples during which group size was observed, but they occurred in 62% of 5-minute point samples where group size was greater than 7 individuals. At no time during follows of calf #203 was group size greater than 7 individuals; this represents an obvious example of the association patterns of a calf influencing its acoustic environment. The acoustic environments of these calves, as well as descriptions of their signature whistle development, are discussed in the next section.

5.3.2.2 Analyses of whistles

5.3.2.2.1 Overall acoustic environment

Total number of whistles recorded, total recording time, and average whistle rates (whistles per minute) for each of the four calves are shown in Table 5.6. Calf #203 was exposed to the lowest overall whistle rates (averaging 0.64/minute), and calf #210 the highest (averaging 0.91/minute). Figure 5.21 shows a breakdown of whistle types recorded during follows of the four calves according to whether they were the stereotyped contour of the mother, another identified individual present, the calf (which includes unstereotyped whistles attributed to a calf), or any other contour. The proportion of the overall acoustic environment comprised by the mother's signature contour is quantified in Figure 5.22. This was calculated by dividing the total number of signature contours of the mother by the total number of whistles recorded, excluding those produced by the calf. Calf whistles were excluded from the total in order to better represent the acoustic environment to which the calf was exposed. Again at the two extremes are calves #203 and #210, which experienced the greatest (20%) and the least (6%) proportion of mother's whistles respectively.

Table 5.6. Total number of whistles recorded, total recording time, and average whistle rates (whistles per minute) for each of the four calves.

Calf ID#	Total # minutes	Total # whistles	Whistles/minute
#210	2501	2282	0.91
#212	1932	1411	0.73
#209	1148	904	0.79
#203	2067	1319	0.64

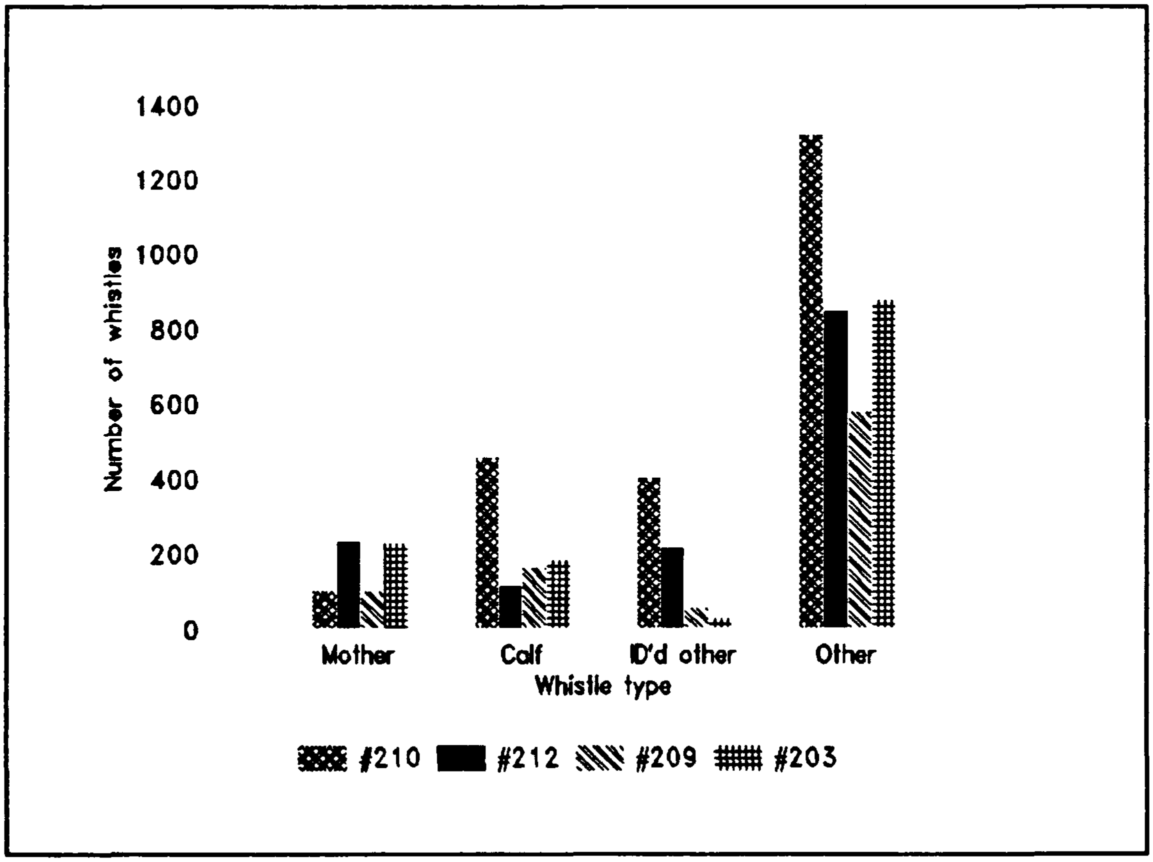


Figure 5.21. Breakdown of whistle contours recorded during follows of four focal calves into four categories: 1) the mother's signature contour; 2) the calf's contour or unstereotyped whistles attributed to the calf; 3) the known contour of an identified individual present (ID'd other); 4) all other whistles.

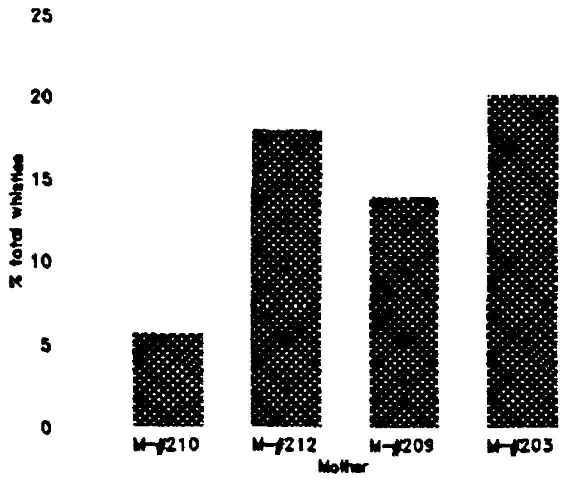


Figure 5.22. The percentage of total whistles (excluding those produced by the calf) comprised by the signature contours of each of the four mothers.

In the 1990 follows, a given group frequently contained more than one of the focal mother-calf pairs, since #210, #212 and #209 were all born within a month of each other.[8] In such a situation, I would choose to observe one of the focal pairs, but would incidentally record whistles from the others as well. Thus, another measure of the frequency of occurrence of the mothers' signature contours is provided by the total numbers of these contours recorded during all follows, not just in follows of their own calf (as in Figure 5.22). This measure will bias against the mother of calf #203, since she was the only one followed in 1989. However, even with this bias, M-#203 was second in overall signature whistle production (Figure

---

[8] Wells et al. (1987) reported that Sarasota mothers with similar-aged calves frequently associate together.

5.23). M-#212 proved to be the most vocal of the mothers (at least in terms of her own signature contour) as measured by the absolute numbers of signature whistles recorded.

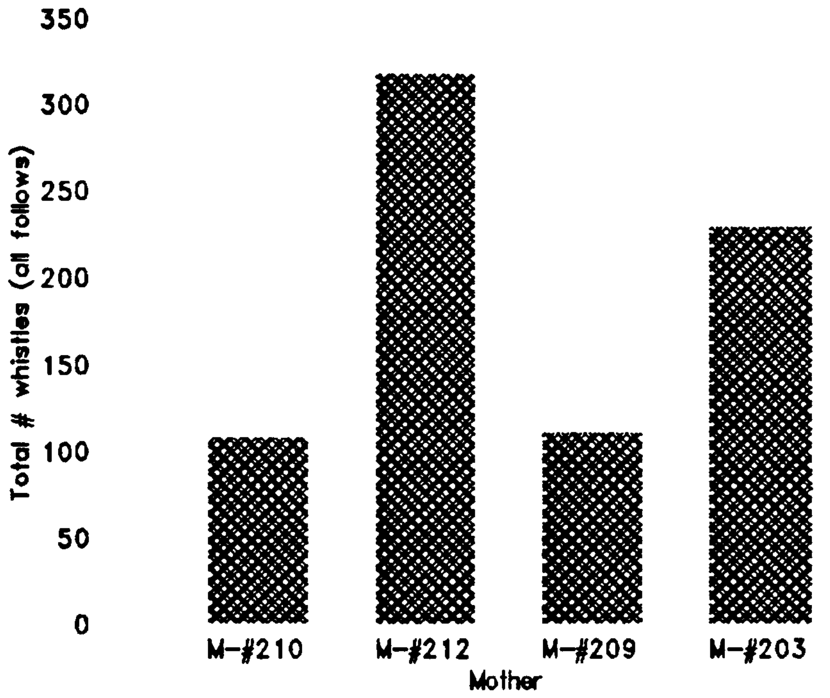


Figure 5.23. Total number of signature contours of each mother recorded in all follows.

5.3.2.2.2 Whistle development

The critical time period for whistle development in these four Sarasota calves was the first 1 to 4 months of life, although there was considerable individual variation. All calves produced unstereotyped whistles (see section 5.3.1.2 for criteria used in attributing these whistles to the calves) at least in their first 1-2 months, and may have continued to do so after developing a stereotyped signature whistle. All of the calves occasionally showed "localized stereotypy" in series of unstereotyped whistles. This is defined as similar contours occurring several times throughout the course of a follow. Since there are few generalities among the four calves beyond those just stated, I will describe the stages of whistle development for each of them separately.

Calf #212

Calf #212 appeared to be producing whistles resembling its crystallized signature whistle as early as one month of age, and was producing a relatively stereotyped whistle by about 2 months (Figure 5.24). Its whistle remained highly stereotyped from that point on, making this calf's whistles the easiest of the four calves to identify (Figure 5.24). Overall, at least 158 occurrences of its signature contour were counted over its first year of life (this includes occurrences of the contour during follows of other calves, when #212 was also present). By one year of age, the overall duration of the flat portion of its whistle was somewhat longer than it had been previously (Figure 5.24), although its whistle was still easily recognizable. The stereotypy of calf #212's whistle production was especially striking after it had been orphaned at about 15 months of age (discussed more in section 5.3.2.2.4).

Calf #203

All follows of calf #203 occurred during his first 5 months of life, after which he was killed by a shark. This calf provided an unusual opportunity for studying whistle development, because a large portion of his time was spent in association only with his mother (see section 5.3.2.1.4). However, this resulted in lower overall whistle rates, since whistle production is correlated with group size (section 5.3.2.1.4). A confounding factor in studying signature whistle development in calf #203 was that his core home range was an area heavily trafficked by boats and heavily populated by snapping shrimp, both of which create a substantial amount of broad-band noise. To compound this problem, his crystallized whistle was apparently a simple upsweep, which commonly occurs as a portion of signature whistles of many individuals, and is also a common type of variant whistle. Thus, signals that were degraded by noise were often difficult to distinguish as his signature contour.

Nonetheless, upsweeps were attributed to calf #203 at as early as 1-2 weeks of age up to the calf's death at 5 months (see Figure 5.25, calf at 1½ months). However, shortly before the calf's death, and after it had already acquired a serious shark-bite wound on its head, a multilooped whistle appeared five times, in addition to frequent upsweeps (Figure 5.25, calf at 5 months). Though I do not consider this a large enough sample to deem it the calf's signature contour, it is possible that the whistle development process was not yet complete at the time of this calf's death.

Figure 5.24. Whistles attributed to calf no. 212 at various stages in its first year of life. Note the similarities in contours produced at 2 months, 7 months and 1 year. Vertical stripes in these figures are echolocation clicks or noise from engines. Settings are as in Figure 5.1.

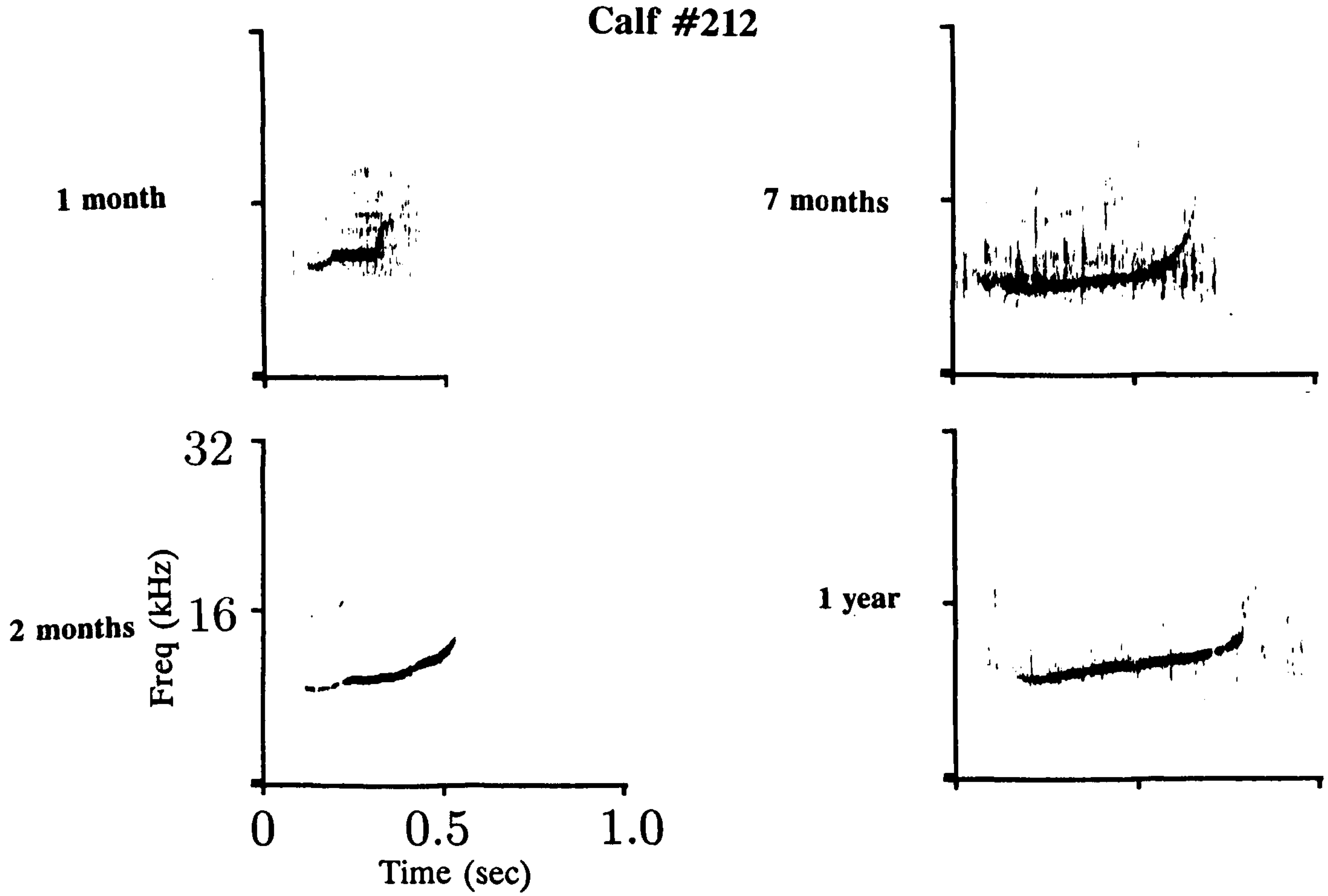
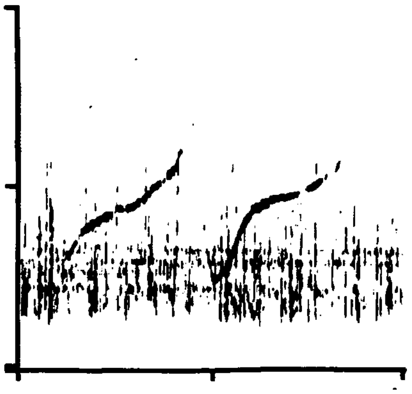
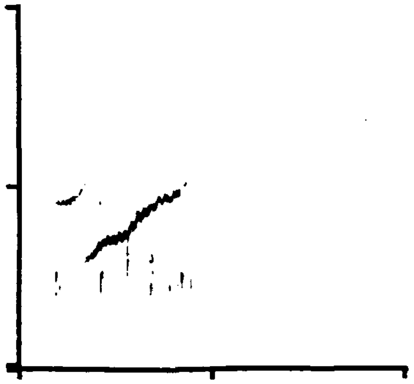

Calf #212
1 month
7 months
2 months
1 year
32
16
Freq (kHz)
0
0.5
1.0
Time (sec)

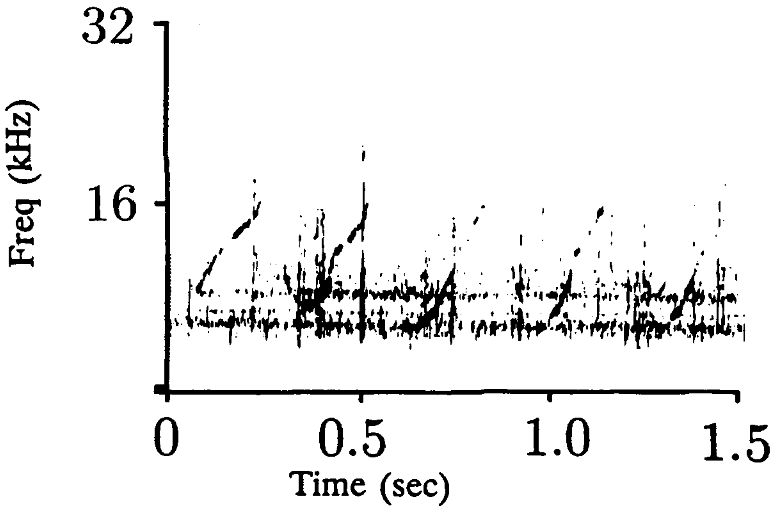
Figure 5.25. A whistle attributed to calf #203 at 1½ months, and a multilooped whistle that he may have produced shortly before his death at 5 months of age. Note the similarity between the calf's whistle at 1½ months and the initial loop of his mother's whistle (discussed in section 5.3.2.2.3). Note also the high levels of background noise due to snapping shrimp or boat engines. Settings are as in Figure 5.1.



