

SIGNATURE WHISTLE PRODUCTION, DEVELOPMENT, AND PERCEPTION IN
FREE-RANGING BOTTLENOSE DOLPHINS

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TABLE OF CONTENTS

ABSTRACT	iv
ACKNOWLEDGEMENTS	vi
LIST OF TABLES	vii
LIST OF FIGURES	viii
CHAPTER 1: WHISTLE PRODUCTION AND DEVELOPMENT IN FREE-RANGING BOTTLENOSE DOLPHINS	1
INTRODUCTION	2
METHODS	6
Sarasota Population	6
Whistle Classification	7
Whistle Crystallization	9
RESULTS	10
Whistle Classification and Distribution	10
Whistle Development	11
FB 39 and Calf	12
FB 65 and Calf	12
FB 59 and Calf	13
DISCUSSION	14
Whistle Classification	14
Signature Whistle Development	16
REFERENCES	20
APPENDIX	33

CHAPTER 2: PLAYBACKS OF WHISTLES OF VARYING LOOP NUMBER AND CONTOUR.....	35
INTRODUCTION	36
METHODS	38
Sarasota Population.....	38
Measures of Response.....	39
Playback Protocol	41
Stimuli Synthesis	42
RESULTS	43
Sample Size.....	43
Responses to Stimulus Presentation	43
Habituation-Dishabituation Protocol	44
DISCUSSION.....	45
REFERENCES	49

ABSTRACT

Data from behavioral observations and acoustic recordings of free-ranging bottlenose dolphins (*Tursiops truncatus*) were analyzed to determine whether signature whistles occur in the wild, and to determine when whistle crystallization occurs in calves. The study animals were part of a resident community of bottlenose dolphins in the waters near Sarasota, Florida. Three mother-calf pairs and their associates were recorded for a total of 141.25 hours between May and August of 1994 and 1995. Each whistle was conservatively classified into one of four categories: signature, probable signature, upsweep, or other. Overall whistle production varied significantly with both activity and group size. Whistles occurred more frequently than expected during socializing and in groups of over five dolphins, and occurred less frequently than expected during travelling and in groups of two dolphins. Signature and probable signature whistles made up approximately 52% of all whistles produced by these free-ranging bottlenose dolphins.

Each of the three calves studied developed its whistle prior to four months of age. Each mother's signature whistle comprised approximately 3% of the whistles recorded during the first year of her calf's life, regardless of social or auditory environment, which varied greatly among the calves. One calf developed a signature whistle similar to that of its mother.

To evaluate whether certain acoustic features of whistles are perceptually important to dolphins, 44 playback experiments were conducted with temporarily captured dolphins near Sarasota, Florida in June of 2000 and 2001. Response measures included number of head turns toward or away from the speaker, echolocation bouts, and whistles. In a modified habituation-dishabituation design, habituation to the first stimulus

did not occur. Additionally, there were low overall response rates to most synthetic stimuli. There were no significant differences in responses to whistles containing differing numbers of loops or differing contours, with the exception that head turn rates were higher in response to modified synthetic upsweeps than to several other synthetic stimuli. In addition, whistle response rates were significantly higher to known, natural whistle stimuli than to synthetic upsweeps. These results suggest that natural whistles and modified upsweeps contain whistle features not adequately conveyed by other synthetic stimuli.

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LIST OF TABLES

Table	Page
1.1	Observed and expected total whistles based on activity and group size.....23
1.2	Observed and expected signature whistles based on activity and group size24
1.3	Observed and expected non-signature whistles based on activity and group size25
1.4	Percent time spent in each activity and group size by each of the focal calves.....26
1.5	Recorded whistle environment for each of the focal calves27
1.6	Overall summary of whistle development for each of the focal calves28

LIST OF FIGURES

Figure	Page
1.1 Average whistles per five-minute interval and average whistles per dolphin	29
1.2 Signature whistles of focal mother-calf pairs	31
2.1 Signature whistle of FB 163 with varying numbers of central loops	51
2.2 Schematic drawing of playback experiment layout	53
2.3 Stimuli used during playbacks to temporarily captured bottlenose dolphins	55

CHAPTER 1: WHISTLE PRODUCTION AND DEVELOPMENT IN FREE-RANGING
BOTTLENOSE DOLPHINS

INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) produce a wide variety of vocal signals to respond to and interact with both their group members and their environment. These vocalizations can be grouped into three different categories: broad-band echolocation clicks; broad-band burst-pulsed sounds; and frequency-modulated, narrow-band whistles (Caldwell et al. 1990). Caldwell and Caldwell (1965) were among the first researchers to scientifically investigate the production of whistles in captive bottlenose dolphins. Their recordings showed that within a group of captive animals, each animal tended to produce the same whistle regardless of context. Although the whistles were shown to vary in intensity, duration, and rate of production, the basic contour of each individual's whistles remained the same overall (Caldwell and Caldwell 1965; Caldwell et al. 1990).

Because these whistles contained distinctively individual characteristics, they were termed "signature whistles" (Caldwell et al. 1990). These unique features allow spectrograms of the signature whistle of one individual to be visually separated from the spectrograms of signature whistles of other individuals and from spectrograms of non-signature whistles (Janik and Slater 1998). Spectrograms of signature whistles are easier to classify visually by human observers than by computer methods because humans are more capable of recognizing the general form of the whistle; naturally-occurring variations are minimized instead of being the impetus for separate whistle classifications (Janik 1999). Variations that may occur include insertions and/or deletions of certain whistle parts and changes in whistle frequencies or duration.

Current data suggest that signature whistles function in the recognition of individuals by others (Caldwell and Caldwell 1965; Caldwell et al. 1990; Sayigh et al.

1999); playback experiments demonstrated that temporarily captured free-ranging dolphins are capable of discriminating between signature whistles of different, familiar individuals (Sayigh et al. 1999).

Signature whistles also appear to function in maintaining group cohesion. Janik and Slater (1998) found that captive bottlenose dolphins primarily produced stereotyped signature whistles when one individual was separate from the rest of the group and that the separated individual primarily produced one stereotyped signature whistle as well. However, when all of the animals were together, they primarily produced non-signature whistles. These data suggest that signature whistles of bottlenose dolphins provide a means to locate and maintain contact with other dolphins. Similarly, Smolker et al. (1993) showed that wild bottlenose dolphin mother-calf pairs whistle commonly while separated, but not as frequently while together. Anecdotal behavioral observations of free-ranging dolphins in Sarasota, Florida noted that separations of large distances and subsequent joinings of animals were often connected to bouts of signature whistle production (Hill 1999).

McCowan and Reiss (1995, 2001), however, found that signature whistles were nonexistent in the vocal repertoire of 10 captive bottlenose dolphins; these dolphins shared a variety of whistle types within and among socially interactive groups. Based on these data, McCowan and Reiss (1995) suggested that signature whistles occur only during times of stress, as they had only been documented in small captive groups or in restrained captive or free-ranging animals.

The first goal of this study was to determine if unrestrained, free-ranging dolphins do produce signature whistles, and if so, to relate this production to factors such as

activity and group size. To date very little research has been done in this area, primarily because of difficulties in identifying the vocalizer. A resident community of bottlenose dolphins near Sarasota, Florida provides a unique opportunity to study signature whistle production because most of the animals have been recorded during temporary capture-release sessions since 1984 (Wells and Scott 1990). Dolphins tend to produce large numbers of stereotyped signature whistles in this context. Thus, vocalizations recorded from free-ranging animals can be compared to those produced by the same animals during temporary capture. These data provide insights regarding whether signature whistles occur naturally in free-ranging dolphins or are artifacts of stressful circumstances.

The second goal of this study was to study signature whistle development in free-ranging bottlenose dolphin calves. Bottlenose dolphins learn their vocalizations (Sayigh 1992; Reiss and McCowan 1993; McCowan and Reiss 1997; Tyack and Sayigh 1997; Janik and Slater 1998), unlike most other non-human mammals (Seyfarth and Cheney 1997). Studies of vocal development in vervet monkeys, squirrel monkeys, rhesus macaques, Japanese macaques, and infants cross-fostered between these two macaque species have shown that vocal production in these primates is largely innate; much of the adult vocal repertoires are found in the calls of very small infants and remain largely unmodified over time (Seyfarth & Cheney 1997). Furthermore, squirrel monkeys deafened, isolated, or raised by mute mothers all produced identical calls, and call production was not hampered in experimentally deafened adults (Hauser 1997). Overall, there are very few data providing evidence that experience or learning play a role in modifying call structures in any primate species (Hauser 1997).

Captive newborn bottlenose dolphin calves are born with the ability to produce narrow-band whistle-like sounds (Caldwell and Caldwell 1979). These whistles are not stereotyped at birth, but calves gradually converge on a stereotyped whistle contour (Caldwell and Caldwell 1979) in a process known as whistle crystallization. Caldwell and Caldwell (1979) reported that 13 of the 14 captive bottlenose dolphin calves in their study had developed a stereotyped signature whistle by three months of age; however, one calf had not developed a stereotyped signature whistle at 17 months of age.