Mother of calf #203



Calf #203 - 1½ months



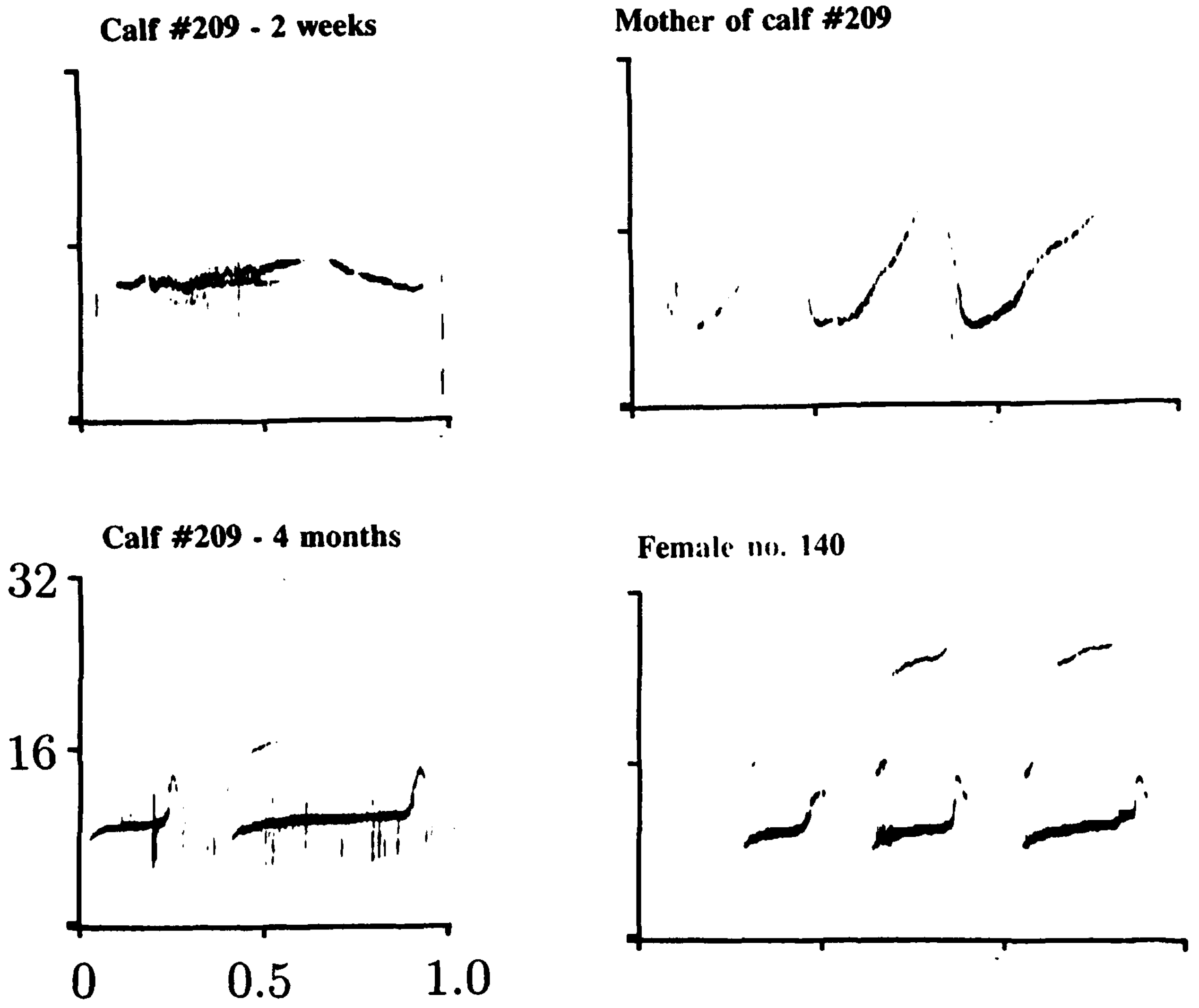
Calf #203 - 5 months?

Calf #209

The crystallization of calf #209's signature whistle occurred when it was between 2 and 3½ months old, during a hiatus in sampling. During its first 2 months of life, only unstereotyped whistles were recorded (Figure 5.26, calf at 1 month). No follows were conducted again until the calf was about 3½ months old, at which time it was producing its crystallized signature whistle (Figure 5.26, calf at 4 months).

A possible example of "teaching", or "modelling" of a distinctive whistle contour by the mother was found when the calf was approximately 2 weeks old. In the middle of a series of unstereotyped whistles characteristic of the calf (see section 5.3.1.2), a stereotyped contour appeared that was not the signature contour of either the mother or the other individual present, who was the older sister of the focal calf. This whistle interrupted one of the unstereotyped whistles produced by the calf (Figure 5.27), and somewhat resembled the eventual signature contour of the calf. An even more striking example of possible modelling by a mother was seen in follows of calf #210, as discussed below.

Figure 5.26 (facing page). An example of an unstereotyped whistle produced by calf #209 at about 2 weeks of age, and its crystallized signature contour at 4 months. Also shown are the mother's signature contour (note the lack of similarity), and the strikingly similar contour of female no. 140 (discussed in section 5.3.2.2.3). Vertical lines are the result of echolocation clicks or engine noise. Settings are as in Figure 5.1.


Calf #209 - 2 weeks
Mother of calf #209
Calf #209 - 4 months
Female no. 140
32
16
0
0.5
1.0

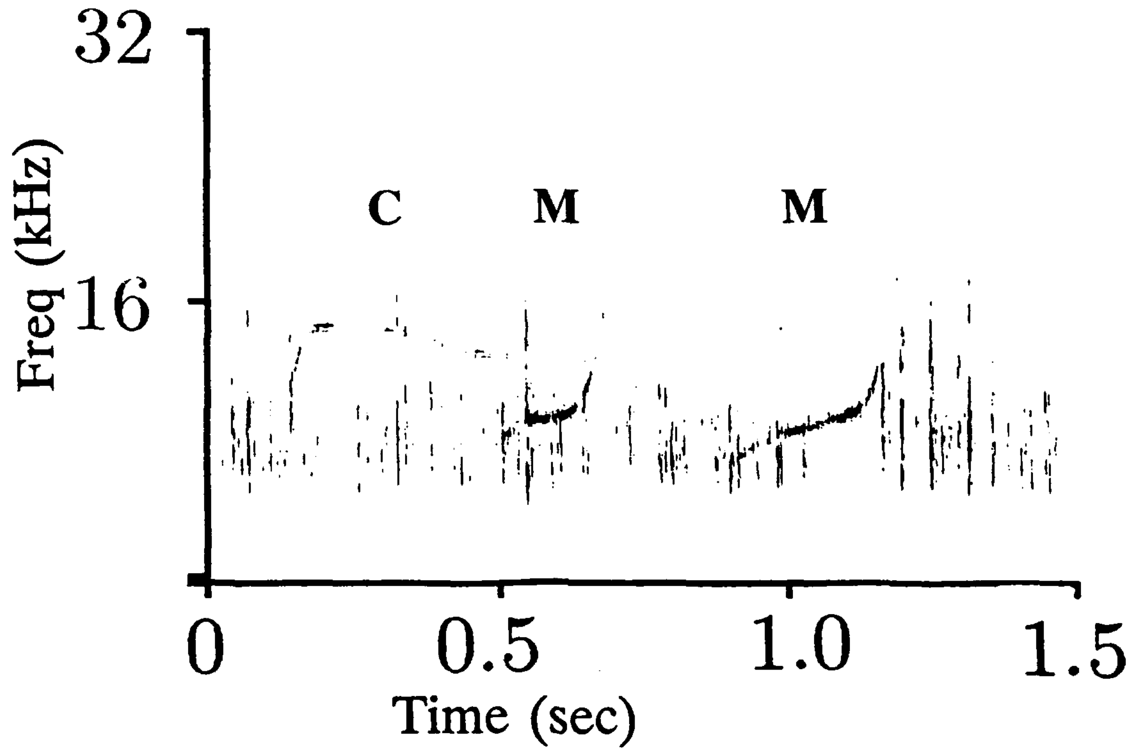


Figure 5.27. This figure shows an unstereotyped whistle attributed to calf #209 (labelled "C" - this was part of a series of unstereotyped whistles), and a stereotyped contour attributed to M-#209 (labelled "M"). This whistle does not resemble the signature contour of M-#209, but it somewhat resembles the contour eventually adopted by the calf (section 5.3.2.2.3). This is tentative evidence for teaching, or modelling of a distinctive contour by M-#209. Settings are as in Figure 5.1.

Calf #210

The whistle development process for calf #210 presents a marked contrast with the other three calves. Crystallization of her signature whistle occurred at some point between 13 and 24 months of age. I will describe details of several stages of her whistle development, since it was more prolonged and variable than for the other three calves.

1) During a follow when she was approximately 1 month old, a prolonged aggressive encounter was observed between calf #210 and her older female sibling. During this encounter, which involved multiple chases and aerial body slams, at least 212 whistles, all relatively unstereotyped, occurred that were likely to have been produced by calf #210 (see section 5.3.1.2 for criteria used in attributions). At least 25% of these whistles contained general features that resembled her eventual signature contour, which was a rough approximation of a sinusoidal pattern of frequency modulation. One example is shown in Figure 5.28 (1 month). However, even these whistles were extremely quavery and unstereotyped. Since animals in stressful situations like capture tend to produce whistles that are highly stereotyped (pers. obs., Sayigh et al. 1990), it seems unlikely that calf #210 had developed her signature whistle by this time.

2) Evidence for possible "teaching" or "modelling" of a distinctive whistle contour by calf #210's mother appeared in several follows, including the one described in detail above. A stereotyped whistle that resembled #210's eventual signature contour appeared at least 10 times during this follow, when the calf was 1 month old and had not yet developed a stereotyped contour. It seems likely that this may have been a model produced by the mother (Figure 5.29). An additional 12 whistles very similar in contour, but less well formed, also were recorded (Figure 5.29). Of the five other individuals present (including the mother), four had known signature contours from recordings made during capture-release projects. This "model" whistle did not match the known contours of any of these individuals. The fifth animal was a 10 month old calf whose signature whistle was not known, but analysis of follows of this calf (#205, Table 5.3) did not indicate that this whistle was its own signature contour. During the time when these potential models occurred, no signature whistles were produced by the mother. Later in the same follow, the mother's signature appears (Figure 5.29), but the hypothesized model does not occur. In addition, this "model" whistle did not occur during several follows of M-#210 that were conducted prior to the birth of calf #210. Many of the whistles produced by calf #210 during her first year (e.g., Figure 5.28, 3 months, 7 months, 1 year; 5.29, 1 year) resembled the contour of this "model" whistle. However, no one repeated, stereotyped contour could be confidently labelled as her signature contour. This was not a problem for the other three calves, for which a stereotyped contour was easily identified as the signature.

3) Calf #210 continued to produce unstereotyped whistles even as a yearling. In one yearling follow, during which she was frequently greater than 50 m away from her mother and her mother's two associates at the time, a total of at least 666 whistles were produced, of which 305 were variations of the sinusoidal type pattern typical of the calf (e.g., as in 5.29, calf at 1 year). One of the mother's associates, male #74, was known to produce a whistle with a similar contour (shown in Figure 5.1). In many cases, however, I recorded loud whistles of this type when the calf was as much as 50-100 m closer to the hydrophone than was male #74, indicating that perhaps she was imitating #74. In support of this conclusion, there were several instances of overlapping contours, similar to the signature contour of #74, which were undoubtedly examples of whistle mimicry (Figure 5.30). Overall, there was still no one consistent, stereotyped contour that could be ascribed to calf #210, only whistles roughly characterized by a sine-wave type structure.

4) I had the opportunity to record calf #210 with a suction-cup hydrophone during temporary capture when she was 2 years old (in June of 1992), and to then compare her crystallized whistle (Figure 5.32 in section 5.3.2.2.3) with others that were recorded during her first year of life. Although the whistle she produced as a two-year old had the general contour that I had expected from analyzing follow recordings, it contained features that were not seen in recordings of her even as a yearling (such as the terminal loop; see Chapter 2). Thus, crystallization of her signature contour must have taken place at some time between 13 and 24 months of age.

Figure 5.28. Whistles attributed to calf #210 during her first year of life. Note the variability in her whistles as compared to those of calf #212 (Figure 5.24). Settings are as in Figure 5.1.