A study comparing fully-developed signature whistles of Sarasota mothers and calves recorded during temporary capture found that approximately 26% of calves developed whistles similar to those of their mothers; this tendency was more pronounced in male than female calves (Sayigh et al. 1995). Nothing is known regarding what factors influence a calf to develop a whistle similar to or different from that of its mother.

Only one study to date has investigated whistle development in free-ranging animals. Sayigh (1992) reported that the critical period for signature whistle development in four free-ranging bottlenose dolphin calves was between one and 13 months of age. Two calves developed whistles similar to those of their mothers, and two did not. A variety of factors, including numbers of associates, numbers of whistles heard, and percent time spent alone with the mother appeared to influence the development process (Tyack and Sayigh 1997). Given the enormous variability and small sample size, more work was clearly needed in this area. Thus, the second goal of this study was to expand on the research of Sayigh (1992), and to further examine the timing and outcome of whistle crystallization in free-ranging bottlenose dolphin calves.

METHODS

Sarasota Population

The data analyzed for this study were collected from a resident community of free-ranging bottlenose dolphins in the waters near Sarasota, Florida (Wells and Scott 1990) during May-August, 1994 and May-July, 1995. Data were collected by Laela Sayigh as part of a study of vocal development, in which acoustic recordings and focal behavioral observations (Altmann 1974) were made of mother-calf pairs. During focal observation sessions (called focal follows) select mother-calf pairs were followed for extended periods of time, often over the course of several hours. In 1994 the focal calves were newborns (less than three months old), and in 1995 the same focal calves were approximately one year old. The data set consisted of 141.25 hours of observations and recordings.

Dolphins were recorded as described by Sayigh et al. (1993). Briefly, two hydrophones with weighted cables were towed while underway in a small boat to enable continuous recording. One hydrophone was connected to a high-pass filter to remove noise from the boat engine. Recordings were made with a Panasonic AG-6400 hi-fi VCR that was capable of recording frequencies up to at least 32 kHz. Verbal comments describing group composition, mother-calf distance, calf's nearest neighbor, activity, location, and group size were recorded onto a third channel at five-minute intervals. Activities included mill, travel, mill/travel, feed/probable feed, rest, and social (see Appendix A for definitions). Group size was divided into three categories: two animals, three to five animals, and over five animals. Also noted was the presence of other animals in the area, but not within the group (a group was defined as animals within a 50-meter

radius of the focal animals). Photographs were taken to ensure proper identification of the animals being studied (Würsig and Jefferson 1990).

The videotapes containing these data were analyzed using Signal/RTSD (Version 3.0, Engineering Design, Belmont, MA), a real time spectrogram sound analysis computer program. The signature whistles of known group members were first studied in the existing Sarasota Bay bottlenose dolphin signature whistle catalog, which contains the predominant whistle produced by each dolphin during temporary capture. This catalog currently contains whistles from 134 animals, many of which have been recorded on multiple occasions.

Whistle Classification

To determine if signature whistles are produced by free-ranging bottlenose dolphins, a conservative tally of signature whistle occurrences was kept as their spectrograms were seen on the computer screen. A signature whistle was defined as a whistle that visually matched the known signature whistle of an animal identified in the group. The remaining whistles were categorized as probable signature whistles, upsweeps, or others. A probable signature whistle was classified in one of two ways. First, it could be a repeated, stereotyped whistle that visually matched the known signature whistle of a catalog animal not positively identified in the group (due to the dynamic nature of dolphin social groups, it was often not possible to identify all group members). Second, a probable signature whistle could be a repeated, stereotyped contour that could be attributed to a group member not in the catalog. For example, if one member of a group had never been recorded during temporary capture, but a repeated, stereotyped whistle was consistently heard when this animal was present, that whistle

would be classified as a probable signature whistle. An upsweep was classified as a whistle consisting of only an increase in frequency over time. Finally, other whistles were defined as those that could not be characterized, often due to poor recording clarity (see Appendix B).

This methodology was not able to account for any possible instances of non-overlapping whistle imitations that may have occurred. In the case of imitations in which two whistles with the same contour overlapped, the first was counted as a signature, probable signature, upsweep, or other whistle (depending on the circumstances), and the second was put in the other category.

Overall percentages of the four whistle categories were calculated. For statistical analyses, signature and probable signature whistles were combined into a grouped signature whistle category, and upsweep and other whistles were combined into a grouped non-signature whistle category. Chi-square tests were used to determine if numbers of overall, signature, or non-signature whistles varied according to activity and group size. Expected distributions were calculated by multiplying the percent time spent in each activity or group size by the total number of whistles, signature whistles, or non-signature whistles. The rationale for this was that if dolphins are whistling equally in all activities and/or group sizes, then numbers of whistles recorded in each activity or group size should closely mirror the amount of time spent recording dolphins in each activity or group size. Average overall whistle rates and average overall whistle rates per dolphin were calculated for each activity to determine if there was an interaction between activity and group size.

Whistle Crystallization

To determine the time of whistle crystallization in the three free-ranging bottlenose dolphin calves that were recorded, identical methods were used. The 1995 videotapes were analyzed first under the assumption that the calves' signature whistles were fully developed at this point (Caldwell and Caldwell 1979). These tapes were analyzed to identify the signature whistle of two of the three focal mothers by comparisons to the whistle catalog; one mother's whistle (FB 39's) was not in the whistle catalog. The whistles recorded in 1995 were then examined to see if there was a second predominant whistle type for each focal mother-calf pair observation; it was then classified as the calf's probable signature whistle. (None of the focal calves had been temporarily captured; therefore, no catalog whistle existed for signature whistle classification.) Signature whistles of FB 39 and her calf were differentiated by analysis of several follows in which the calf came into very close proximity to the hydrophone and whistled loudly.

The 1994 videotapes were then analyzed to determine the approximate age at which whistle crystallization occurred by identifying the first recording of each calf's signature whistle. The recordings made in 1994 were used to describe the acoustic environment of each calf around its time of whistle crystallization. For example, proportions of the total whistles comprised by the mother's signature whistles, other signature whistles, and other whistles were calculated, as were overall whistle rates during each calf's period of signature whistle development. Finally, the social environment of each calf during focal observations was described, with respect to numbers of associates and percent time spent alone with the mother.

RESULTS

Whistle Classification and Distribution

Of the 3208 whistles analyzed, 664 were visually classified as signature whistles; this represents 20.7% of the data. Probable signature whistles accounted for 31.5% (1011), upsweep whistles 19.0% (609), and other whistles 28.8% (924). The average number of whistles per five-minute interval was found to be 1.89 ± 0.10 S.E..

The distribution of total whistles across activities and group sizes differed significantly from expected values based on the percent time spent in each activity or group size category ($\chi^2 = 2960$, $p < 0.001$ for activity; $\chi^2 = 1910$, $p < 0.001$ for group size; Table 1.1). Whistles were much more likely to occur during socializing and much less likely to occur during travelling than expected. In all other activities, observed whistle frequencies corresponded fairly closely to expected values, with the exception that slightly more whistles occurred during milling than expected. With respect to group size, whistles were much more likely to occur in groups of over five animals and were much less likely to occur in groups of two animals than expected (Table 1.1). In groups of three to five animals, observed whistle frequencies corresponded fairly closely to expected values.

The average overall whistle rates ranged from 0.9 whistles per five-minute interval during travelling to 12 whistles per five-minute interval during socializing (Fig. 1.1). Average whistle rates during milling, milling/travelling, feeding, and resting were all approximately two whistles per five-minute interval. Average overall whistle rates per dolphin across activities generally mirrored results for total whistles. Rates ranged from 0.3 whistles per dolphin per five-minute interval during travelling and resting to 1.6

whistles per dolphin per five-minute interval during socializing (Fig. 1.1). Average whistle rates per dolphin during milling, milling/travelling, and feeding were 0.5, 0.8, and 0.5 whistles per dolphin per five-minute interval, respectively.

Numbers of grouped signature (signature and probable signature) whistles and grouped non-signature (upsweep and other) whistles were also highly significantly different than expected based on the percentage of time spent in each activity and group size category (signature: $\chi^2=723$, $p<0.001$ for activity; $\chi^2=1000$, $p<0.001$ for group size; non-signature: $\chi^2=2760$, $p<0.001$ for activity; $\chi^2=914$, $p<0.001$ for group size; Tables 1.2 & 1.3). More signature and non-signature whistles occurred during socializing and fewer occurred during travelling than expected; this finding mirrored the trends of the data set of total whistles (Table 1.1). The slight increase in total whistles that was observed during milling (Table 1.1) was entirely caused by an increase in signature whistles during milling (Table 1.2). During resting, more signature whistles and fewer non-signature whistles occurred than expected. During feeding, fewer signature and more non-signature whistles occurred than expected.

Whistle Development

Percent time spent in each activity and group size category for all three mother-calf pairs is shown in Table 1.4. Data on whistle rates, percent signature whistles, percent non-signature whistles, and percent signature whistles of the mother are summarized in Table 1.5. Numbers of whistles, whistle rates, percent signature whistles, percent non-signature whistles, and percent mother's signature whistles were all calculated after removing the calves' signature whistles from the sample sizes. Data for each mother-calf pair are presented separately below.

FB 39 and Calf

Twelve focal follows of FB 39 and her calf took place between June 1, 1994 and June 29, 1995, totaling 30.8 hours of observations and recordings (370 five-minute intervals). The first stereotyped whistle recorded from FB 39's calf was on August 19, 1994 when it was approximately four months old (birthdate: April, 1994). During 18.0 hours of observations and recordings of FB 39's calf in 1994, 33 whistles were recorded, averaging 0.15 ± 0.13 S.E. whistles per five-minute interval. During 12.8 hours of observations and recordings in 1995, 116 whistles were recorded, averaging 0.75 ± 0.22 S.E. whistles per five-minute interval. Of the total of 149 whistles recorded in 1994 and 1995, 71.8% were signature whistles, and 28.2% were non-signature whistles. Additionally, FB 39's probable signature whistle comprised 3% of the recorded whistles in 1994 (1/32) and 17% in 1995 (10/59). One signature whistle was recorded from FB 39's calf in 1994 and 57 were recorded in 1995. In 1994, FB 39 and her calf spent most of their time travelling, milling, and feeding, and almost all of their time by themselves (90.3%; Table 1.4). FB 39 and her calf were seen with only one associate in 1994. Additionally, FB 39's calf was less than three meters from its mother during 91.3% of five-minute samples in 1994, and 62.8% in 1995. Anecdotal behavioral observations noted that very few sounds were ever produced by FB 39 or her calf—including echolocation and other feeding sounds during obvious periods of feeding. FB 39's calf did not develop a signature whistle similar to that of its mother (Fig. 1.2).

FB 65 and Calf

Twenty-five focal follows of FB 65 and her calf took place between May 31, 1994 and July 6, 1995, totaling 63.25 hours of observations and recordings (759 five-

minute intervals). The first stereotyped whistle recorded from FB 65's calf was on July 18, 1994 when it was approximately three months old (birthdate: April 7, 1994). During 21.3 hours of observations and recordings of FB 65's calf in 1994, 275 whistles were recorded, averaging 1.07 ± 0.18 S.E. whistles per five-minute interval. During 41.9 hours of observations and recordings in 1995, 883 whistles were recorded, averaging 1.76 ± 0.19 S.E. whistles per five-minute interval. Of the total of 1158 whistles recorded in 1994 and 1995, 59.8% were signature whistles, and 40.2% were non-signature whistles.

Additionally, FB 65's signature whistle comprised 3% of the recorded whistles in 1994 (9/262) and 3% in 1995 (24/857). Thirteen signature whistles were recorded from FB 65's calf in 1994 and 26 were recorded in 1995. In 1994, FB 65 and her calf spent over half (50.8%) of their time travelling; additionally, they spent 38.7% of their time by themselves (Table 1.4). FB 65 and her calf were seen with 20 associates in 1994.

Additionally, FB 65's calf was less than three meters from its mother during 91.1% of five-minute samples in 1994, and 67.9% in 1995. FB 65's calf did not develop a signature whistle similar to that of its mother (Fig. 1.2).

FB 59 and Calf

Nine focal follows of FB 59 and her calf took place between June 28, 1994 and July 5, 1995, totaling 30.2 hours of observations and recordings (362 five-minute intervals). The first stereotyped whistle recorded from FB 59's calf was on June 29, 1994 when it was 14 days old (birthdate: June 15, 1994). During 21.3 hours of observations and recordings of FB 59's calf in 1994, 539 whistles were recorded, averaging 2.1 ± 0.19 S.E. whistles per five-minute interval. During 8.8 hours of observations and recordings in 1995, 986 whistles were recorded, averaging 9.3 ± 0.43 S.E. whistles per five-minute

interval. Of the total of 1525 whistles recorded in 1994 and 1995, 40.1% were signature whistles, and 59.9% were non-signature whistles. Additionally, FB 59's signature whistle comprised 3% of the recorded whistles in 1994 (16/537) and 6% in 1995 (55/986). Two signature whistles were recorded from FB 59's calf in 1994 and none were recorded in 1995 (FB 59 and calf were followed only three times in 1995). In 1994, FB 59 and her calf spent most of their time travelling and milling (Table 1.4), and they spent only 17.6% of their time by themselves. FB 59 and her calf were seen with 27 associates in 1994. Additionally, FB 59's calf was less than three meters from its mother during 94.7% of five-minute samples in 1994, and 69.6% in 1995. FB 59's calf did develop a signature whistle similar to that of its mother (Fig. 1.2).

A summary of data pertaining to whistle development in all three calves is provided in Table 1.6.

DISCUSSION

Whistle Classification

These data show that approximately 52% of all whistles produced by free-ranging bottlenose dolphin groups containing mother-calf pairs in Sarasota, Florida are signature or probable signature whistles. Thus, signature whistles clearly are not merely artifacts of stressful circumstances. Signature whistles occurred more often than expected during milling, resting, and socializing, and in groups of over five animals. It is possible that as group spread and group size increase, vocal contact to maintain group cohesion is more necessary. In all of these activities (milling, resting, and socializing), dolphins do not tend to form cohesive groups and are often spread out over a wide area. Signature whistles

occurred less often than expected during travelling and feeding. During travelling, animals tend to stay closer together and surface in consistent directions; therefore, physical and/or visual contact may help animals keep track of one another. Thus, the theory that signature whistles are used as cohesion calls (Janik and Slater 1998) was supported by these data. Additional support came from behavioral notes that indicated that signature whistles were often produced when mother-calf pairs were separated by a distance of over 100 meters, when one of the calves was in close proximity to the boat, or when foreign objects like swimmers were in the area. Subsequent joining of the animals often occurred shortly after the whistle bouts were produced.

Non-signature whistles occurred more often than expected during feeding and socializing. It is possible that non-signature whistles contain information relevant to these two activities; for example, Janik (2000a) found that dolphins produce low frequency brays only while feeding.

The high whistle rates during socializing (averaging 12 whistles per five-minute interval) could have been simply due to the presence of more dolphins. However, when whistle rates per dolphin were calculated, a strong increase during socializing was also found. Thus, although socializing often occurs in groups of over five animals, these findings show that each individual animal in the group is, on average, producing more whistles. Jones and Sayigh (2002) also reported that the average number of whistles per dolphin in Sarasota, Florida was significantly higher while dolphins were socializing than while they were travelling or milling/travelling; thus, the increase seen during socializing was not due entirely to the presence of more dolphins.

The research done by McCowan and Reiss (1995, 2001) concluded that bottlenose dolphins shared certain whistle types, and that the predominant shared whistle type, an upsweep, functioned as a contact call with individually distinct features (2001). McCowan and Reiss (1995, 2001) also concluded that the use of signature whistles by bottlenose dolphins was rare or even non-existent. However, their studies were conducted with dolphins that were housed in the same tank; if signature whistles function as a means of cohesion, they would not be expected to occur in such a context because the animals were never separated from each other by large distances (Janik and Slater 1998; Janik 2000b). The present study supports the idea that upsweeps play an important role in the bottlenose dolphin whistle repertoire, as 19% of all whistles recorded were classified as upsweeps. However, it appears that the recording conditions of the captive dolphins in the McCowan and Reiss studies stimulated upsweep, rather than signature whistle, production; Tyack (1986) reported upsweeps comprising only 6% of the whistle repertoires of two captive dolphins. Free-ranging, undisturbed dolphins produce a combination of signature whistles and upsweeps in their natural repertoire. The present study clearly demonstrates that signature whistles play an important role in the natural communication system of dolphins.

Signature Whistle Development

Focal observations of FB 39, FB 65, FB 59, and their calves show that signature whistle development occurred between less than two weeks and several months of age. These results support the findings of Caldwell and Caldwell (1979) and Sayigh (1992). However, it is difficult to pinpoint the exact time of whistle crystallization since no unstereotyped whistles were attributed to any of the calves.

FB 39 and her calf spent the majority of their time alone (90%), while FB 59 and her calf spent only 18% of their time alone. Although it was expected that FB 39's calf might develop a whistle similar to that of its mother, given that they rarely associated with other individuals, this did not occur. FB 39's calf's signature whistle was not obviously similar to that of the one associate with which FB 39 and her calf were observed in 1994. FB 39's calf developed its whistle over the course of a maximum of four months, while FB 59's calf developed its whistle over the course of several days. It is possible that the amount of time spent in larger groups necessitated the earlier signature whistle development for FB 59's calf; it is harder for a mother to keep track of her calf when many animals are present. Additionally, during the first few months of life overall whistle rates 14 times higher were recorded during follows of FB 59's calf than during follows of FB 39's calf. This could have also influenced the rapid signature whistle development of FB 59's calf. Perhaps exposure to large numbers of whistles stimulates and/or necessitates rapid whistle development. Large groups and high whistle rates could have also influenced FB 59's calf's development of a signature whistle similar to that of its mother, if this similarity might facilitate mother-calf recognition. Captive dolphins have been shown to mimic each other's signature whistles (Tyack 1986) possibly as a means of identifying group members.