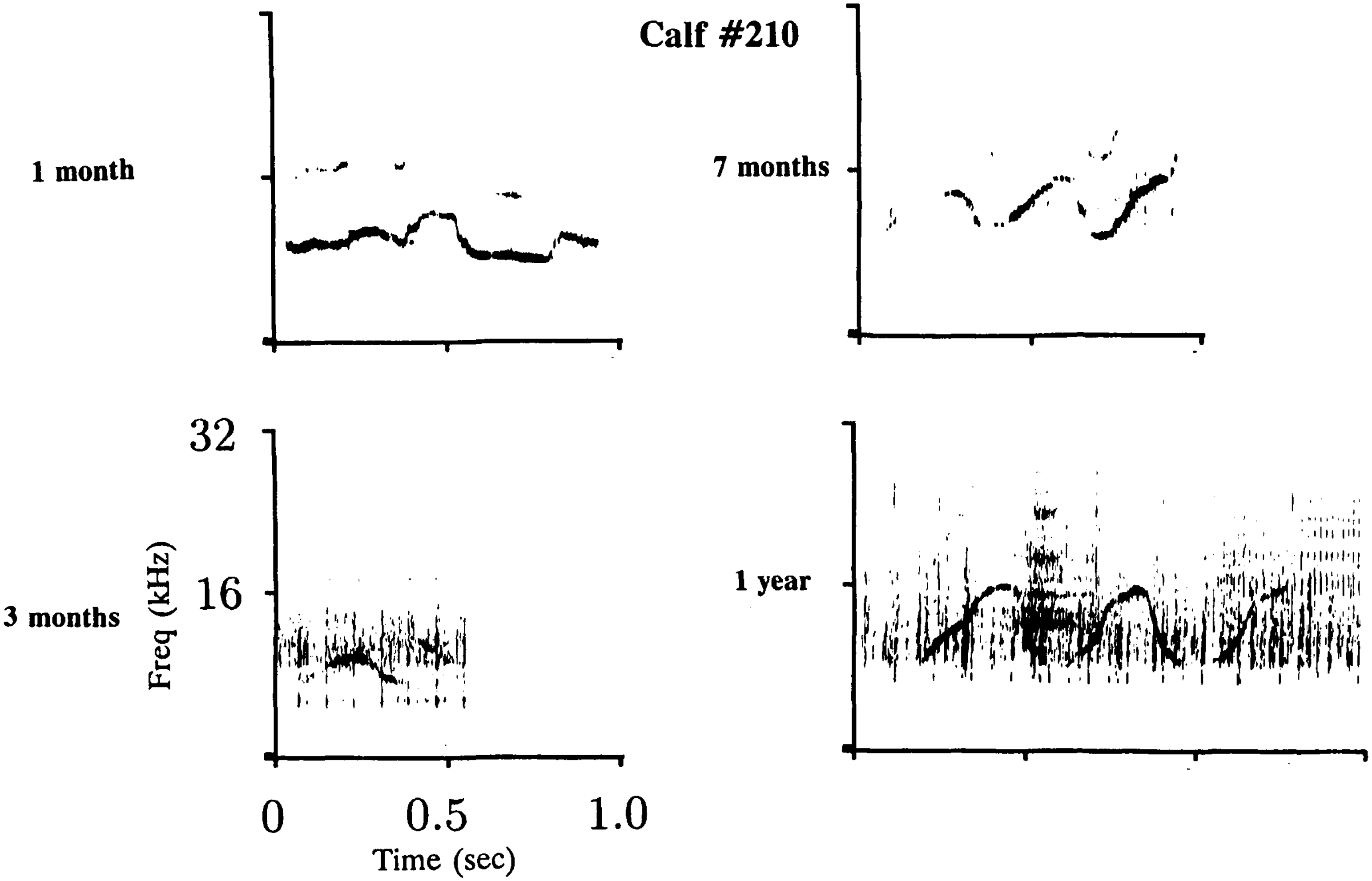
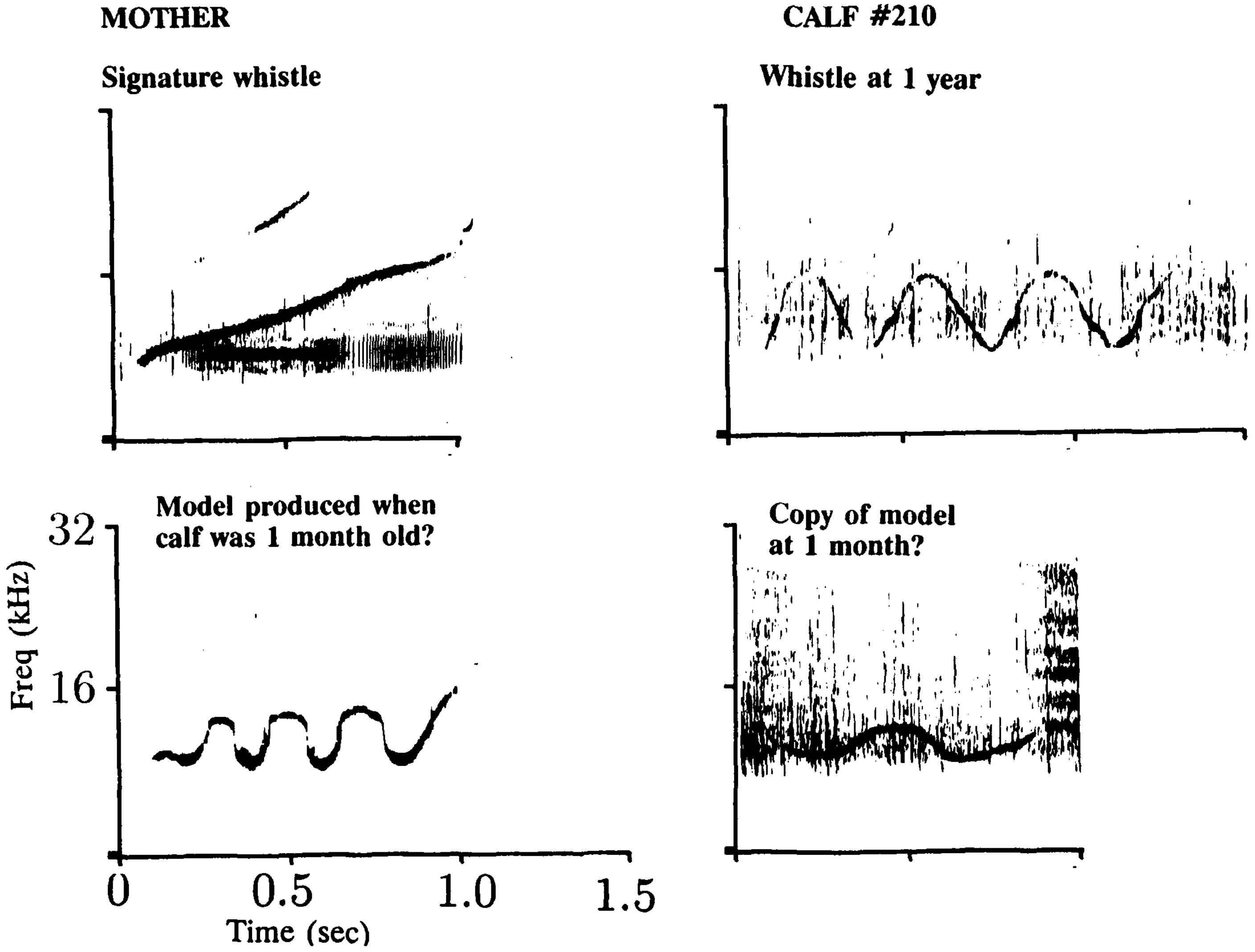

Calf #210
1 month
7 months
3 months
1 year
32
16
Freq (kHz)
0
0.5
1.0
Time (sec)

Figure 5.29. Comparisons of the signature whistle of M-#210, a whistle contour attributed to calf #210 as a yearling, and whistles suspected to be a model produced by M-#210 early in the calf's life, and a copy of that model by the calf. This is tentative evidence for "teaching", or "modelling" of a distinctive contour by M-#210. Settings are as in Figure 5.1.


MOTHER
Signature whistle
CALF #210
Whistle at 1 year
Model produced when
calf was 1 month old?
Copy of model
at 1 month?
32
16
Freq (kHz)
0
0.5
1.0
1.5
Time (sec)

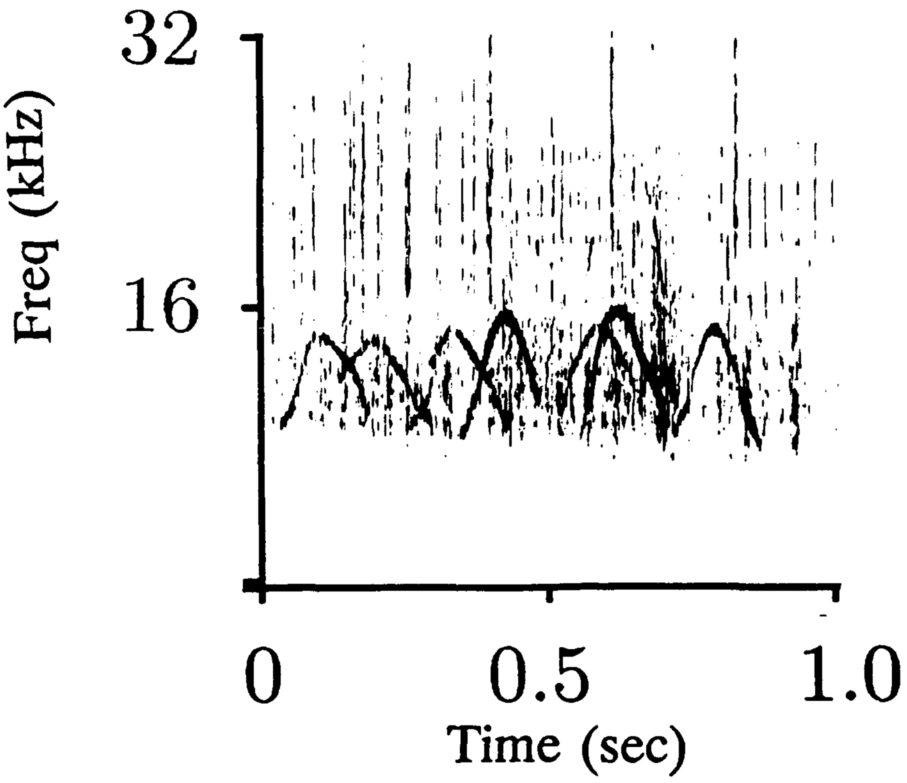


Figure 5.30. Overlapping similar whistle contours, representing probable whistle mimicry by calf #210 of male no. 74 (see Figure 5.1). These contours resemble the stereotyped contour of no. 74. Calf #210 produced many similar contours throughout the course of one yearling follow. Settings are as in Figure 5.1.

5.3.2.2.3 Similarity to the mother or other individuals

A qualitative judgement of similarity of the signature contours of the four calves to those of their mothers indicates that calves #203 and #212 produced contours resembling those of their mothers, and calves #209 and #210 produced whistle contours quite distinct from those of their mothers. I will describe each of these four comparisons in detail.

1) The simple upsweep that apparently characterized calf #203's signature whistle strongly resembled the first loop of his mother's signature contour (Figure 5.25). As previously noted, characterization of upsweeps is somewhat problematic, since they are commonly produced and are part of the signature contours of many individuals. However, calf #203 may have started to produce a multilooped whistle shortly before his death, which even more closely resembled his mother's contour (Figure 5.25).

2) Although at first glance the signature contour of calf #212 did not resemble that of its mother, the two whistles did share several features in common (Figure 5.31). Calf #212's contour was similar to a single, elongated loop of its mother's whistle. These types of perturbations in the duration of whistle segments are common sources of variation in repetitions of a single individual's contour (e.g., see Figure 4.1). The initial and terminal portions of #212's whistle more closely resembled those of its mother. However, as this calf got older, it appeared to have increased the overall

duration of its whistle, with the result that it less resembled the whistle of its mother (e.g., see Figure 5.24, 1 year).

3) The signature contour of calf #209 was quite distinct from that of its mother. The only feature shared in common was its repetitive, "looped" (Chapter 2) structure (Figure 5.26). However, a rather striking similarity was apparent between calf #209's contour and that of a subadult female (#140) in the community (Figure 5.26). This young female did not associate with calf #209 at all during the focal observations.

4) The signature contour of calf #210 shared no features in common with that of her mother, as was seen in Figure 5.29. Her mother's contour consisted of a long frequency upsweep, and #210's crystallized whistle was a repetitive, sine-wave type pattern of frequency modulation (Figure 5.32). As was the case with calf #209, there was a similarity between the whistle of calf #210 and a young female in the community (#175; Figure 5.32). This female was a persistent associate of calf #210. She was present in 5 follows, for a total of 11% of the total time that #210 was followed. However, only 9 possible occurrences (all were too faint to verify) of her whistle were documented during follows of calf #210.

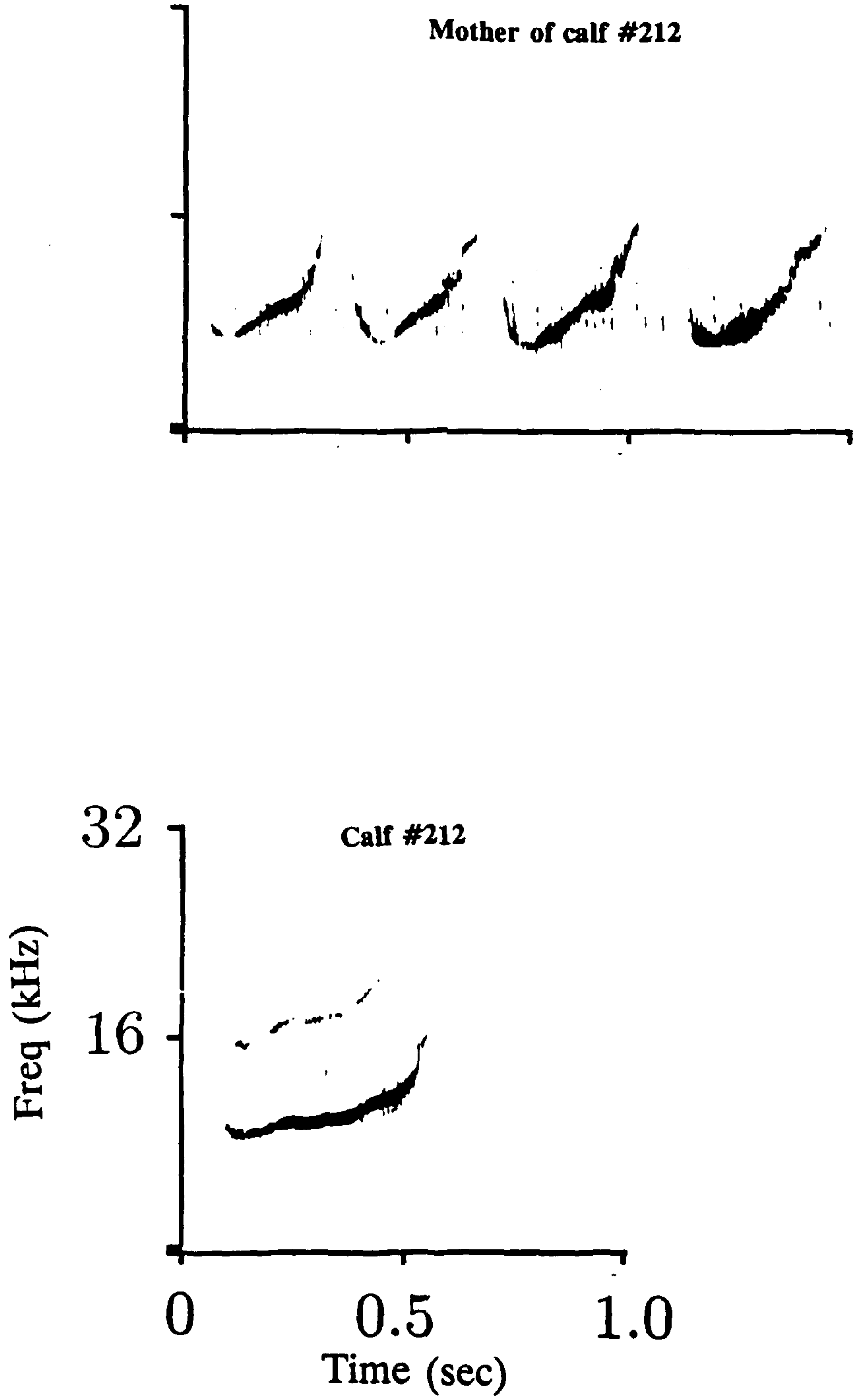


Figure 5.31. Signature contours of calf #212 and its mother. Note the similarity between the calf's contour and a single, elongated loop of its mother's whistle. Settings are as in Figure 5.1.

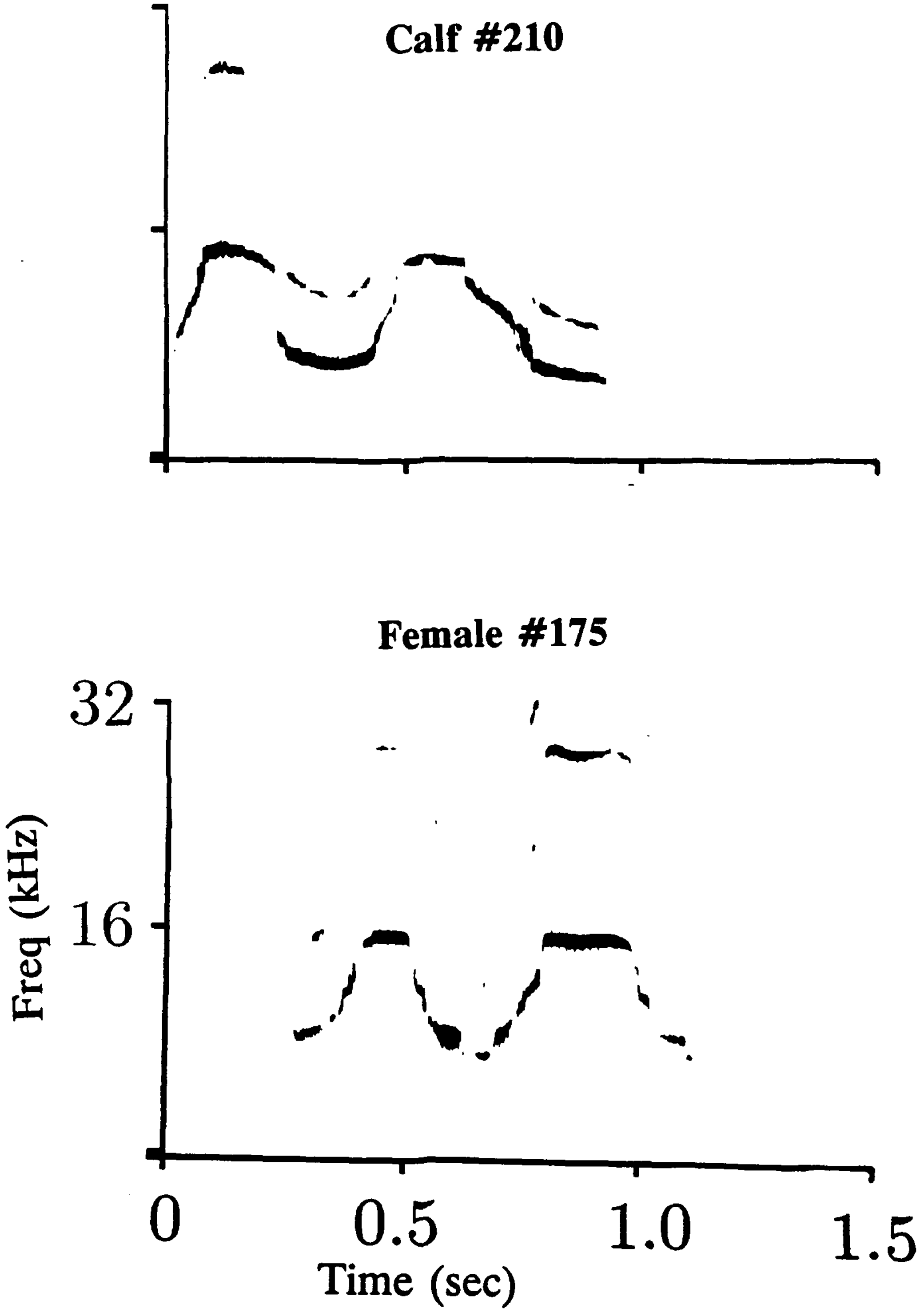


Figure 5.32. The crystallized signature contour of calf #210, recorded when she was 2 years old. Note the lack of similarity to her mother's contour (Figure 5.29). Also shown is the similar contour of female #175, a persistent associate of calf #210. Settings are as in Figure 5.1.