FB 65's calf developed its signature whistle over the course of a maximum of three months, and its observed social and auditory environment was intermediate between those of FB 39's and FB 59's calves'. FB 65 and her calf spent less than half of their time alone (38.7%), and the calf was exposed to recorded whistle rates comparable to those of FB 59's calf. These results suggest that similar vocal environments do not necessitate

similar vocal development; both Caldwell and Caldwell (1979) and Sayigh (1992) had similar findings. For example, Sayigh (1992) reported that although two calves both exhibited early whistle development, one had few associates besides its mother while the other had many.

Like FB 39's calf, the signature whistle of FB 65's calf did not obviously resemble that of any of its observed associates. However, these observations represent only a brief snapshot of the developmental period. Thus, it is likely that the calves of FB 39 and FB 65 did learn their whistles from associates other than their mothers. Captive bottlenose dolphin calves have been shown to develop signature whistles similar to whistles present in their acoustic environment (Tyack and Sayigh 1997; Tyack et al. unpublished data; Miksis et al. unpublished data).

Previous studies have found that calves were exposed to proportionately more of their mothers' whistles during their first year of life (Caldwell and Caldwell 1979; Sayigh 1992); however, in this study the proportion of each mother's signature whistles either increased from the calf's first year of life to its second or remained relatively constant. (Only about 3% of the whistles recorded during each calf's first year of life were those of its mother.) These results lend further support to the theory of signature whistles functioning as cohesion calls (Smolker et al. 1993; Janik and Slater 1998), given that bottlenose dolphin calves venture farther away from their mothers with increasing age (Mann and Smuts 1999). All of the calves in this study spent over 90% of their time less than three meters from their mothers during their first year of life and 62-70% during their second year of life. Additional support for this idea comes from the fact that more

signature whistles were recorded from two of the three calves during their second year of life than their first.

This study demonstrates that signature whistle development in free-ranging bottlenose dolphins is both a complex and difficult process to observe and to explain. Further studies are needed that use localization techniques to positively identify the vocalizing animals and to determine how signature and non-signature whistles are used. Further studies are also needed that increase the amount of time spent observing and recording calves during the critical developmental period in order to elucidate factors that affect the timing and outcome of whistle development. Overall, this study has shown that signature whistles make up over half of the whistle repertoire of free-ranging bottlenose dolphins, and that signature whistle development in these animals is a complex and variable process.

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Activity or Group Size	Number of 5-min. Intervals	Percent Time	Observed Whistles	Expected Whistles
Mill	504	29.73	1100	954
Travel	704	41.53	666	1332
Mill/Travel	166	9.79	310	314
Feed	183	10.80	360	346
Rest	86	5.07	165	163
Social	52	3.07	607	99
2 animals	782	46.14	418	1480
3-5 animals	473	27.90	981	895
Over 5 animals	440	25.96	1809	833

Table 1.1 Observed and expected total whistles based on activity and group size. Expected whistles were calculated by multiplying the total number of whistles by the percent time in each activity or group size, respectively. (n=3208, $\chi^2=2660$, p<0.001; $\chi^2=1910$, p<0.001)

Activity or Group Size	Number of 5-min. Intervals	Percent Time	Observed Whistles	Expected Whistles
Mill	504	29.73	621	498
Travel	704	41.53	394	696
Mill/Travel	166	9.79	178	164
Feed	183	10.80	142	181
Rest	86	5.07	124	85
Social	52	3.07	216	51
2 animals	782	46.14	226	773
3-5 animals	473	27.90	498	467
Over 5 animals	440	25.96	951	435

Table 1.2 Observed and expected signature whistles based on activity and group size. Expected whistles were calculated by multiplying the total number of signature whistles by the percent time in each activity or group size, respectively. (n=1675, $\chi^2=723$, $p<0.001$; $\chi^2=1000$, $p<0.001$)

Activity or Group Size	Number of 5-min. Intervals	Percent Time	Observed Whistles	Expected Whistles
Mill	504	29.73	479	456
Travel	704	41.53	272	637
Mill/Travel	166	9.79	132	150
Feed	183	10.80	218	165
Rest	86	5.07	41	78
Social	52	3.07	391	47
2 animals	782	46.14	192	707
3-5 animals	473	27.90	483	428
Over 5 animals	440	25.96	858	398

Table 1.3 Observed and expected non-signature whistles based on activity and group size. Expected whistles were calculated by multiplying the total number of non-signature whistles by the percent time in each activity or group size, respectively. (n=1533, $\chi^2=2760$, $p<0.001$; $\chi^2=914$, $p<0.001$)

Focal Calf	Year	Number of 5-min. Intervals	Mill	Travel	Mill/ Travel	Feed	Rest	Social	2	3-5	Over 5
39	94	216	26.4	29.6	14.8	25.0	3.7	0.5	90.3	9.3	0.5
	95	154	45.5	17.5	14.3	22.1	0.6	0	92.2	7.8	0
	Total	370	34.3	24.6	14.6	23.8	2.4	0.3	91.1	8.6	0.3
65	94	256	29.3	50.8	10.2	9.0	0.4	0.4	38.7	39.1	22.3
	95	503	27.0	49.3	8.0	6.0	6.6	3.2	54.5	15.7	29.8
	Total	759	27.8	49.8	8.7	7.0	4.5	2.2	49.1	23.6	27.3
59	94	256	35.9	39.8	13.3	7.0	2.3	1.6	17.6	42.6	39.8
	95	106	19.8	26.4	2.8	10.4	10.4	30.2	0.9	17.0	82.1
	Total	362	31.2	35.9	10.2	8.0	4.7	9.9	12.7	35.1	52.2

Table 1.4 Percent time spent in each activity and group size by each of the focal calves of FB 39, FB 65, and FB 59.

Focal Calf	Year	Number of 5-min. Intervals	Number of Whistles (excluding calf)	Whistle Rates (whistles/5-min. interval)	Percent Signature Whistles	Percent Non-signature Whistles	Percent Mother's Signature Whistle
39	94	216	32	0.1	28.1	71.9	3.1
	95	154	59	0.4	67.8	32.2	16.9
	Total	370	91	0.2	53.8	46.2	12.1
65	94	256	262	1.0	65.3	34.7	3.4
	95	503	857	1.7	56.2	43.8	2.8
	Total	759	1119	1.5	58.4	41.6	2.9
59	94	256	537	2.1	39.5	60.5	3.0
	95	106	986	9.3	40.3	59.7	5.6
	Total	362	1523	4.2	40.0	60.0	4.7

Table 1.5 Recorded whistle environment for each of the focal calves of FB 39, FB 65, and FB 59. Numbers of whistles, whistle rates, percent signature whistles, percent non-signature whistles, and percent mother's signature whistle were all calculated after removing the calves' signature whistles from the sample sizes.

Focal Calf	Number of Hours Observed	Max. Time of Whistle Development	Percent Time Spent Alone (1994)	Average Whistles/Minute (1994)	Total Whistles (% Mother's) (1994)	Number of Associates (1994)	Calf Similar to Mother?
39	30.8	4 months	90.3	0.15	32 (3.1)	1	No
65	63.25	3 months	38.7	1.07	262 (3.4)	20	No
59	30.2	2 weeks	17.6	2.1	537 (3.0)	27	Yes

Table 1.6 Overall summary of whistle development for each of the focal calves of FB 39, FB 65, and FB 59.

Figure 1.1 Average whistles per five-minute interval and average whistles per dolphin per five-minute interval versus activity.