5.3.2.2.4 Contexts of whistle production

For the purposes of this chapter, only general contexts of whistle production that were obvious in analysis of the follows will be discussed. In the future, correlation of the continuous behavior record with the occurrence of whistles should provide a fine scale analysis of the behavioral contexts of whistle production.

One of the most persistent contexts of whistle production involved approaches, wherein the signature contour of an animal visibly approaching a focal group would be heard repeatedly. There were several instances in which an individual in a focal group exchanged whistles with a more distant animal, and then abruptly turned in the direction of the distant animals. In at least one case, the whistles of the distant animal were not heard in real time, and it was not until analysis of the tape that the situation was fully understood. This case involved a series of whistle exchanges between one of the focal mothers (M-#212) and her own mother.

Whistles were less commonly associated with individuals leaving. Examples of this include one instance when the signature contour of one individual was heard repeatedly shortly before that individual left the group. On another occasion, faint whistles were heard from a distant mother-calf pair, and immediately following these, the focal mother (M-#209) rapidly porpoised toward this other pair.

Overlapping contours that were similar in structure (e.g., Figure 5.30) were relatively common, suggesting whistle mimicry. I had no means to quantify the occurrence of non-overlapping whistle imitations, as this would require a means to positively identify which dolphin was vocalizing.

The most common context of whistle production during the mother-calf follows were mother-calf separations. Obviously, this represents the bias of my sampling, as mother-calf pairs were the focus of my observation and recording sessions. Whistle exchanges between at least four different mother-calf pairs in addition to the four focal pairs were clearly documented during the follows (e.g, Figure 5.33). In several instances (especially involving M-#212), there were multiple whistles from the mother, followed by a mother-calf joining. Other cases involved series of unstereotyped whistles (in young calves), which stopped after whistles from the mother occurred.

An especially striking example of signature whistles being used as contact calls comes from calf #212, who was orphaned at 15 months of age. During several recording sessions approximately three weeks after the death of its mother, localized periods of extremely high whistle rates (hundreds of stereotyped whistles, at rates of approximately 9 whistles/minute) were recorded. These may have represented attempts by the orphan to make contact with its mother.

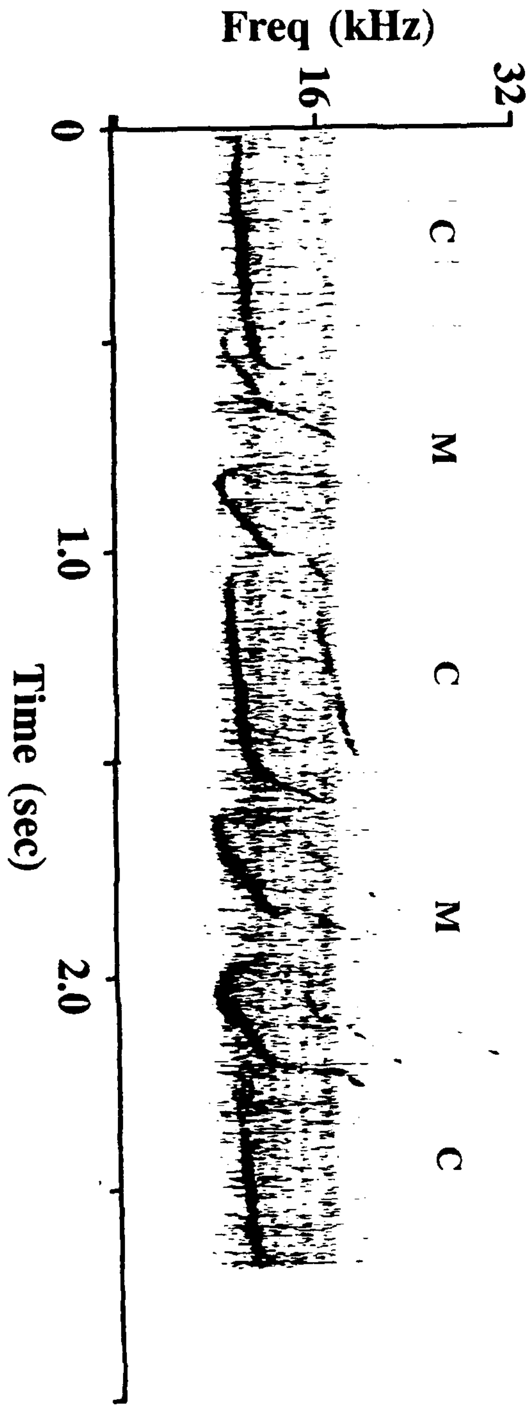


Figure 5.33. A whistle exchange between M-#212 and her calf, #212. Whistles are labelled "M" and "C", respectively. Settings are as in Figure 5.1.

All of the contexts of whistle production described seem to fit into the broad category of establishing or maintaining contact. An increased occurrence of whistles during feeding episodes by the mothers is likely to fit into this category as well, since these represent periods of increased mother-calf separation (e.g., section 5.3.2.1.1). Another activity that was associated with the occurrence of whistles (as well as a wide variety of burst-pulsed sounds) was socializing. However, since socializing animals are often in close proximity, it appears that in this context whistles may be serving a function different from a simple contact call.

5.3.3 DISCUSSION

Since data strongly suggest that signature whistle structure is learned (see section 5.2), differences among calves in whistle development are likely due to differences in their early social and/or auditory environments. These effects were explored by means of focal observations and acoustic recordings of free-ranging mother-calf pairs.

There is scant information available in the literature to which the results of this study can be compared. My data on mother-calf distance in four Sarasota calves are in broad agreement with the results of Janet Mann, Rachel Smolker, and Barbara Smuts from their work on free-ranging bottlenose dolphins in Shark Bay, Western Australia (Mann and Smuts 1991, Smolker et al. submitted). Their data, which were collected from older calves (ranging from 4 months to 4 years of age), showed a great deal of individual variability in each calf's association with its mother, as measured by mother-calf distance. Such variability was beginning to become apparent in mother-calf distance data from the late and yearling stages in Sarasota. Even the middle stage showed some variability, since one calf spent a significant amount of time with its older sibling. The early period was characterized by high degrees of mother-calf proximity in all four calves; this period was not examined in Shark Bay.

Data from Sarasota and Shark Bay (Mann and Smuts 1991) show that mother-calf separations generally become more frequent as calves get older. Data from a wide variety of mammals (e.g., chimpanzees: Rijt-Plooij and Plooij 1987; bison: Green 1992; right whales: Taber and Thomas 1982) show the same general pattern of increased mother-offspring distance with age. This is an obvious indicator of increasing offspring independence.

A consistent association between the occurrence of mother-calf separations of 1 meter or more and activities other than travel was noted for all four calves. Since animals engaged in these activities tend to remain in one general location, it is not surprising that separations would be more likely to occur. Close proximity during travel is likely to prevent mothers and calves from losing track of one another. Beyond broad measures such as this, however, individual variability among the calves was more prevalent than were consistent trends. For example, occurrences of asynchronous mother-calf surfacings, as well as occurrences of individuals other than the mother as a calf's nearest neighbor, varied considerably among the four calves at different ages.

Data on association patterns of Shark Bay mother-calf pairs do not appear to be similar to data from Sarasota, since Smolker et al. (submitted) noted that the mother-calf pairs in their samples were often alone. This finding differs markedly from the present study, in which three of the four focal calves spent only 7-26% of their time alone with their mothers. The fourth calf spent an average of 63% of his time alone with his mother. One focal calf (#212) had a minimum of 43 different associates in a sample of 13 follows over the calf's first year of life. The number of persistent associates (defined as those individuals present in more than two follows) ranged from between 3 and 15 individuals for each of the four pairs.

Individual variability in the four focal calves was also seen in their signature whistle development. Calves #212 and #203 produced stereotyped whistles by 1-2 months of age, although there was a possibility that #203 began to produce a multilooped whistle at about 5 months, shortly before his death.[9] Calf #209 developed a stereotyped whistle between 2 and 3½ months of age, and calf #210 did not develop a fully stereotyped whistle until between 13 and 24 months of age, although some stereotypy was evident as early as 2-3 months.

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[9] The possible development of a multilooped whistle by calf #203 at 5 months of age is in accordance with the findings of Caldwell and Caldwell (1979), who reported that most calves first developed single-looped whistles, and gradually began producing loop repetitions as they got older.

The whistles of calves #203 and #212 resembled those of their mothers. These two calves also exhibited the most rapid whistle development. Calves #209 and #210 both exhibited more prolonged whistle development, and they both produced whistles very different from those of their mothers. There was preliminary evidence for two possible sources (which were not mutually exclusive) of the contours eventually adopted by these two calves: "teaching", or "modelling" of a distinctive whistle contour by the mother during the calf's first few months of life; and learning from another individual present in the community. With respect to the first of these, the mothers of both calves #209 and #210 apparently produced "model" whistle contours quite different from their own, which resembled the eventual contours adopted by their calves. Second, both of these calves also produced whistles which showed strong similarities to whistles of young females present in the community (#140 and #175). These could be simply chance similarities, due to there being a finite number of possible signature contours. Alternatively, these calves may have learned their signature whistles from these young females. Female #140 was never seen in association with calf #209 during focal observations, but the fewest number of hours (20) were spent following this calf. Thus, this discrepancy could be due to insufficient sampling. Female #175 was a persistent associate of calf #210, although no positive occurrences of her whistle were documented during follows of calf #210.

Even if these two calves did learn their signature whistles from these young females, it is very unlikely that they were simply copying the most common sound in their respective acoustic environments, as may have been the case for calves #203 and #212. It seems likely that whistle production may have been in some way reinforced by the mother, perhaps by production of models, or other more subtle means. Studies of zebra finches raised in captivity indicated that individuals were likely to copy the song of an adult with which it had interacted aggressively during the period of song development (Slater et al. 1988, Clayton 1987). Another study showed a preference to learn from high-ranking individuals (Payne 1983). These intriguing results raise the possibility that additional behavioral interactions could play a role in the whistle development process. The scope of the observations conducted to date was not extensive enough to define the factors contributing to the ultimate choice of whistle contour by these calves.

However, some consistent differences among the four calves do suggest some of the factors that may affect the time course and ultimate outcome of whistle development. In many of the measures looked at, calves #210 and #203 showed the greatest differences; these two calves were also strikingly different in their whistle development. Calf #203 showed fairly stereotyped whistle production at an early age, and adopted a whistle contour similar to that of his mother. He associated more closely with his mother than did the other three calves, as measured by his low percentage of asynchronous surfacings and his overall low level of associations with other individuals. Calf #210 showed extremely variable whistle production during her first year of life and eventually adopted a signature contour highly distinct from that of her mother. In addition, when viewed with respect to the time course of her whistle development, calf #210 showed differences from the other calves in her association with her mother. For example, all calves sampled after the middle period showed a general increase in independence from the mother as they got older, as evidenced by increased percentages of separations of 1 meter or more, increased percentages of asynchronous surfacings, and increased occurrences of nearest neighbors other than the mother. For calves #209 and #212, this increased independence took place after the signature whistle had fully crystallized. For calf #210, increased independence took place before whistle crystallization. Thus, perhaps the greater variability in calf #210's whistle development can be attributed to her exposure to a greater variety of interactions during this period. This does not explain, however, why calf #210 did not develop a crystallized whistle in the early or middle periods, as had the other calves.

A possible factor affecting the delayed crystallization of calf #210's signature whistle may have been the more diverse acoustic environment to which this calf was exposed. Calf #210 experienced the highest average whistle rates, expressed as average whistles per minute, and the lowest absolute number and percentage of her mother's signature whistle (6%). Therefore, compared to the other calves she heard more whistles, and her mother's whistle contour was not as dominant an element in her acoustic environment. Conversely, calf #203 experienced the lowest average whistle rates, and the highest percentage of his mother's signature whistle (20%). M-#212 was similar to M-#203 in the percentage of total whistles comprised by her signature contour (18%), and she also produced the greatest absolute number of signature whistles (but this measure biased against M-#203, as discussed in section 5.3.2.2.1). It is perhaps noteworthy that the two calves which heard the greatest numbers and percentages of their mothers' signature contour also developed signature whistles somewhat resembling those of their mothers, and exhibited relatively rapid whistle development. The calf which experienced the most diverse acoustic environment and the lowest percentage of her mother's signature contour developed a whistle highly distinct from her mother, and exhibited prolonged and variable whistle development. The acoustic environment of calf #209 fell somewhere in the middle; it was second to calf #210 in overall whistle rates (0.79 whistles/min), and showed the second lowest proportion of signature contours of the mother (14%). Calf #209's whistle development was intermediate in time course and the crystallized contour was distinct from that of the mother.

Whistle development in the four Sarasota calves can be compared with what is known from captive dolphins. Tyack et al. (submitted) found that three captive calves held in the same community tank at the Miami Seaquarium all underwent relatively rapid whistle development, occurring in the first few days to 1-2 months of life. All three calves were exposed to a similar acoustic environment, in that they were born within a few months of each other and were all housed with the same individuals. Whistle rates were extremely high, averaging 7.4 whistles per minute (Tyack et al. submitted). All apparently incorporated sounds present in their acoustic environment in developing their own signature whistle. The oldest calf produced a whistle markedly similar to the trainer's "bridge" whistle, used in reinforcing trained behaviors. The second calf developed a whistle quite similar to that of the oldest calf. The third calf produced a whistle similar to that of two highly vocal subadults present in the tank. Association patterns of these calves were not observed during the whistle development process, so it is not known what factors shaped the final outcome for each calf.

The study of Caldwell and Caldwell (1979) of 14 captive calves housed in different acoustic environments provided some intriguing parallels with the present study. Although eight of the calves in this study were not recorded until they were at least 9 months of age, at which time they were all producing stereotyped signature whistles, six of the calves were recorded within their first few months of life. Of these six, all were found to produce quavery, unstereotyped whistles in the first 1-2 months. Two calves developed a stereotyped whistle by the time they were about 1½-2 months of age. A third calf produced relatively stereotyped whistles at 2½ months of age. Two calves did not produce stereotyped whistles at 1½ months, and then were not recorded again until 4 and 7½ months respectively, at which time each was producing a stereotyped whistle. Thus, the precise time of whistle crystallization for these calves was not known. The sixth calf was recorded for 17¼ months, and was never found to produce a highly stereotyped whistle, although there was some similarity among his whistles.

One of the two calves that developed a stereotyped whistle by 1½-2 months of age was housed exclusively with his mother, except for a brief exposure to a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*). Surprisingly, this white-sided dolphin produced a whistle similar to that of the calf's mother, so the calf was exposed to only one general whistle contour. Caldwell and Caldwell speculate (1979; pp. 385-6):

> The fact that the infant heard the mother's whistle almost exclusively may possibly have influenced the rapid development of the whistle. ...[T]here was a close similarity of the infant's whistle to that of the mother...[which] may be the result of learning or genetics or may only be a coincidence.

The situation described by Caldwell and Caldwell (1979) bears a strong resemblance to that observed for Sarasota calf #203. Through low interaction rates with other individuals, he was exposed to relatively fewer whistles than were the other calves, and to proportionately more whistles of his mother. He also exhibited rapid whistle development.

A further parallel in the Caldwell's study is seen between their infant #1 and calf #210. Infant #1 was still not producing a stereotyped whistle at 17¼ months of age, "[a]lthough considerable similarity [did] exist between many of the whistles after three months" (Caldwell and Caldwell 1979, p. 376). They continue:

> It is not known whether the presence of the two eastern Pacific white-sided dolphins in the tank contributed to this absence of development of stereotypy. There is some slight degree of similarity between the whistles of this infant and those of the more vocal white-sided dolphin of the two. This latter animal also had a more variable whistle than most dolphins (M.C. Caldwell and D. K. Caldwell 1971, animal number 1, Figs. 2-12). The possibility that these whistles may have affected the whistle development of the infant bottlenosed dolphin cannot be eliminated.

Calf #210 also experienced a relatively diverse acoustic environment, and had not yet developed a stereotyped whistle by 12 months of age.

However, the situation is not entirely clear-cut. The only other infant for which Caldwell and Caldwell (1979) describe any features of the acoustic environment was their infant #2, which was housed in the same community tank as infant #1 (discussed above). Although the whistles of infant #2 were not classified as stereotyped during recording sessions up to 5½ months of age, "there was considerable similarity between most of his whistles after 2½ months" (Caldwell and Caldwell 1979, p. 381). Thus, exposure to similar rearing conditions can still result in very different outcomes. Another apparent exception is Sarasota calf #212, which exhibited rapid whistle development similar to that of calf #203, and produced a whistle somewhat resembling that of its mother, but which associated with many more individuals than did calf #203. However, like calf #203, calf #212 did show a low level of asynchronous mother-calf surfacings in the early period, which was when whistle crystallization occurred. Also, M-#212 was the most vocal of the mothers, so her whistle still comprised a large proportion of calf #212's acoustic environment.

A tentative conclusion from the results of this study as well as from the data presented in Chapter 4 (documenting a greater tendency for male calves to produce signature whistles similar to those of their mothers, and for female calves to produce whistles highly distinct from those of their mothers), is that males are more likely than females to copy whistle contours that are common in their acoustic environment. In most, if not all cases, the mother's whistle would be one of the most common whistles that a calf hears, as was certainly the case for the one known male calf in this sample. Perhaps mothers of some male calves facilitate this process by producing many signature whistles (such as M-#212, although the sex of calf #212 is still unknown), or by isolating their calves from other individuals (such as M-#203).

The situation for females appears more complicated. Since females have a strong tendency to produce whistle contours that are highly distinct from those of their mothers (Chapter 4), it seems unlikely that the choice of contour is a random process. This study provides limited evidence for "teaching" or "modelling" of a distinctive whistle contour by two mothers; one of the calves was a known female. Another (not mutually exclusive) possibility is that female calves copy a whistle that is less common in their acoustic environment, and perhaps this choice is in some way facilitated by the mother. This idea could also be supported by the observation that these same two calves (only one known to be female) produced whistles similar to those of individuals present in the Sarasota community.

Finally, the finding that signature whistles function broadly to establish or maintain contact among individuals is in accordance with other reports in the literature. McBride and Kritzler (1951) noted that captive mothers and calves that were separate from one another frequently whistled until reunited. Sayigh et al. (1990) reported that temporarily captured mother-calf pairs in Sarasota often exchanged whistles back and forth. Smolker et al. (submitted) report that free-ranging calves in Shark Bay, Western Australia appear to use signature whistles to announce an interest in or an intention to reunite with their mothers during separations, although they do not use them to maintain continuous contact.

This study of whistle development in free-ranging calves has raised more questions than it has answered. Since there is so much individual variability, future research should aim to study a greater number of individuals, and to obtain larger samples from each individual. It was difficult to reach firm conclusions about whistle development in the wild because of difficulties in identifying the vocalizing individuals. Thus, work should be attempted in areas with good water clarity, so techniques for identifying which individual is making a sound may be utilized. For example, it could be possible to observe animals releasing bubbles from the blowhole while whistling. In addition, a technique is currently being developed at the Woods Hole Oceanographic Institution to localize which individual is producing a sound, using passive acoustic localization (Freitag and Tyack, in prep.). This technique requires clear water, such that the vocalizing animal can be identified on a video image.

However, although water clarity is generally poor in the Sarasota study area, there exists a much richer potential for fully understanding signature whistle development, because the ages, sexes and matrilineal relationships of most of the individuals are known (Chapter 2). It has taken 22 years to build up the body of knowledge presently available for the Sarasota dolphin community (e.g., Hohn et al. 1989, Irvine and Wells 1972, Irvine et al. 1981, Wells et al. 1987, Scott et al. 1990, Wells 1991), so studies at other sites would be more limited in their potential to assess the strength and subtleties of associations among individuals. In addition, the temporary capture and release program provides opportunities to sex individuals (once they reach two years of age), and to record signature whistles from known individuals with suction-cup hydrophones (Chapter 2). This ability too greatly enhances the possibilities for understanding signature whistle development. Perhaps a device that identifies which individual in a captive group is making a sound, such as the datalogger (Tyack and Recchia 1991), could be modified into a semi-permanent, recoverable device to get around the problem of poor visibility in Sarasota.

Ideally, studies should be conducted at several different field sites, to allow comparisons among communities subject to different social and ecological conditions. This would lead to a broader understanding of the factors affecting signature whistle development in free-ranging bottlenose dolphins.

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CHAPTER 6: SUMMARY AND CONCLUSIONS

6.1 Thesis summary

The goal of this thesis was to address basic questions regarding the development and functions of signature whistles in free-ranging bottlenose dolphins (*Tursiops truncatus*). These individually distinctive vocalizations were first documented by Caldwell and Caldwell in 1965, when they recorded isolated captive dolphins. Research on signature whistles has since been done with dolphins in captivity (e.g., Caldwell and Caldwell 1979, Caldwell et al. 1970, 1971, 1972, Tyack 1986, Tyack et al. submitted), but, beyond studies describing general contexts of whistle production (e.g., Tyack 1976, Smolker et al. submitted), very little work has been done on communication in free-ranging dolphins. This is due to several factors. First, it is very difficult to identify which dolphin in a group is making a sound, since there is generally no external movement associated with vocalization. Techniques have been designed to overcome this problem in captivity (Tyack 1985, Tyack and Recchia 1991), but there are currently no techniques available for use in the wild (although they are being developed; e.g. Freitag and Tyack (in prep.)). Second, even though systematic behavioral sampling techniques are beginning to come into use in studies of free-ranging dolphins (e.g., Mann and Smuts 1991, Chapter 5 of this thesis), the level of observable detail is frequently considerably less than for most terrestrial animals, since dolphins spend the majority of their time underwater. This is an added constraint to learning about behavior and communication in these animals. Finally, and perhaps most importantly, in order for recordings of free-ranging dolphins to provide anything more than very general information about the contexts of vocal production, the identities and relationships of the animals being recorded must be known.

An ongoing, long-term research program studying a resident community of free-ranging *Tursiops* in waters near Sarasota, Florida (described in Chapters 1 and 2) has overcome one of these hurdles by providing the kind of detailed background information necessary for meaningful study of dolphin communication. Since 1970, Blair Irvine, Michael Scott, Randall Wells and numerous collaborators (e.g., Irvine et al. 1981, Scott et al. 1990, Wells et al. 1987) have amassed a large amount of background data on the members of the Sarasota dolphin community. These data include information on age, sex, and genetic relationships of individuals, life history, movement patterns, behavior, association patterns and social structure. Some of these data were collected during a temporary capture-release program, during which individuals could be handled for sampling.

These temporary capture situations provided a unique opportunity to record whistles from known, free-ranging bottlenose dolphins. Recordings were made with suction cup hydrophones placed directly on the head of each individual. These recordings were integral to every aspect of the research described in this thesis, and they have also contributed to a large database of sounds (Watkins et al. 1991) that have been used in the development of automated techniques for whistle detection, contour extraction, and quantitative contour comparisons (Buck and Tyack submitted).

Background information on the Sarasota dolphin community and signature whistles were presented in Chapters 1 and 2. The remaining chapters were divided into three main topics: 1) the use of signature whistles in individual recognition (Chapter 3); 2) sex differences in signature and variant whistle production (Chapter 4); and 3) factors affecting signature whistle development (Chapter 5). The main results of each of these chapters are summarized below.

6.1.1 Individual recognition

Playback experiments conducted during the Sarasota capture-release projects demonstrated that dolphins are capable of discriminating among signature whistles of familiar individuals (Chapter 3). A paired playback design was used, wherein the same two whistle sequences were predicted to evoke opposite responses from two different target animals. This design controlled for any unknown cues that may have been present in the playback stimuli. Target animals included mothers with independent offspring present in the community, offspring that had separated from their mothers, and females from different female bands. Paired stimuli that were used in each of these experiments were independent offspring, mothers, and females from different bands, respectively. Thus, a target mother was exposed to whistles of her own independent offspring and whistles of a familiar, similar-aged non-offspring, with the prediction that she would respond more strongly to her own offspring. The same two stimuli would then be played back to the mother of the non-offspring in the previous playback, with the prediction that she would respond in the opposite direction (more strongly to her own offspring).

Target animals were significantly ($p = 0.0002$) more likely to respond to the predicted stimuli, with responses measured by the number of head turns toward the playback speaker. These results were discussed in the context of what is known about individual recognition in other animal species. Although these experiments only demonstrate that bottlenose dolphins are able to discriminate among different familiar whistles, it seems highly likely that they are able to associate a particular whistle with a particular individual. In bottlenose dolphins societies, stable, individual-specific relationships are intermixed with fluid patterns of association among individuals (Shane et al. 1986). In primate species that live in similar "fission-fusion" type societies, individual recognition is commonplace. Individual associations are based on knowledge of the relationships among individuals and memories of the histories of interactions (e.g., Dasser 1985, Essock-Vitale and Seyfarth 1986, de Waal 1982). Thus, when taken in the context of what is known about the social structure and behavior of bottlenose dolphins, the playback experiments strongly suggest that individual recognition occurs.

6.1.2 Sex differences in vocal production

Analyses of recordings of mother-calf pairs made during the Sarasota capture-release projects revealed a sex difference in the tendency of calves to produce signature whistles similar to or different from those of their mothers. Naive judges rated the similarity of whistle contours of 42 mothers and calves on a scale of 1 (not similar) to 5 (very similar). Effective reliabilities of these mean similarity scores were high (ranging from 0.94 to 0.96). Mean scores were divided into three equal categories: not similar (1 - 2.33), somewhat similar (2.34 - 3.66), and very similar (3.67 - 5.00). A significant ($p < 0.001$) difference was found in comparison of the numbers of male and female calves in the not similar and very similar categories. Males were more likely than females to produce signature whistle contours very similar to those of their mothers and females were more likely than males to produce signature whistle contours highly distinct from those of their mothers.

Data from a sample of four male and eight female calves (Chapter 4, Sayigh et al. 1990) also indicated that males may be more likely than females to produce whistles other than the signature (called "variant" whistles). However, these data must be viewed as preliminary, because of the small sample size and because serial dependence of whistle types prevented statistical analysis of whistle counts.

These sex differences in whistle production may be related to different roles that males and females play in the social structure of the community. Signature whistles are known to function in establishing and/or maintaining contact between mothers and calves (McBride and Kritzler 1951, Sayigh et al. 1990, Smolker et al. submitted, Chapter 5), and matrilineally related females tend to associate together in Sarasota. Thus, in order for a calf to be able to maintain contact with its mother, it may be particularly important for matrilineally related females to produce whistles that are distinctive from one another. Similarly, production of variant whistles by females could interfere with the maintenance of mother-calf contact. Males, which tend to disperse into the community, do not face similar constraints on their whistle production. The similarities of whistles of some males and their mothers may function to maintain contact with kin, avoid inbreeding, or advertise dominance relationships. Only further research will be able to establish the appropriateness of these possible explanations for the sex differences seen in Sarasota (see section 6.2).

6.1.3 Signature whistle development

Comparisons of signature whistles of parents and offspring, both from the wild (Sarasota) and from captivity (Miami Seaquarium) do not indicate that whistle structure (i.e., the distinctive pattern of frequency changes over time) is strictly inherited. Instead, a variety of evidence indicates that signature whistle structure is most likely learned (Caldwell and Caldwell 1979, Tyack et al., submitted, Chapter 5). Although learning to match vocal production to auditory input is commonplace among songbirds (e.g., Kroodsma 1982) and of course humans, it is rare among terrestrial mammals. Thus, dolphins provide a rare opportunity to study the role of learning in vocal development in a non-human mammal.

Focal observations and recordings of four undisturbed mother-calf pairs over the calves' first year of life focused on differences in the early social and auditory environments that might affect the time course and eventual outcome of whistle development. Although there was considerable individual variability among the four calves, there were some apparent correlations between the association patterns of these calves, the acoustic environments to which they were exposed, and their whistle development. For example, one male calf that exhibited rapid whistle development (within 1-2 months) and produced a whistle contour resembling that of his mother had a very strong association with his mother, and few associations with other individuals. Of the four calves, he was exposed to the lowest overall whistle rates, and to the greatest percentage of his mother's whistle. At the other extreme, one female calf that exhibited prolonged (13 - 24 months) and variable whistle development and produced a whistle contour highly distinct from that of her mother showed relatively greater independence from her mother, and had many associations with other individuals. Of the four calves, she was exposed to the greatest overall whistle rates, and to the lowest percentage of her mother's whistle. The other two calves fell in between these two extremes.

Thus, although this study was based on a sample of only four calves, it demonstrated that there is potential for understanding the effects of the early social and auditory environment on whistle development in free-ranging calves. Suggestions for further research in this area are given in section 6.2.

6.1.4 Conclusions

Overall, this thesis attempted to address fundamental questions regarding the development and functions of signature whistles in free-ranging bottlenose dolphins. Results suggest that signature whistles are likely to be used for individual recognition. Factors affecting signature whistle development may include the association patterns of a calf with its mother or with other individuals, and the overall acoustic environment to which it is exposed. These data add to the growing body of evidence (Caldwell and Caldwell 1979, Tyack et al. submitted) that dolphin signature whistles are learned, unlike the vocalizations of all other non-human mammals studied to date.

Comparisons between bottlenose dolphins and some non-human primate species reveal similarities with respect to the "fission-fusion" nature of their societies, in which long-term, individually-specific associations are intermixed with fluid patterns of association among many individuals. Thus, it is likely that this species possesses a communication system similar to those of many non-human primates. Non-human primates use vocal signals to communicate many things, including individual identity and kinship, as well as "semantic" information such as the type of aggressive encounter in which an individual is engaged (Gouzoules et al. 1984) or alarm calls specific to each type of predator that is frequently encountered (Seyfarth et al. 1980). Primates rely on visual cues to convey additional information; this modality is frequently unavailable to dolphins living in murky water. Vocal signals are likely to be the primary means by which dolphins convey information to one another. Thus, it is almost impossible to imagine that there is not a great deal of work still left to be done in order to unravel the subtleties of how these animals communicate with one another. A large class of dolphin sounds, so called "burst pulsed" sounds, remain virtually unstudied. In addition, there is evidence that dolphins may systematically vary features of whistles to convey information in addition to individual identity (Caldwell et al. 1970, Tyack 1991). Researchers are beginning to amass knowledge about dolphin social behavior (e.g., Connor et al. 1992, Östman 1991, Samuels et al. 1991); as this work progresses, it will provide the needed context for a more complete understanding of the natural communication system of bottlenose dolphins.

In addition to these questions, many more have been raised by the research in this thesis. Some of these are outlined in more detail in the following section.

Publications that have been generated while working on this thesis, as well as those that are in preparation, are listed below. These formed the basis for Chapters 3-5 and Appendix II.

Sayigh, L. S., P. L. Tyack, R. S. Wells, and M. D. Scott 1990. Signature whistles of free-ranging bottlenose dolphins, *Tursiops truncatus*: stability and mother-offspring comparisons. Behav. Ecol. Sociobiol. 26: 247-260

Sayigh, L. S. and P. L. Tyack 1990. Do young dolphins learn to imitate sound from their mothers? Ann. Rep. (1989) of the Woods Hole Oceanographic Institution, Woods Hole, MA 02543

Sayigh, L. S., P. L. Tyack, and R. S. Wells. In press. Recording underwater sounds of free-ranging bottlenose dolphins while underway in a small boat. Mar. Mamm. Sci.