AVERAGE WHISTLES/5-MIN. INTERVAL AND AVERAGE WHISTLES/DOLPHIN/5-MIN. INTERVAL VS ACTIVITY

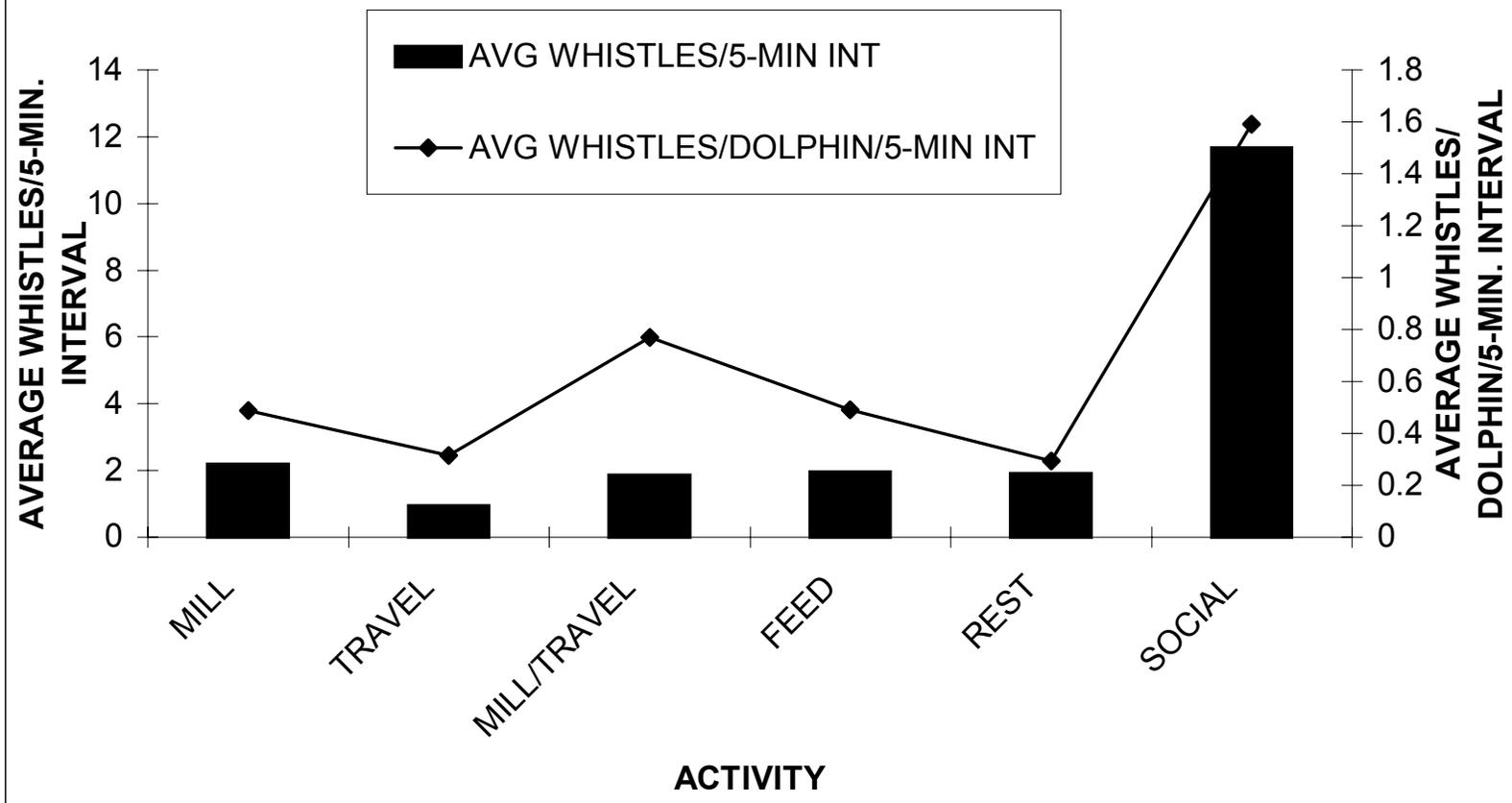
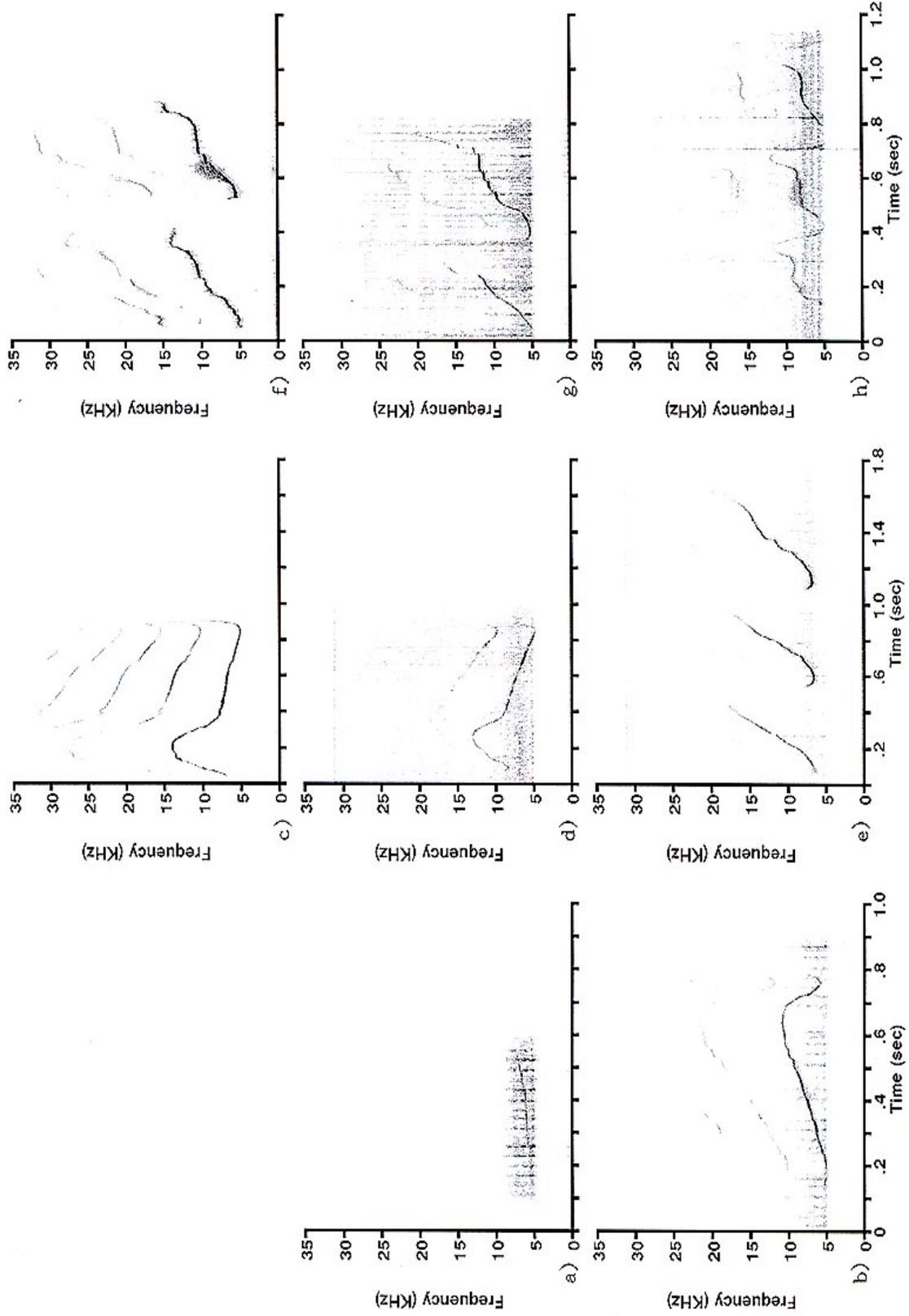


Figure 1.2 Signature whistles of focal mother-calf pairs. a) FB 39's whistle during a focal follow, b) FB 39's calf's whistle during a focal follow, c) FB 65's whistle during capture, d) FB 65's whistle during a focal follow, e) FB 65's calf's whistle during a focal follow, f) FB 59's whistle during capture, g) FB 59's whistle during a focal follow, h) FB 59's calf's whistle during a focal follow. Spectrograms were made using Signal/RTSD Version 3.0, with a sample rate of 80 kHz, a 512 point FFT, and a Hanning window.



APPENDIX

Appendix A. Activities assigned to focal mother-calf pairs and their groups (Sayigh 1992).

Milling—non-directional movement; frequent changes in direction

Travelling—directed movement in one direction; not necessarily in a straight line

Milling/Travelling—combined milling and travelling

Feeding—obvious evidence of feeding; e.g., fish in mouth, diving birds, etc.; this study also included probable feeding; e.g., lunging

Resting—quiescent, slow movements with no indication of other activities

Socializing—active interactions with one or more other dolphins

Appendix B. Definitions of whistle types for focal mother-calf pairs and their groups.