Sayigh, L.S., P. L. Tyack, and R. S. Wells. (In preparation). Sex difference in whistle production in free-ranging bottlenose dolphins, *Tursiops truncatus*

Sayigh, L. S., P. L. Tyack, and R. S. Wells. (In preparation). Possible evidence for vocal teaching in free-ranging bottlenose dolphins.

Sayigh, L. S., P. L. Tyack, R. S. Wells, M. D. Scott, and A. B. Irvine. (In preparation). Playback experiments provide evidence for individual recognition in free-ranging bottlenose dolphins, *Tursiops truncatus*.

Solow, A., P. Tyack and L. Sayigh. (In press). The statistical analysis of whistle exchanges in dolphins. Applied Stochastic Models and Data Analysis.

Tyack, P. L. and L. S. Sayigh. 1989. Those dolphins aren't just whistling in the dark. Oceanus 32: 80-83.

6.2 Suggestions for future research

The study of bottlenose dolphin signature whistles, especially in free-ranging animals, is still in its infancy. Although the research presented in this thesis addressed some questions regarding the development and functions of whistles, it has also suggested many additional areas that would be worthy of further study. Several of these are outlined below.

1) As described in Chapter 3, there is much potential for future research on individual recognition in bottlenose dolphins. Playback experiments could explore the extent to which individuals recognize relationships among other individuals, akin to studies that have been done with primates (e.g., Cheney and Seyfarth 1986). For example, playback experiments in which whistle exchanges between a mother-calf pair were contrasted with whistle exchanges between the same mother (or calf) and a different individual could perhaps begin to detect recognition of affiliations. Playbacks could be conducted opportunistically in situations where relationships among individuals are changing, such as before and after a calf separates from its mother, or when males in a coalition shift affiliations (Connor et al. 1992). Studies with captive dolphins would provide opportunities for experimental manipulations, but these should be validated with studies of wild dolphins as well.

2) Additional carefully designed playback experiments have the potential to shed light on complexities of signature and variant whistle functions and usage.

Preliminary data presented in Chapter 3 indicated that possibly the female - female pair was using whistles differently than were the mother - independent offspring pairs. Only the female - female pair showed significant differences in signature and variant whistle responses to playbacks. Again, studies could be conducted in the wild as well as in captivity, where experiments can be more carefully controlled.

3) It would be of great interest to determine whether qualitative judgements of whistle similarity (Chapter 4) made by visually inspecting spectrograms match what dolphins themselves perceive as similar or different. Experiments designed to look at this question would also have the potential to begin teasing apart which features of whistles may carry information other than individual identity (e.g., Tyack 1991).

4) Whistle sequences produced by many different individuals should be analyzed, taking into account the serial dependence of whistle types. This is the only to way to confirm or refute the preliminary sex difference in variant whistle production reported in Chapter 4.

5) Techniques are being developed (e.g., Buck and Tyack, submitted) which will allow quantitative assessments of similarity of variant whistles to a catalogue of signature and variant whistles of individuals in the Sarasota community. This work promises to shed light on the functions of variant whistles.

6) Detailed behavioral observations of free-ranging dolphins, such as those that have been undertaken with captive animals (e.g., Östman 1991, Samuels et al. 1991), could begin to provide information on subtleties of relationships among individuals, such as whether or not dominance hierarchies exist. In turn, this research could shed light on some of the hypothesized functions of the sex differences in vocal production seen in the Sarasota dolphins (Chapter 4). Such observations, if conducted with simultaneous acoustic recordings, could also provide additional information on functions of signature and variant whistles. Techniques for identifying which individual is producing a sound (e.g., Freitag and Tyack in prep.) should be used when they become available.

7) Additional studies of signature whistle development, both in the wild and in captivity, should strive for larger samples both of individuals and of observation and recording time. It is clear from this study and from captive studies (Caldwell and Caldwell 1979, Tyack et al. submitted) that there is a large amount of individual variability in whistle development, and that whistle crystallization can occur at any time from the first few days to over 1 year of age. This calls for intensive sampling regimes to ensure that the critical time periods are not missed. Studies in captivity should take advantage of improved visibility to correlate association patterns of calves with the whistle development process. In addition, work at several different field sites should be attempted in order to understand the effects of larger scale social and ecological factors.

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APPENDIX I. Samples of the original and revised score sheets used in the judges' ratings experiments. Sample set of 10 calves' whistles and 10 mothers' whistles have been reduced from their original size.

@

GROUP A

DOLPHIN WHISTLE LAB 23 OCTOBER 1989

Rate the similarity of each combination that I specify: for example, when I say 10F, rate on a scale of 1 to 5 the similarity of calf 10 to mother F.

SIMILARITY SCALE: 1 - no similarity .. 5 - very similar

MOTHERS

CALVES	A	B	C	D	E	F	G	H	I	J	
1											1
2											2
3											3
4											4
5											5
6											6
7											7
8											8
9											9
10											10
	A	B	C	D	E	F	G	H	I	J	

- Remember to compare shapes, (or contours) of whistles rather than absolute frequencies or durations.

- Ignore echolocation clicks (they appear as vertical lines).

- There are no right or wrong answers!

GROUP A

DOLPHIN WHISTLE SIMILARITY JUDGEMENTS

Judge the similarity of the shape or contour of whistles, ignoring features such as absolute duration or frequency (these are plots of frequency versus time). Compare the combinations of whistles in the order listed below (for example, "B7" means compare whistle B and whistle 7).

Rate the whistle similarity on a scale of 1 to 5, with 1 being not similar and 5 being very similar. Give yourself about 15-20 seconds for each judgement - the whole set should take about 30 minutes.

1) J7
2) B7
3) B10
4) G7
5) J4
6) I10
7) D1
8) B2
9) J1
10) A1
11) I7
12) D4
13) H3
14) G1
15) H4
16) F9
17) I3
18) H8
19) I9
20) B8
21) E6
22) I1
23) C4
24) E4
25) D7
26) I6
27) C3
28) A6
29) J8
30) A7
31) D9
32) A2
33) G3
34) E10
35) C2
36) F3
37) B6
38) C10
39) I5
40) E5
41) G8
42) A10
43) J3
44) E8
45) C9
46) F1
47) C7
48) J6
49) F6
50) C6
51) C8
52) J2
53) G5
54) B1
55) D8
56) J10
57) B3
58) E9
59) J5
60) F2
61) J9
62) E2
63) E1
64) D10
65) H2
66) I2
67) H6
68) G4
69) H5
70) D2
71) F7
72) D3
73) E7
74) H9
75) D5
76) I4
77) A5
78) G2
79) F5
80) H10
81) C5
82) A4
83) H7
84) D6
85) A8
86) G9
87) E3
88) B4
89) A3
90) F8
91) F4
92) F10
93) I8
94) C1
95) A9
96) B5
97) B9
98) G10
99) G6
100) H1

GROUP A - CALVES

PAGE 1

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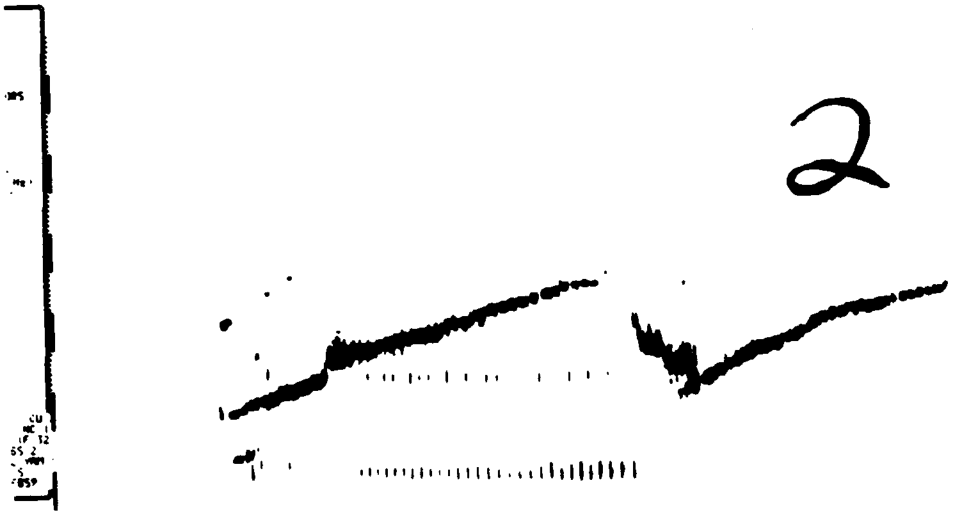

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GROUP A - CALVES PAGE 2

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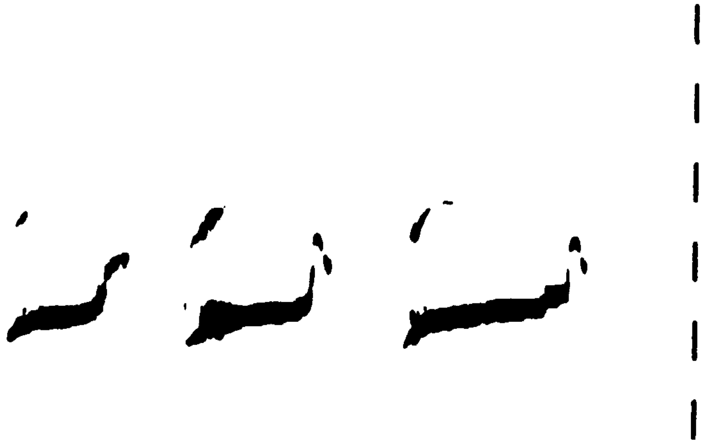

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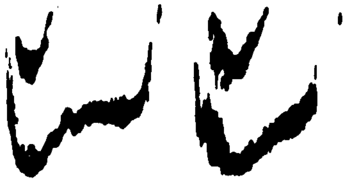

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GROUP A - CALVES PAGE 3

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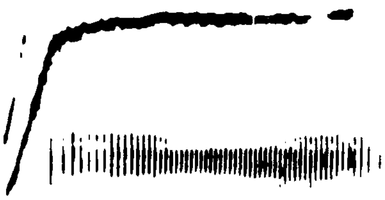

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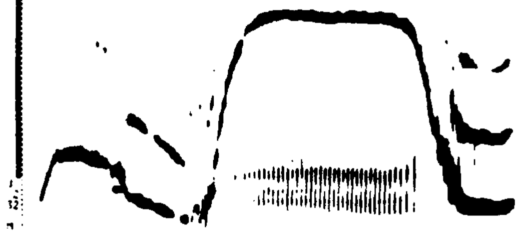
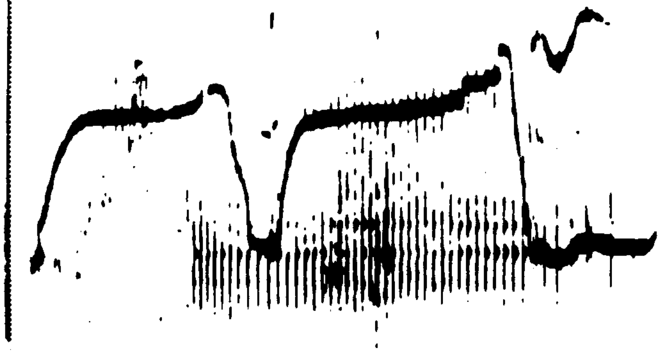
GROUP A - MOTHERS PAGE 4



A

B



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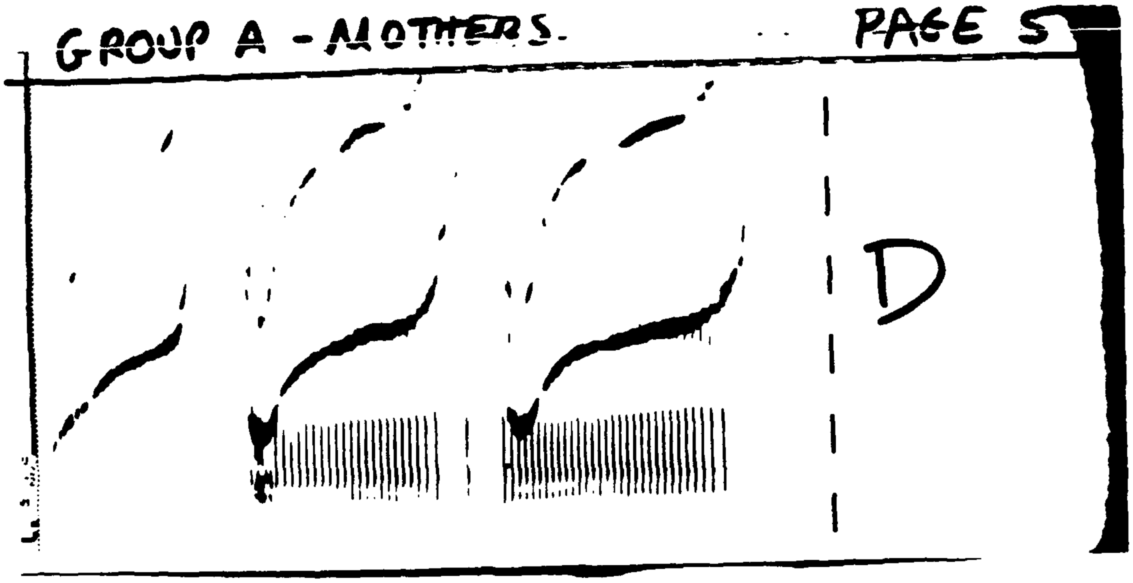
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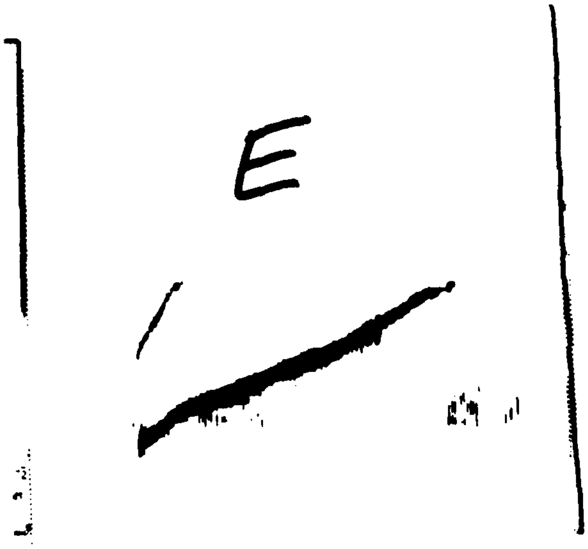
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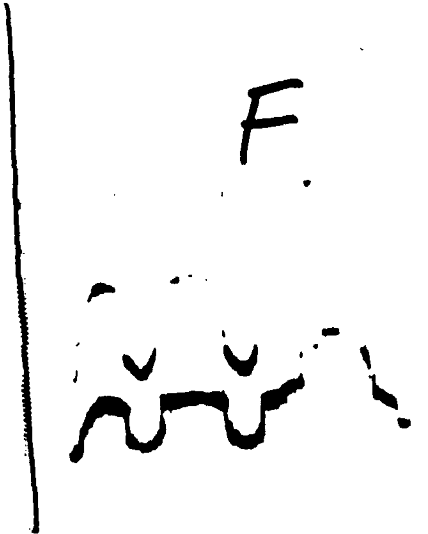
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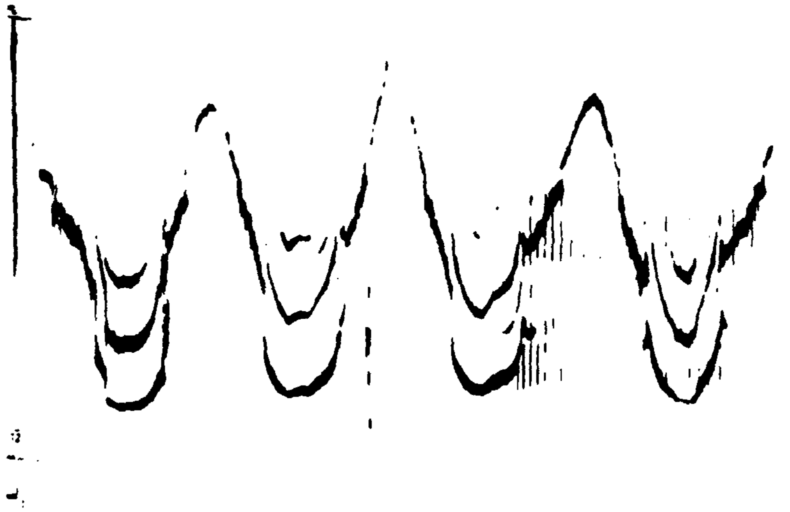
G

GROUP A - MOTHERS PAGE 6

H



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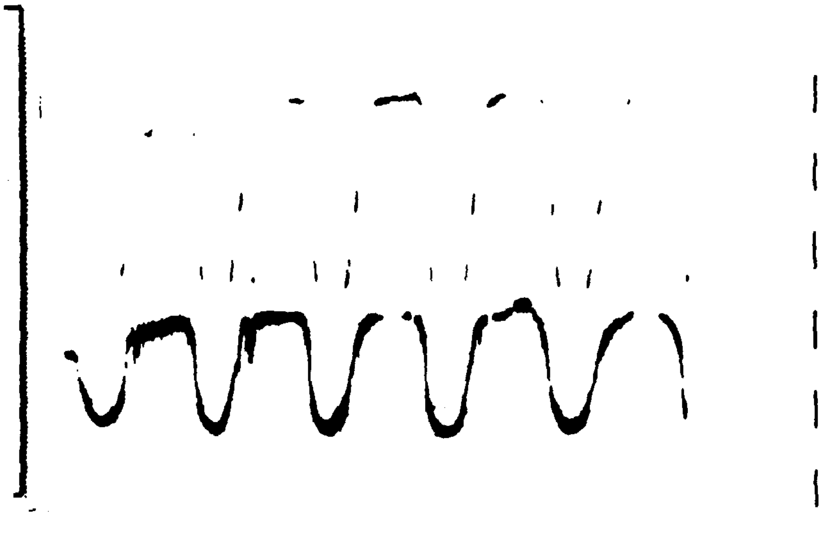

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APPENDIX II.

RECORDING UNDERWATER SOUNDS OF FREE-RANGING DOLPHINS WHILE UNDERWAY IN A SMALL BOAT

Laela S. Sayigh[1], Peter L. Tyack[1] and Randall S. Wells[2,1]

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In press, Marine Mammal Science

Few studies of vocalizations of free-ranging cetaceans have successfully linked continuous, underwater recordings with ongoing behavioral observations. Noise from engines and/or water flowing around the hydrophone generally limited researchers to recording sounds from stationary sites (e.g. Watkins and Schevill 1974, Watkins et al. 1987) or from boats with their engines turned off (e.g., Norris et al. 1985, Watkins and Schevill 1972), especially if the sounds of interest were in the same frequency range as that of engine or flow noise. But unless the animals stay in one place, these techniques do not allow for long-term recording sessions, or for simultaneous detailed behavioral observations. Sailboats are more difficult to maintain at a steady distance from the animals, and they still produce substantial flow noise around a towed hydrophone. Existing towed hydrophone systems (Schevill et al. 1964, Watkins 1981) are unwieldy and not practical for use by one or two persons in a small power boat, especially in areas heavily trafficked by boats. Therefore, we designed an inexpensive, portable system tailored to record whistles (ranging from about 5 to 25 kHz) of bottlenose dolphins (*Tursiops truncatus*), while they are being followed in a small boat.

We utilized this technique in studies of free-ranging bottlenose dolphins in waters near Sarasota, Florida. This area typically provided excellent recording conditions. The inshore waters are protected by a chain of barrier islands, resulting in calm seas much of the year. A resident community of bottlenose dolphins inhabits the area. Nearly every individual is recognizable, and most are of known sex and age (Scott et al. 1990, Wells 1991). The dolphins are habituated to the presence of small power boats as a result of local recreational boating activity. Observations and recordings were made from a small (5-6 m) boat with a 60 or 110 horsepower engine.

If an unweighted hydrophone is towed alongside a moving boat, its bouyancy will cause it to bounce at the surface, creating an enormous amount of noise. In order for it to stream underwater alongside the boat, the hydrophone cable must be weighted. Thus, for our hydrophones we threaded the cable (NEGLEX 2534 microphone cable) through approximately 10-15 small lead fishing weights, which had been drilled through the center to accomodate the diameter of the cable. The weights spanned approximately the last meter of the cable, to within 1-2 cm of the hydrophone, and their total weight was approximately 1 kg. They were separated by strands of nylon line to prevent them from hitting together.

Two 1.5 m sections of rigid, 5 cm diameter PVC pipe were joined together with a "T" joint, and tied across the gunwales at the bow of the boat, extending approximately 1 m on each side (Figure 1). Approximately 2 m of cable (of which 1 m was weighted) extended from the end of the pipe into the water on each side. At speeds of 2-3 knots, the hydrophones streamed underwater at a depth of approximately 1 m, and the weighted cables considerably reduced strumming and flow noise. The rigid PVC pipe kept the cables away from the hull of the boat, and provided enough separation between the hydrophones to allow later calculation of rough bearings for vocalizing individuals by using differences in sound arrival times (Spiesberger and Fristrup 1990). These bearings were limited by the accuracy with which we were able to visually locate individuals. This was generally not much better than about 45 degrees, since dolphins were usually not in sight (i.e., they were underwater) when whistles were produced.

The hydrophones we used were developed specifically for recording dolphin whistles (Tyack 1985). They had built-in 1-2 kHz high pass filters to reduce engine noise, and above this, their frequency response was flat to 25 kHz. They were cylindrical, 17 cm long and 4 cm in diameter, and weighed approximately 100 g. Overall, they were streamlined and towed well underwater.

Hydrophone cables extended from the the center of the PVC pipe to the deck of the boat, where they were plugged into an additional, two-channel passive high-pass filter. This filter (designed to our specifications by Allen Avionics, Mineola, NY) had a flat frequency response from 5-30 kHz. This low frequency cut-off was chosen, after evaluation of hundreds of hours of recordings, to maximize reduction of engine noise and retention of whistle frequencies. Outputs of the filter were connected to the two high fidelity inputs of a portable VHS recorder (Panasonic model AG-6400), which had a flat frequency response from 20 to 20000 Hz. A lapel microphone was used on a third (low fidelity) channel for voice commentary, and a video camera was used on a fourth VCR channel. The camera was either mounted onto a tripod or manually operated. Thus, two channels of high fidelity audio, one comment channel, and video were recorded simultaneously onto the same tape. A battery operated speaker was used to monitor the recorded sounds in real time, and whistles were noted on a check sheet for correlation with behavioral data.

Examples of whistles recorded a) with the engine off, and with no external high pass filters; b) while underway, with the portable high pass filter; and c) the same as b), but with additional high pass filtering at 9 kHz during analysis, are shown in Figure 2. This shows the high quality of recordings that are attainable with this system.

For focal animal behavioral sampling (Altmann 1974), we attempted to remain within about 20 m of the animal. Recording and observation sessions lasted for up to six hours, and the animals being followed appeared to habituate rapidly to our presence. Depending upon their activity, the dolphins generally moved at speeds up to 3 knots, and at these speeds whistles could easily be discerned above the engine noise, even without the portable high-pass filter. Echolocation clicks and other broadband "burst pulse" sounds also were audible, and could be noted for presence or absence. However, this system did not provide complete representation of all dolphin sounds due to the filtering of low frequencies.

This is a low-cost, easy to use technique that enables continuous underwater recording of dolphins from small boats. Our understanding of the natural contexts of dolphin vocalizations were enhanced by combining this technique with simultaneous behavioral observations and with background information on the dolphins being recorded.

Acknowledgements

We would like to acknowledge the generous support of Dolphin Biology Research Institute of Sarasota, Florida for providing the R/V Fandango. We also wish to thank William Watkins for reviewing the manuscript, and Alessandro Bocconcelli and Andy Bowen for drafting the figure. Financial support was provided by Ocean Ventures Fund Awards (WHOI) to LSS, National Science Foundation Doctoral Dissertation Grant No. BNS-9014545 to LSS, NIH Grant No. 1R29NS25290 to PLT, and ONR Grant No. N00014-87-K-0236 to PLT. This work was conducted under marine mammal permit no. 638 to R. S. Wells. This is contribution number 8092 from the Woods Hole Oceanographic Institution.

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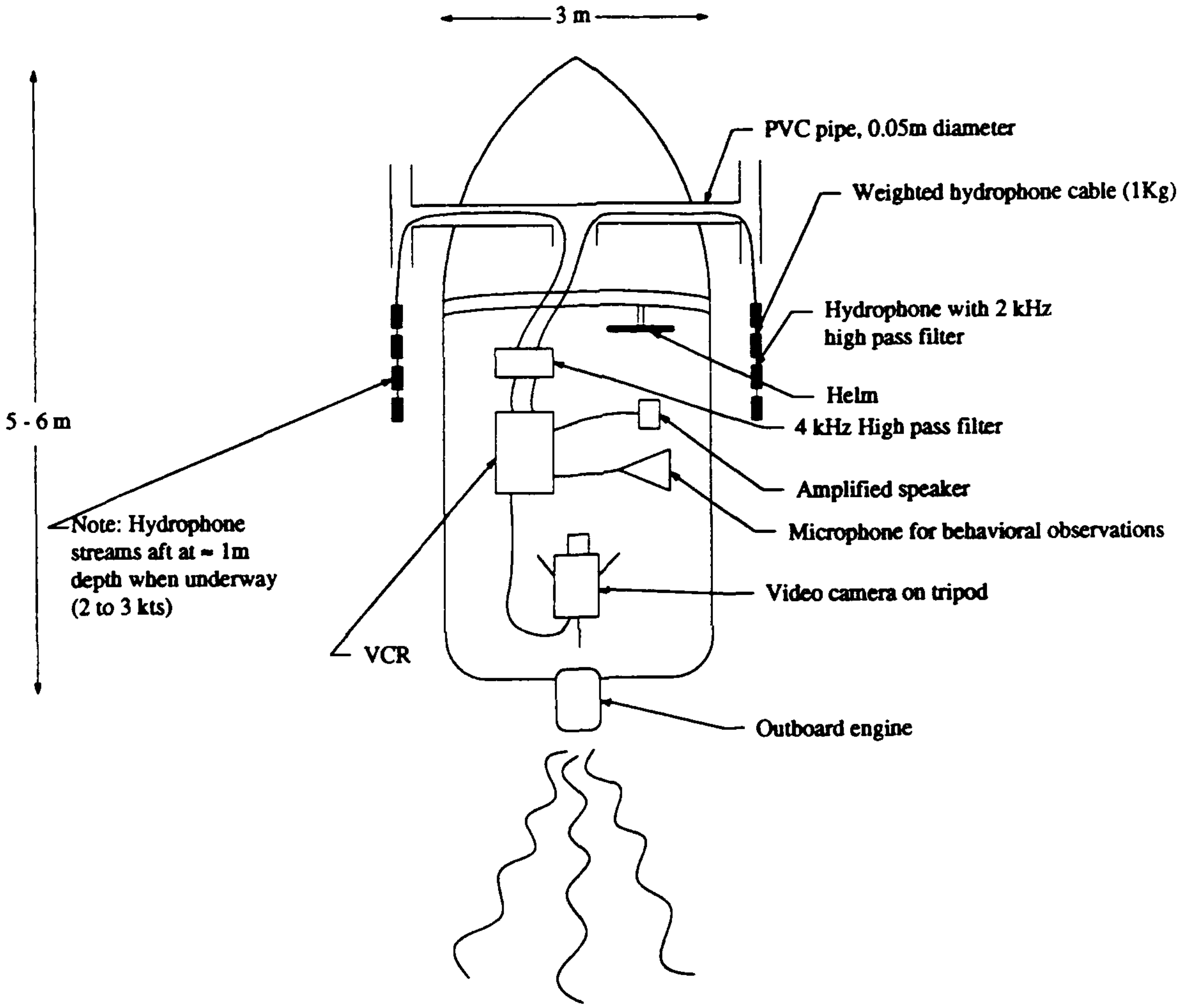
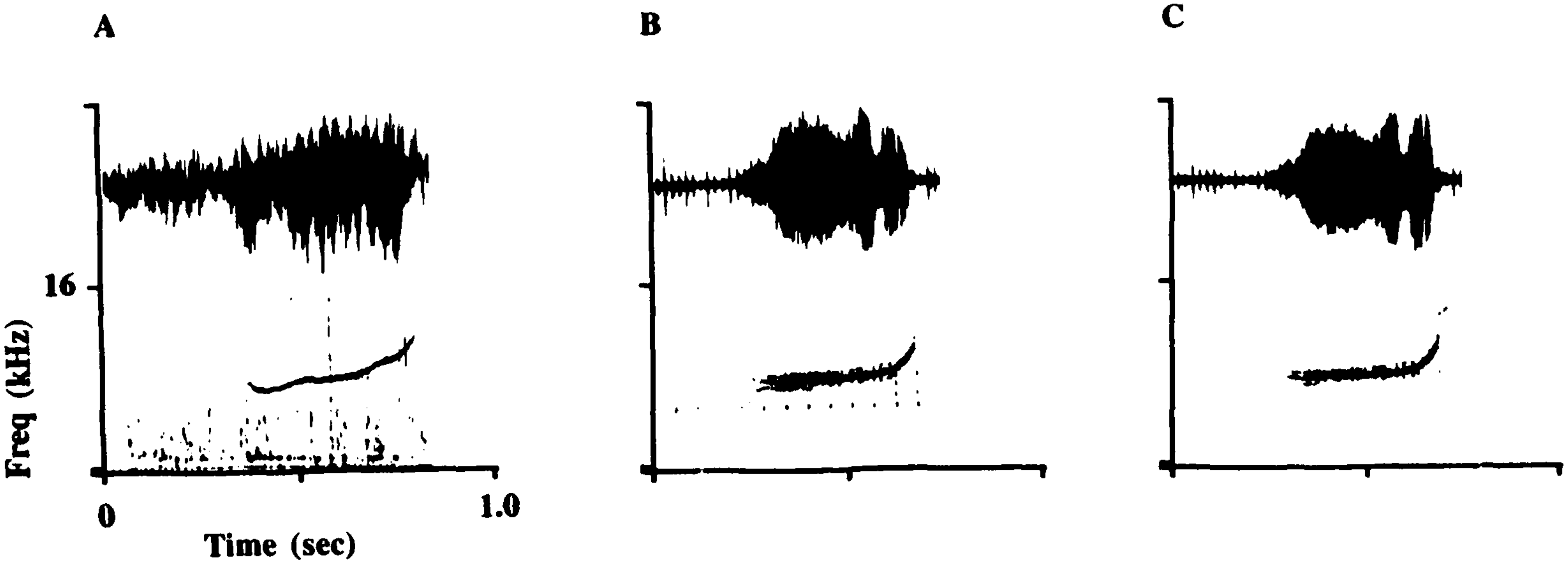


Figure 1. Schematic drawing of recording set-up.

Figure 2. A: whistle recorded with the engine off, and no external high pass filters. B: whistle recorded with the boat underway, using the portable, 4kHz high pass filter. C: same whistle as B, additionally high pass filtered at 9kHz during analysis. Spectrograms and waveforms were created on a Kay Elemetrics Corp. Model 5500 Digital Signal Processing system. Analysis settings included a sample rate of 40,960 Hz, a 256 pt. FFT, and a Hamming window.


A
B
C
16
Freq (kHz)
0
1.0
Time (sec)

Appendix III

PROTOCOL FOR BEHAVIORAL OBSERVATIONS OF FREE-RANGING MOTHER-CALF PAIRS

Laela S. Sayigh, Amy Samuels, and Peter L. Tyack

1. Objectives

The main objectives of the focal observations (also called "follows") of mothers and calves were: a) to study whether experiential factors affect signature whistle development; b) to track the whistle repertoire of calves during the first year of life; c) to characterize the overall acoustic environment of young calves; d) to determine general behavioral correlates of whistle production.

2. Protocol

2.1 Recording set-up

Focal observations were conducted in a small (5-6m) boat with a 60 or a 110 horsepower engine. A 3m piece of PVC pipe was tied onto the bow of the boat, with hydrophones coming out of both ends of the pipe. This kept the hydrophones at more or less a fixed distance apart, making it possible to obtain information on time delays between them. Also, this arrangement keeps the hydrophones from hitting against the hull of the boat. The cables of the hydrophones were each weighted with approximately 1 kg of weights, so that they streamed under water, rather than flopping at the surface. These hydrophones (designed by Peter Tyack) were equipped with 1-2 kHz highpass filters, so water noise did not swamp the dolphin sounds. In addition, they were channeled into a 4kHz high-pass filter to get rid of most of the engine noise. Additional engine noise was filtered out during analysis. Recording equipment consisted of a Panasonic AG-6400 hifi VCR, a Panasonic video camera on a tripod, and a clip-on microphone for comments. This recording system was described in detail in Sayigh et al. (in press), which is included as Appendix II.