Signature—whistle visually matches known signature whistle of animal identified in the group

Probable Signature—stereotyped, repeated contour that visually matches signature whistle of catalog animal not known to be in group OR stereotyped, repeated contour that can be attributed to group member, but not in catalog

Upsweep—whistle consists of only an increase in frequency over time and no distinctiveness

Other—whistle cannot be characterized; shows no distinctiveness, often due to poor recording clarity

Grouped Signature—combination of signature and probable signature whistles

Grouped Non-signature—combination of upsweep and other whistles

CHAPTER 2: PLAYBACKS OF WHISTLES OF VARYING LOOP NUMBER AND
CONTOUR

INTRODUCTION

Bottlenose dolphins have an impressive ability to both produce and perceive an array of signals including echolocation, burst pulse sounds, and whistles. In a behavioral study of free-ranging bottlenose dolphins in Sarasota, Florida, Hill (Chapter 1) reported that approximately 52% of all whistles produced were signature whistles. Many bottlenose dolphin signature whistles have a multi-looped structure (72.8% in Sarasota, FL; Sayigh 1992), in which there may be an introductory loop, a terminal loop, and varying numbers of central loops (Fig. 2.1). Most researchers classify multi-looped whistles as the same whistle regardless of the number of loops (i.e., Tyack 1986; Sayigh 1992; Janik et al. 1994). However, other researchers (i.e., McCowan and Reiss 1995) treat any loop that is disconnected from the other(s) as a separate whistle for classification purposes. Using this method, the spectrograms in Figure 2.1 would consist of two whistles, one whistle, and two whistles (top to bottom). This adds another problem in that a lot of recording equipment loses sensitivity at higher frequencies; it is therefore possible that some loops may appear disconnected even if they are not. It is currently not known how dolphins perceive multiple loops in whistles.

Several researchers have reported the common occurrence of upsweep whistles in the vocal repertoire of bottlenose dolphins (Tyack 1986; McCowan and Reiss 1995, 2001; Janik unpublished data). McCowan and Reiss (1995, 2001) reported upsweeps to be the predominant shared call in captive dolphins, while Hill (Chapter 1) found them to compose 19% of all whistles produced by free-ranging bottlenose dolphins. Clearly, upsweeps are another important and common whistle type. They are composed of an increase in frequency over time, and are classified into a single whistle category by most

researchers. However, it is unknown how variations in upsweep parameters are perceived by dolphins; therefore, it is also unknown whether or not these whistles are correctly or incorrectly classified into the same category.

The best way to resolve the issue of how to classify multi-looped whistles or upsweeps would be to test how they are perceived by the dolphins themselves. However, very little work has been done on whistle perception in bottlenose dolphins. The only work that has examined dolphins' responses to playbacks of whistles has focused on the dolphins' abilities to discriminate among a variety of exemplars of signature whistles of several individuals (Caldwell et al. 1969, 1972; Sayigh et al. 1999; Harley unpublished data).

The goal of this study was to examine how dolphins perceive whistles with varying loop numbers or frequency contours by means of playback experiments. Synthetic whistles were used in order to control for all variables except the ones being tested and because they were unfamiliar to the target animals. Three specific questions were examined during the playback sessions:

- 1) Is the number of loops in a multi-looped whistle a behaviorally significant cue? Synthetic whistle sequences contained the same overall numbers of loops, but the loops were divided into different whistle segments. For example, one sequence consisted of repetitions of one four-looped whistle and the other consisted of repetitions of four one-looped whistles. All other loop parameters, including duration, frequency range, and amplitude were held constant. Three different contours were tested—a sine wave, a cosine wave, and an upsweep—and each consisted of one, two, three, or four loops for a total of twelve different whistles (see Methods).

2) Is whistle contour a behaviorally significant cue? Synthetic whistle sequences contained whistles of slightly differing contours while other whistle features (including numbers of loops, duration, frequency range, and amplitude) were held constant. Four different contour pairs were tested—sine/flat sine, cosine/flat cosine, upswEEP/s-shaped upswEEP, upswEEP/hooked upswEEP—for a total of seven different whistles (see Methods).

3) Do synthetic whistles evoke a lesser response than natural whistles of familiar or non-familiar individuals? Analyses of playbacks utilizing synthetic whistles in 2000 yielded overall low levels of response, which prompted the design of experiments to address this question. A sequence of synthetic double upswEeps was followed by a sequence of natural whistles from either familiar Sarasota, Florida animals or non-familiar Wilmington, North Carolina animals (see Methods).

METHODS

Sarasota Population

Playback experiments were conducted with bottlenose dolphins during temporary capture-release sessions in Sarasota, Florida in June 2000 and 2001. These captures occur annually in Sarasota in order to study many aspects of dolphin biology (Wells 1991). The objective of the playback experiments was to determine whether dolphins' behavioral responses systematically varied with the presence of whistles containing different acoustic features.

Dolphins were caught using a 300m X 4m seine net that was circled around the dolphins, creating a corral (Wells 1991). Target animals were positioned in shallow waters (less than two meters) at a 90° angle to the playback speaker. The animal was

loosely restrained by human volunteers during the entire experiment. Tape measures were held in the air in a grid over the target animal to help measure head turns toward or away from the speaker (Sayigh et al. 1999; Fig. 2.2).

The playback apparatus consisted of a Lubel underwater speaker, a Radio Shack car stereo amplifier, and a Panasonic AG 6400 hi-fi VCR, with a system frequency response from approximately 20 Hz to 20 kHz. Amplifier gain was adjusted so that all stimuli were presented to the target animals at amplitudes similar to those of natural whistles heard from identical distances. The target animal's responses were videotaped with a Panasonic 5100 HS super-VHS or a Sony Digital 8 Handycam camera for later analysis, and the target animal's vocalizations were recorded using a Panasonic AG 7400 hi-fi VCR and a suction cup hydrophone placed on the melon of the dolphin (Tyack 1985).

Measures of Response

Head turns directed toward the playback speaker were scored as a measure of response to the synthetic and natural stimuli. Head turns toward the speaker likely represent the target animal's efforts to locate the source of the stimulus visually and/or by means of echolocation (Sayigh et al. 1999). Since echolocation is highly directional, a dolphin must be oriented toward an object in order to effectively "visualize" it (Au 1993). All head turns greater than 20° were scored and counted from the videotapes. Any head turns less than 20° were not scored, as anything less than 20° was considered to be within the normal range of movement of the animal (Sayigh et al. 1999). Head turns away from the speaker were also scored as a measure of increased level of arousal, as were overall head turns.

All playbacks were scored for head turns (both toward and away from the speaker) twice by the author, and the results were highly consistent. In addition, eleven playbacks (25%) were scored for head turns by Nikki Vollmer (an undergraduate research assistant). Vollmer was unfamiliar with both the playback stimuli and which stimuli were predicted to evoke a stronger response. The number of head turns scored by both Vollmer and the author were compared for each playback. Vollmer consistently scored more turns both toward and away from the speaker, but 68% of compared scores differed by five or fewer counts across an entire playback experiment. Therefore, for consistency only the scores of the author were used in analysis.

In order to evaluate potential acoustic responses to the playbacks, audio recordings of all playback experiments were analyzed using RTSD, a real-time spectrogram program (Engineering Design Belmont, MA). Duration of echolocation bouts was approximated to the nearest second, and all whistles produced were classified as either the animal's signature whistle or as non-signature whistles. For all animals, the signature whistle was classified as the predominant whistle produced. For most of the target animals (33 out of 45), the signature whistle was established by evaluating recordings made during earlier capture sessions. For the remaining 12, the signature whistle was established by evaluating recordings made immediately prior to the playback experiment. Non-signature whistles were those that could not be classified as the target animal's signature whistle. Whistles were classified as a response to the playback stimulus if they occurred during a stimulus or within one second thereafter.

Playback Protocol

In each experiment two different whistle sequences were played back in adjacent time blocks, following the protocol used by Sayigh et al. (1999). Response rates to the different whistle sequences were then compared using Wilcoxon signed-rank tests and analyses of variance. Wilcoxon tests compared response rates of the same individual to two different whistle sequences, thus accounting for the large amount of individual variability in response rates. ANOVAs were used to compare response rates per minute to all of the stimuli, averaged across all target animals.

Additionally, a modified habituation-dishabituation protocol was used. In a generic habituation-dishabituation design, the first stimulus is systematically presented to the target animal until habituation occurs (Hauser 1997). Habituation is measured by a decrease in response eventually leading to low or no response. A single example of the second stimulus is then presented to the target animal. If an increase in response is observed, it can be concluded that dishabituation occurred and that the two stimuli were perceived as different. If no increase in response is observed, it can be concluded that the two stimuli were perceived as similar. In the present experiments, response rates per minute were compared across the first two-minute playback presentation to look for evidence of habituation. Rates for the last minute of the first stimulus were also compared to the rates for the first minute of the second stimulus to look for evidence of dishabituation. After no evidence of habituation in June 2000, the duration of the first stimulus presentation was increased to four minutes in 2001 to enhance the likelihood of habituation.

Playbacks were conducted as follows: 1) a 120-s pre-trial period to allow the target animal to adjust to the experimental set-up; 2) a 120-s (2000) or 240-s (2001) playback consisting of the first stimulus; and 3) a 120-s playback consisting of the second stimulus. Total experimental time was either six (2000) or eight (2001) minutes. Playback sequences consisted of the same contour with varying numbers of loops (total numbers of loops in both sequences were constant; 2000), varying contours with the same number of loops (2001), or synthetic upsweeps followed by natural whistles (2001). To avoid pseudoreplication (an inappropriate replication of playback stimuli in an experiment), sine waves, cosine waves, upsweeps, and several natural whistles were used as stimuli (Catchpole 1989; McGregor et al. 1992). Presentation orders of synthetic playback sequences were varied to avoid the effect of surprise (the tendency of a target animal to respond more strongly to the first stimulus) biasing the results.

Stimuli Synthesis

Synthetic stimuli were created using the software package Signal (Engineering Design Belmont, MA). All synthetic stimuli had a low frequency of 2 kHz and a high frequency of 12 kHz. The overall contours of synthetic stimuli were influenced by naturally occurring whistle contours; characteristics of natural whistles such as duration, repetition rate, and frequency content were replicated in designing these stimuli. For the experiments examining responses to numbers of loops in multi-looped whistles, synthetic stimuli included one, two, three, and four loops of three basic contours (sine, cosine, and up-sweep). For the experiments examining responses to contour variability, each basic contour was modified to yield changed contours: sine waves (Fig. 2.3a) were modified to flat sine waves (Fig. 2.3b), cosine waves (Fig. 2.3c) were modified to flat cosine waves

(Fig. 2.3d), and upsweeps (Fig. 2.3e) were modified to both s-shaped upsweeps (Fig. 2.3f) and hooked upsweeps (Fig. 2.3g).

In addition to synthetic whistles, natural whistles were also used in playback experiments conducted in June 2001. The durations and frequencies of these whistles were not manipulated for the playback experiments; exemplars used had high signal-to-noise ratios. Natural whistles consisted of two known whistles from the Sarasota bottlenose dolphin population, FB 90 (Fig. 2.3h) and FB 35 (Fig. 2.3i), and two whistles unknown to Sarasota animals from the Wilmington, NC, bottlenose dolphin population, FB 727 (Fig. 2.3j) and FB 706 (Fig. 2.3k).

Watch Sample Playback Experiment

RESULTS

Sample Size

A total of 24 playback experiments was performed in 2000; four playbacks were not included in the data set due to faulty acoustic recordings. The remaining 20 playbacks were analyzed for all response variables. A total of 25 playback experiments was performed in 2001; two playbacks were not analyzed for head turns due to poor video quality, but all remaining response variables were analyzed.

Response to Stimulus Presentation

In order to determine if numbers of whistle loops or changes in whistle contours caused differential response rates, these rates were compared between the two two-minute response periods using Wilcoxon signed-rank tests. Comparisons of all measured response rates to whistles of more loops and whistles of fewer loops yielded no significant differences ($p > 0.05$). Comparisons of all measured response rates to whistles of basic contours and whistles of changed contours yielded no significant differences,

with the exception of head turns away from the speaker ($p=0.031$; $p>0.05$ for remaining response rates). The rate of head turns away from the speaker was significantly higher during unchanged contours than during changed contours.

Overall responses to synthetic stimuli were low. Sayigh et al. (1999) reported head turns toward the speaker at a mean rate of 3.1/minute in response to natural whistles of familiar individuals; this is significantly higher than the mean rate of 1.7/minute in response to synthetic stimuli that was observed in this study ($F=22.2701$; $p<0.0001$). Because of these low response rates, a comparison was made between synthetic stimuli and natural whistles. Although most response rates to synthetic upsweeps and natural whistles did not differ significantly, whistle response rates were significantly higher (and overall head turns rates were significantly lower) to known whistle stimuli than to synthetic upsweeps ($p=0.031$ for both). Analyses of variance (ANOVAs) were used to compare response rates per minute for upsweeps, modified upsweeps (s-shaped and hooked upsweeps), waves (sine and cosine waves), modified waves (flat sine and flat cosine waves), known natural whistles, and unknown natural whistles. In terms of head turns toward the speaker, modified upsweeps had significantly higher response rates than either upsweeps or waves ($p=0.0082$). In terms of both head turns away from the speaker and overall head turns, modified upsweeps had significantly higher response rates than either waves or modified waves ($p=0.0025$, $p=0.0011$).

Habituation-Dishabituation Protocol

To look for evidence of habituation, the first minute of the first stimulus was compared to the last minute of the first stimulus for all response measures. No significant decline in any of the response rates occurred for either the two- or four-minute presentations of the first stimuli ($p>0.05$ for all). To look for evidence of dishabituation,

the last minute of the first stimulus was compared to the first minute of the second stimulus. No significant increase in any of the response rates occurred for any of the playbacks ($p > 0.05$ for all). Evidence for habituation/dishabituation was also looked for in the experiments that yielded the strongest differential response in the two-minute comparisons. These were synthetic upsweeps versus known natural whistles (which showed significant differences in whistle responses and overall head turns). No significant difference was found in comparisons of the first fifteen seconds of the first stimulus and the last fifteen seconds of the first stimulus ($p = 0.375$ for whistles; $p = 0.125$ for overall head turns).

DISCUSSION

During playback experiments, temporarily captured dolphins did not generally differ in their responses to synthetic whistles with differing numbers of loops or with slightly varied contours. There are at least four possible explanations for these results. First, the measurements of responses might not have been sensitive enough to detect actual differences shown by the animals. However, Sayigh et al. (1999) used the same experimental protocol and found that head turns toward the speaker were robust in detecting responses. Second, the animals might have detected a difference between the stimuli, but each stimulus elicited the same response, or third, the animals might have detected no difference between the stimuli (McGregor 2000). Finally, the animals might not have perceived the stimuli as important sounds, and thus did not respond. This last explanation is likely given the overall low levels of response to synthetic playback

stimuli. Rates of head turns toward the speaker were significantly lower than the average rate reported by Sayigh et al. (1999) in response to natural stimuli.

Pseudoreplication, as defined by McGregor et al. (1992), is “the use of an n (sample size) in a statistical test that is not appropriate to the hypothesis being tested”. Thus, it would be inappropriate to use only a single exemplar to represent a class of stimuli, and to then analyze the results as if multiple replicates were performed (Catchpole 1989; McGregor et al. 1992). The issue of pseudoreplication was addressed in these experiments by using several different exemplars for each whistle parameter being tested. For example, to examine how dolphins responded to differing numbers of loops in multi-looped whistles, exemplars of sine waves, cosine waves, and upsweeps were used; additionally, each of these contours consisted of one, two, three, or four loops. Therefore, 12 different exemplars were used to examine this question. Multiple exemplars were also used to examine each of the two additional questions posed in this study.

No habituation occurred during either two- or four-minute presentations of synthetic whistles of varying contours. It is possible that the time periods were too short for habituation to occur; Janik and Rey (in press) reported similar findings. It is also possible that overall levels of response were too low, i.e., synthetic whistles do not elicit a sufficient response. Thus, it is not possible to draw conclusions about how dolphins may or may not perceive differences in loop number or whistle contours from these experiments.

Whistle response rates were significantly higher to known natural whistles than to synthetic upsweeps, although overall head turn rates were significantly lower. Since signature whistles are known to be used as contact calls, it may be that the target animals

were attempting to establish contact with the individuals whose whistles were being played back. Dolphins may only be motivated to whistle to known individuals. The fact that the only experiments that showed a significant difference in whistle responses involved known, natural whistles versus synthetic upsweeps suggests that natural whistles may convey information not adequately conveyed by synthetic whistles.

However, the fact that overall head turn rates were lower to natural whistles than synthetic upsweeps seems to contradict this finding. Similarly, the greater amount of head turns away from the speaker to unchanged versus changed contours is also difficult to explain. It is not clear if head turns away from the speaker are a useful response category, given that no significant differences were found in this category by Sayigh et al. (1999). Head turns away from the speaker may result from the animal orienting toward people, boats, or even other dolphins that might have been in the area, and thus may be unrelated to the playback stimuli.

For the ANOVA results comparing response rates per minute, modified upsweeps showed higher rates of head turns toward the speaker than either synthetic upsweeps or waves. These results suggest that modified upsweeps may contain certain whistle features that are more salient to bottlenose dolphins than the features contained in other types of synthetic whistles. Thus, variations in up-sweep contours may be important to dolphins, and it may be appropriate to subdivide this category of whistles. However, additional experiments are needed to test this idea. For example, future playback experiments could examine additional types of contour changes in upsweeps in order to identify specific whistle features that may cause increased response rates. In addition, future playbacks could evaluate the importance of loop numbers or contour variations by examining

responses to natural, rather than synthetic, whistles with varying numbers of loops and with varying contours or durations. Experiments could include longer trial periods or flexible trial periods in order to maximize the likelihood of habituation.

Another way of approaching these questions could involve training captive dolphins to respond to various whistles using “same-different” operant conditioning; dolphins would be trained to recognize very different whistle contours as different whistles and identical whistles as same whistles. Then novel whistles of varying loop numbers, contours, or durations would be introduced to the repertoire for the dolphin to categorize as either “same” whistles or “different” whistles. These techniques would provide information as to how the dolphins themselves identify and classify whistles, and as to which parts of the whistles are most salient to the animals. Clearly, understanding whistle perception is critical to understanding how whistles function in the natural communication system of bottlenose dolphins.