2.2 Pre-follow

When a group containing a mother-calf pair was sighted, a decision was made whether to begin a follow based on these criteria: if a newborn calf was present, it was followed it unless it had been followed successfully in the previous few days; if more than one newborn calf was present, the choice was based on whether one of them had been followed recently (if not, *ad lib*). If no newborn calves were present, but a target pair of older calves that had not been followed recently was present, they were the focal pair. Target pairs of older calves were ones that had been followed in previous years and recorded during temporary captures (see Sayigh et al. 1990); since their whistles were well known, they were the most likely to yield information about behavioral correlates of whistle production. In other conditions, judgements were made in accordance with the likelihood of finding other suitable animals, which varied with conditions (e.g., weather, time of day, boat traffic). If no suitable mother-calf pair was present, an *ad lib* sample was taken for each mother-calf pair. This consisted of noting on a check sheet information equivalent to one five-minute point sample during a follow (see below).

If a suitable focal pair was present, information required for standard sighting data sheets was obtained, which included identifying visually all animals, taking identification photographs, and noting location, conditions, etc. If only two people were present, one person drove the boat and kept track of the animals, attempting to identify them. The other person took photographs and filled out the data sheet.

When this was completed, one person set up the equipment while the other drove the boat and kept track of the animals. Equipment set-up involved putting hydrophones overboard, plugging them into the filter and VCR, setting up the camera on the tripod and white balancing the camera, and setting up the external microphone. At this time, if the animals were still in sight, recording began and the 5 minute timer was set. One person began making verbal comments onto one track of the tape, starting with the date, time, and a general description of the situation. The other person filled out the header information on the check sheet, which included date, reel number, observers present, platform, focal animals, follow number and page number (see attached check sheet). If a third person was present, he/she helped to keep track of the focals, looked for other animals, and oriented the video camera in the appropriate direction.

2.3 Focal sampling

Once the survey data collection and equipment setup was completed, the follow began. Data for the five-minute point samples was collected at the first surfacing that occurred after each time the five-minute timer went off. During the follow, one person (the observer) was selected to perform the job of driving the boat and verbally recording data from each surfacing and from the five minute points onto the comment track of the tape. The other person (the recorder) simultaneously recorded data directly onto check sheets from the five minute points and behaviors that occurred throughout the five minute period. The recorder helped the observer to keep track of the animals and prompted the observer for information at the five minute points when necessary. The recorder also took photos if new animals joined the focals. Whenever possible, either person occasionally checked the video equipment (gain, battery level, tape).

If possible, focal sampling was conducted of both dolphins in the pair. If that was not possible, the calf was the focal subject.

2.3.1 Information recorded verbally at each surfacing, and on check sheets every 5 minutes (except behavior column (#13), see attached check sheet).

Column 2) Azimuth - position of mother and calf relative to heading of boat using clock direction

Column 5): Calf nearest neighbor - the identity of the animals that were closest to the calf, with the relevant distance code (see column 6, mother-calf distance)

Column 6) Distance between mother and calf, using the following codes

BP - baby position: calf was slightly behind and usually below mother, <1m away

0 - <1m

1 - between 1m and 3m (within approximately one adult body length)

2 - greater than 3m (a body length), but less than 10m

3 - between 10 and 50 m

4 - greater than 50m - at this distance, both individuals can not be reliably observed. Therefore, the calf was observed and the distance of the mother estimated frequently.

Column 7) Mother calf synchrony - synchrony was defined as any overlap in the surfacings of mother and calf. The main points of interest here were whether or not the mother and calf were surfacing synchronously, and if they were not, whether the calf was surfacing synchronously with another animal. Also of interest was whether an additional animal(s) was (were) also surfacing synchronously with the mother-calf pair. This column was also used to note if only the calf were seen. Coding as follows:

Y - mother and calf synchronous

N - mother and calf asynchronous

Y+63 - mother, calf and FB63 all synchronous

C+63 - mother and calf asynchronous, calf synchronous with FB63

M+63 - mother and calf asynchronous, mother synchronous with FB63

C - calf only seen (NOTE: if only the mother were seen, it would be a missed point, since the calf is the focal in situations when the pair can not be followed)

Column 13) Behavior - Behaviors were noted verbally and on the check sheet continuously throughout the 5 minute periods. Since the range of possible behaviors is enormous, the list was restricted to behaviors that were believed (based on previous observations) to be relevant either to the development of the calf's whistle, or to the broad definition of social functions of whistles (i.e., general contexts of whistle production: feeding, socializing, changes in group status). These behaviors were divided into general categories using information from earlier observation sessions of mother-calf pairs. It is by no means an exhaustive list, and the categories are not mutually exclusive.

BEHAVIORS ASSOCIATED WITH FEEDING

TL - tail lob

LG - lunge

FW - fish whack

FM - fish in mouth

CS - calf at surface (infants only)

BEHAVIORS ASSOCIATED WITH SOCIALIZING

SO - general socializing

HO - head out

LP - leap (body out of the water)

PP - porpoise (body clears surface, making forward motion)

FS - fast surface (body does not clear surface)

CH - chuff

CN - chin slap

GROUP BEHAVIORS INVOLVING CHANGE IN STATUS

CD - change direction ($\leq$90 degrees)

ACD - abrupt change in direction (>90, $\leq$180 degrees)

AG - focals approach another group (head in general direction)

AVG - focals avoid another group (head in other than general direction)

GS - group containing focals splits

GJ - group containing focals joins another group

BEHAVIORS RELEVANT TO WHISTLE DEVELOPMENT PROCESS

AP - approach - animal crosses a distance category boundary during the surfacing (or visible underwater) toward the focal pair (e.g., FB63 AP)

LV - leave - animal crosses a distance category boundary during the surfacing (or visible underwater) away from the focal pair (e.g., FB63 LV)

CAP - calf approaches mother

MAP - mother approaches calf

MA - mutual approach (mother and calf)

MCJ - mother and calf join

CLV - calf leaves mother

MLV - mother leaves calf

AW - calf greater than distance category 1 away from mother

LD - calf leading mother by >1m

TR - calf trailing mother by >1m

IB - another animal in between mother and calf

CIB - calf in between mother and someone else (e.g., CIB-FB63)

CSY - calf synchronous with someone else (e,g, CSY-63)

CNN - calf's nearest neighbor is someone other than mother (e.g., CNN-63)

BP - calf in baby position

CUP - calf up alone

MUP - mother up alone

2.3.2 Information recorded only every 5 minutes, both verbally and on check sheet

Column 1) Time of day

Column 3) Group composition - all animals present in the group were listed, and distances of neighbors of mother and calf were noted, using distance codes as described for column 6. For the purposes of the behavioral observations, animals greater than 50m away were not considered part of the group. These animals were noted in column 14.

Column 4) Total number of animals in the group

Column 8) Spread - distance codes defined for column 6 were used to describe distances present in the group. E.g., two animals less than 1m apart separated by a distance of 12 meters from a trio of animals each less than 1m from the next was 0,3. A group of animals each 1m from its nearest neighbor was 1. Information on formation, e.g. line abreast, single file, was also included.

Column 9) Activity of focal pair - it was also noted if this was not the same as general group activity. Activities included (as defined informally by Randy Wells):

FD - Feeding - obvious evidence of feeding; e.g., fish in mouth, parts of fish at surface, frigate birds diving on dolphins, etc.

Column 9) Activity of focal pair, cont.

ML - Milling - non-directed movement; frequent changes in direction; can occur in conjunction with most other activities; can be accomplished by a lone dolphin.

TR - Travel - directed movement from one area to another - not necessarily straight line (note slow, fast, zigzag)

SZ - Socializing - active interactions with one or more other dolphins

PL - Playing - interactions with non-dolphin objects (*e.g.*, boats)

RE - Resting - quiescent, slow movements with no indication of other active activities; rest can occur while travelling (rarely) or milling (more often)

Column 10) Heading of group (compass direction)

Column 11) Location - Randy Wells' general location codes were used, as well as more specific information, such as GF(grassflats), C(channel), SS(sandy shallows), CE(channel edge), P(near pilings). The recorder marked the position of the focals on a map every 30 minutes.

Column 12) Distance from boat, in meters

Column 14) Other animals in sight - approximately how far away, heading, activity, and if possible, how many and who they are

Column 15) Roll and frame numbers of any photos taken of animals in the group or of other animals

Column 16) If whistles were heard, this was stated verbally on the tape. On the check sheet, the whistle box of the current 5 minute interval was checked.

Column 17) Comments - anything notable that is not coded, regarding the focal group, boats, equipment (reel changes, battery changes, etc.).

2.4 Analysis

Data from the check sheets (see attached) were entered into the relational database program *PARADOX* (Borland International, Scotts Valley, CA).

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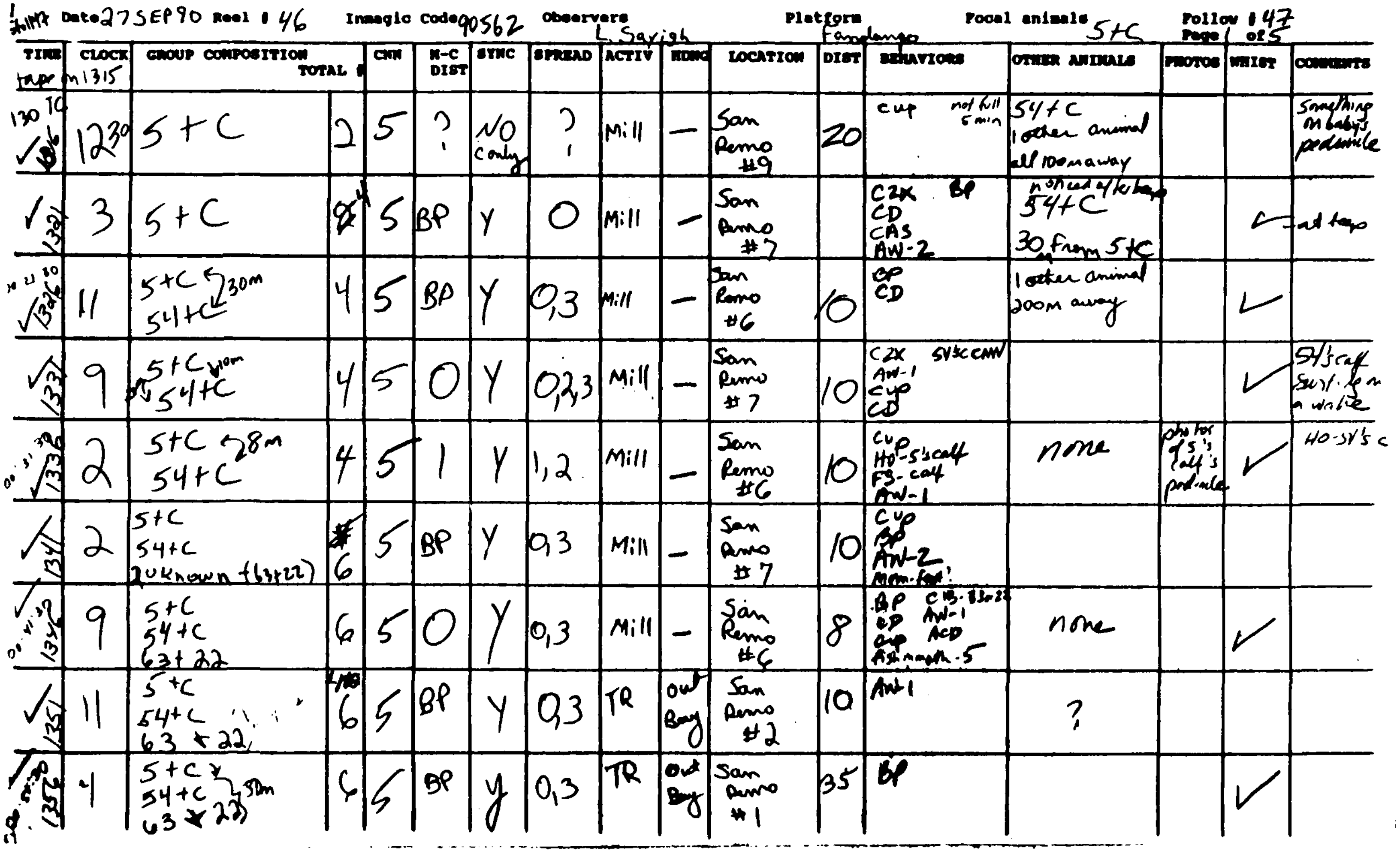

Date 27SEP90 Reel # 46 Inmagic Code 90562 Observers L. Sayigh Platform Fandango Focal animals 5+C Follow # 47 Page 1 of 5

TIME	CLOCK	GROUP COMPOSITION	TOTAL #	CNN	M-C DIST	SYNC	SPREAD	ACTIV	HDNG	LOCATION	DIST	BEHAVIORS	OTHER ANIMALS	PHOTOS	WHIST	COMMENTS
tape	m1315															
130 10 ✓ 1316	12 30	5+C	2	5	?	NO C only	?	Mill	—	San Remo #9	20	cup not full 5 min	54+C 1 other animal all 100m away			Something on baby's peduncle
✓ 1321	3	5+C	~~2~~ 4	5	BP	Y	0	Mill	—	San Remo #7		C2X BP CD CAS AW-2	noticed after tape 54+C 30m from 5+C		✓	at tape
30 21 30 ✓ 1326	11	5+C ↰ 30m 54+C	4	5	BP	Y	0,3	Mill	—	San Remo #6	10	BP CD	1 other animal 200m away		✓	
✓ 1331	9	5+C 40m 54+C	4	5	0	Y	0,2,3	Mill	—	San Remo #7	10	C2X 54'sC CNN AW-1 cup CD			✓	54's calf surf. for a while
00 31 30 ✓ 1336	2	5+C ↰ 28m 54+C	4	5	1	Y	1,2	Mill	—	San Remo #6	10	cup HO-5's calf FS-calf AW-1	none	photos of 5's calf's peduncle	✓	HO-54's c
✓ 1341	2	5+C 54+C 2 unknown (63+22)	~~#~~ 6	5	BP	Y	0,3	Mill	—	San Remo #7	10	cup BP AW-2 Mom-fed?				
00 41 30 ✓ 1346	9	5+C 54+C 63+22	6	5	0	Y	0,3	Mill	—	San Remo #6	8	BP C13-33-22 BP AW-1 cup ACD AS-[illegible]-5	none		✓	
✓ 1351	11	5+C 54+C 63+22	6	5	BP	Y	0,3	TR	out Bay	San Remo #2	10	AW-1	?			
00 51 30 1356	1	5+C ↰ 50m 54+C 63+22	6	5	BP	y	0,3	TR	out Bay	San Remo #1	35	BP			✓	

A sample check sheet used in the mother-calf follows.

BIOGRAPHICAL NOTE

The author attended the University of Pennsylvania from 1981-1985, and graduated *summa cum laude*, with distinction in biology and environmental studies, and a minor in music. She entered the MIT/WHOI joint program in Biological Oceanography in June of 1986.

Honors and awards:
- Dean's list, University of Pennsylvania, 1981-1985
- Adam's Prize for independent research in Biology, 1985
- Phi Beta Kappa, 1985
- Ocean Ventures Fund Awards (funds for research), 1987-88
- National Science Foundation Doctoral Dissertation Research Grant (BNS-9014545), 1990
- American Cetacean Society (funds to attend two conferences), 1991
- Associate member, Sigma Xi, 1991

Professional societies: Phi Beta Kappa, Sigma Xi, Animal Behavior Society, Society for Marine Mammology, North Atlantic Marine Mammal Association, Acoustical Society of America, Association for Women in Science.

Teaching and professional experience: Laboratory assistant, University of Pennsylvania, 1985-6; Teaching fellow, Harvard University, 1988; Teaching assistant, Boston University Marine Program, Marine Biological Laboratory, 1989.

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Research papers

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16. Abstract (Limit: 200 words)

This thesis investigated the development and functions of individually distinctive signature whistles of free-ranging bottlenose dolphins, *Tursiops truncatus*, in waters near Sarasota, Florida. First, results of playback experiments strongly suggested that dolphins use signature whistles for individual recognition. Second, male calves were more likely than females to produce signature whistle contours similar to those of their mothers, whereas females were more likely to produce whistles distinct from those of their mothers. Male calves appeared to produce more whistles other than the signature (called "variant" whistles) than did females. Finally, several sources of data indicate that learning plays a role in signature whistle development; this contrasts with what is known about vocal development in other non-human mammalian species. Focal observations and acoustic recordings of mother-calf pairs were conducted to examine the effects of the early social and auditory environment on signature whistle development. This provided preliminary insights into factors affecting both the time course of whistle development and whether or not a calf develops a contour similar to that of its mother; these included strength of the mother-calf association, number of associates, overall number of whistles heard, and number of whistles produced by the mother.

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