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Figure 2.1 Signature whistle of FB 163 with varying numbers of central loops. a) one, b) two, and c) three central loops. Spectrograms were made using Signal/RTSD Version 3.0, with a sample rate of 80 kHz, a 512 point FFT, and a Hanning window.

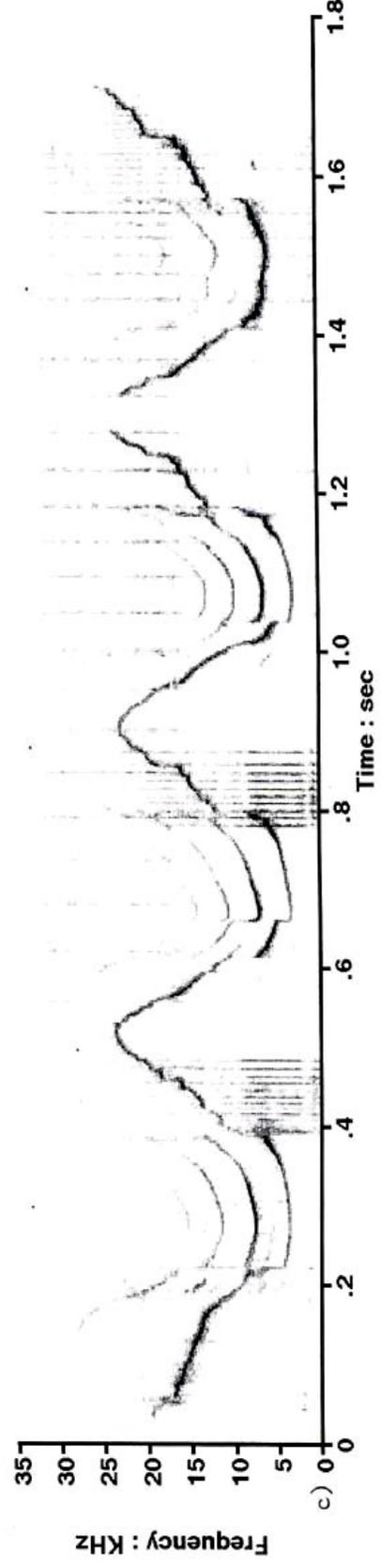
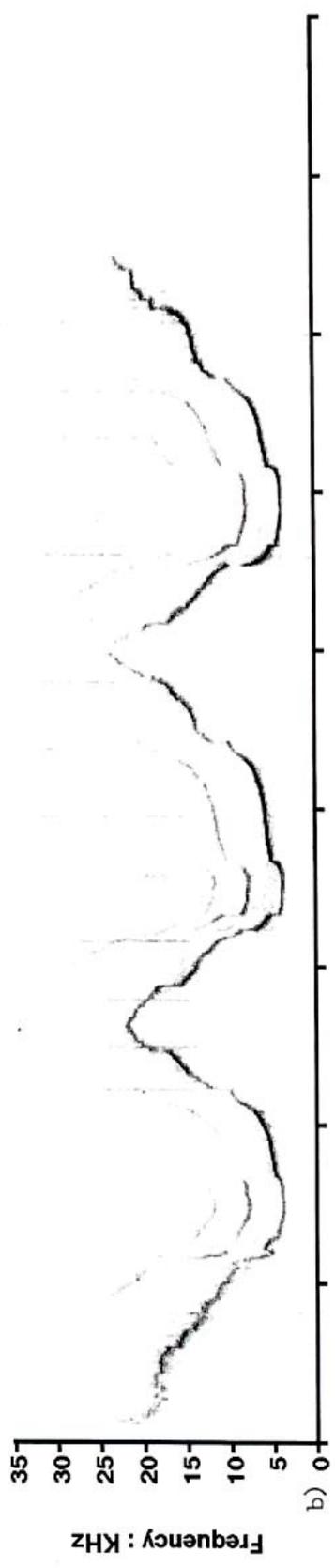
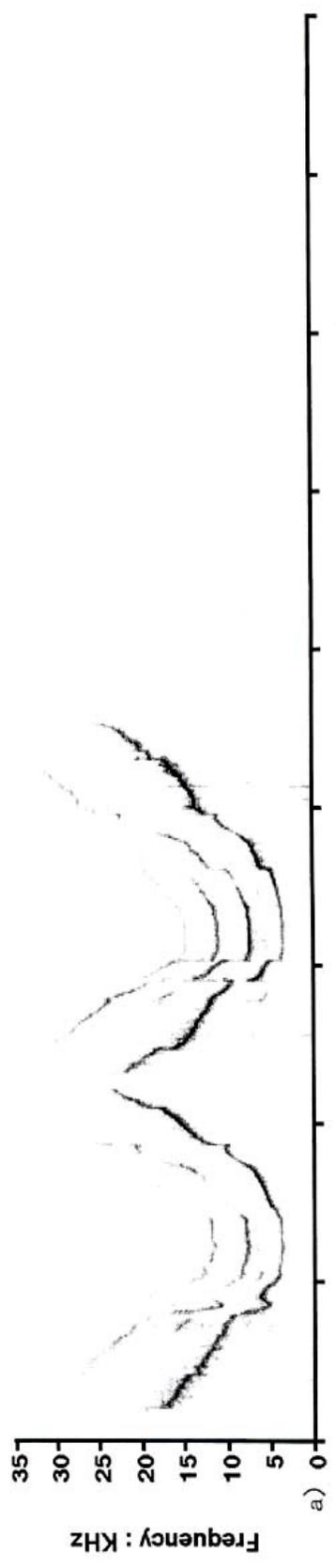


Figure 2.2 Schematic drawing of playback experiment layout (from Sayigh et al. 1999, © Association for the Study of Animal Behaviour).

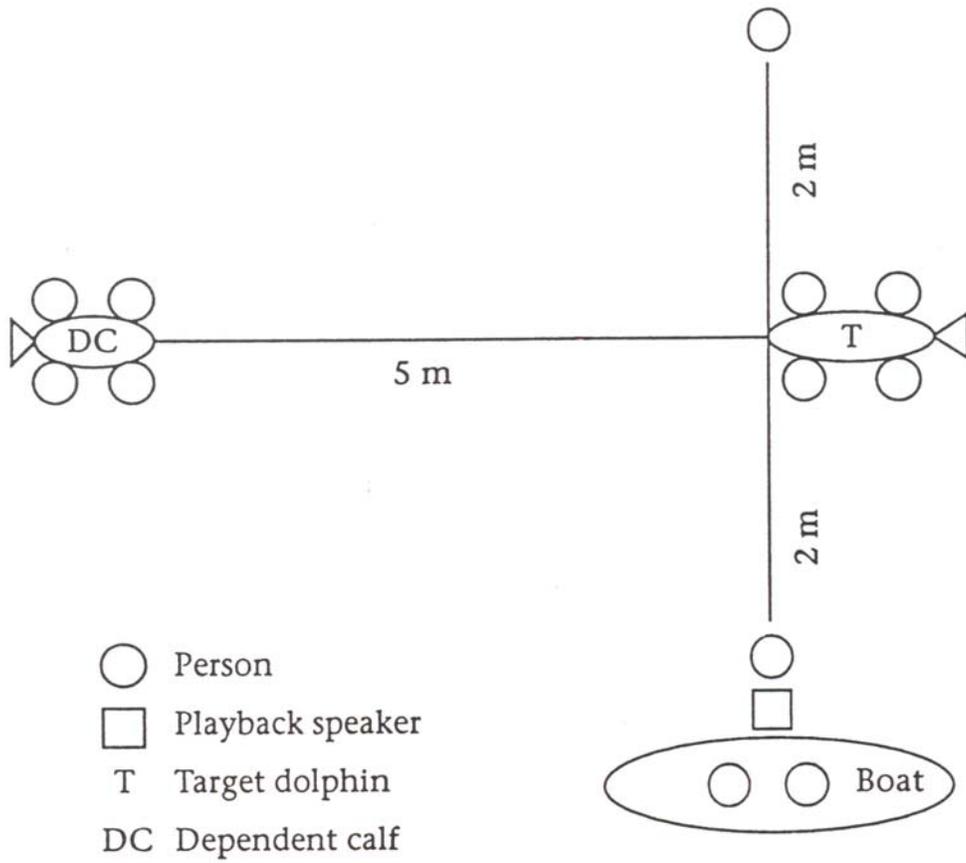


Figure 2.3 Stimuli used during playbacks to temporarily captured bottlenose dolphins. a) sine wave, b) flat sine wave, c) cosine wave, d) flat cosine wave, e) upsweep, f) s-shaped upsweep, g) hooked upsweep, h) FB 90, i) FB 35, j) FB 727, and k) FB 706. Spectrograms were made using Signal/RTSD Version 3.0, with a sample rate of 80 kHz, a 512 point FFT, and a Hanning window.

