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DEVELOPMENT AND SOCIAL FUNCTIONS OF SIGNATURE WHISTLES IN BOTTLENOSE DOLPHINS *TURSIOPS TRUNCATUS*

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ABSTRACT

Bottlenose dolphins *Tursiops truncatus* produce individually distinctive signature whistles. Dolphins recognize the signature whistles of animals with which they share a social bond. Signature whistles develop within the first few months of life and are stable for a lifetime. Vocal learning appears to play a role in the development of signature whistles in bottlenose dolphins. The signature whistles of most female dolphins and about half of male dolphins differ from those of their mothers. Some dolphin calves born in captivity develop a signature whistle that matches either man-made whistles or those of an unrelated dolphin. Dolphins retain the ability as adults to imitate the whistles of animals with which they share strong individual-specific social relationships, bonds which may change throughout their lifetime. The exceptional imitative abilities of dolphin infants and the retention of this ability in adults may be related to the maintenance of changing individual-specific social relationships. Individual recognition by the voice may differ in marine vs terrestrial mammals. Diving marine mammals may not be able to rely upon involuntary voice cues for individual recognition, but rather may require vocal learning to maintain a stable signature as their vocal tract changes shape with increasing pressure during a dive.

Key words: bottlenose dolphins, *Tursiops truncatus*, vocal development, vocal learning, signature whistle.

INTRODUCTION

The remarkable abilities of marine mammals to imitate man-made sounds stand in marked contrast to the very weak evidence that auditory input modifies vocal output in non-human terrestrial mammals. Evidence for vocal learning in marine mammals spans taxa from seals (Ralls et al. 1985), to dolphins (Evans 1967, Richards et al. 1984, Sigurdson 1993), to beluga whales (Ridgway et al. 1985, Eaton 1979) and humpback whales (Payne and Payne 1985). Bottlenose dolphins show particularly exceptional skills of vocal imitation. Adult dolphins can imitate synthetic whistle sounds spontaneously within a few seconds after the first exposure (Herman 1980), or after only a few exposures (Reiss and McCowan 1993), and have also repeatedly been trained to imitate synthetic whistle sounds (Evans 1967, Richards et al. 1984, Sigurdson 1993). Not only is there little comparable evidence for imitation in terrestrial non-human mammals, but even such drastic treatments as deafening at birth or raising in isolation do not prevent vocalizations from developing normally (Buchwald and Shipley 1985, Winter et al. 1973).

Since vocal learning plays such an important role in the development of human communication, there has been a strong focus on comparative research on vocal learning. Decades of research on non-human primates have yielded little evidence of vocal learning, and songbirds have proven better subjects for research on vocal learning (Nottebohm 1991). Yet there remains a gap in studies of vocal development in the one mammalian group with strong evidence for vocal learning: marine mammals.[1] Why have there been so few studies of vocal development in marine mammals? Studying development requires either longitudinal studies of individual animals as they age or cross-sectional studies of animals of known ages. Studying the social functions of communication signals is more effective in the context of a long term study of identified individual animals. We are not yet able to conduct these kinds of studies for most cetacean species because we cannot count on being able to determine the age and sex of individuals and reliably continue to resight them for months or years. I will focus here on the bottlenose dolphin *Tursiops truncatus* because it breeds well in captivity, where individuals can be followed in great detail. Long-term studies of this species in the wild also allow longitudinal studies of mothers and calves in the environment in which dolphin communication evolved. The dolphin vocal repertoire includes a variety of pulsed and tonal sounds, but most research on vocal development focuses upon frequency modulated whistle sounds. While the sample sizes of studies of vocal development in dolphins to date are limited, I hope to illustrate the diversity of promising methods to study vocal development in these animals. I will focus on two main questions in this review: What is the role of vocal learning in the development of dolphin whistles? What are the functions of whistle imitations among dolphins?

Research on dolphin whistles divides into two different approaches. One approach assumes that dolphins share a species-specific repertoire of whistles, each of which is produced by each individual in a particular behavioral context. This was the dominant approach of researchers before 1965 (e.g. Dreher and Evans 1964, Lilly 1963). For example, Lilly (1963) suggested that dolphins produce a

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[1] The seals and cetaceans evolved from different terrestrial mammals. If their ancestors were not capable of imitation, then vocal learning evolved independently in these two taxa.

particular whistle with a rise and then fall in frequency when in distress. The second approach emphasizes how each dolphin tends to produce its own individually distinctive whistle, which was called a signature whistle in the seminal paper by Caldwell and Caldwell (1965). Caldwell et al. (1990) reviewed a lifetime of work on signature whistles from 126 captive bottlenose dolphins of both sexes and a wide range of ages. These dolphins tended to produce signature whistles whether recorded soon after they had been caught from the wild or after a lifetime in captivity and in a variety of behavioral contexts recorded in captivity. Most of the whistles were recorded when the dolphins were isolated, and signature whistles made up about 94% of each individual's whistle repertoire in this data set (Caldwell et al. 1990). The Caldwells reported that signature whistles are distinctive among individuals, and that each individual dolphin produces a stereotyped signature whistle that is stable over many years.

Signature whistles have also been studied in wild dolphins inhabiting waters near Sarasota, Florida. More than 100 individual dolphins in this area can be identified by distinct markings, and some individuals have been followed for over two decades (Scott et al. 1990, Wells et al. 1987, Wells 1991). The study includes an annual capture-release component, in which dolphins are briefly captured to be measured, aged, sexed, sampled, marked, and then released. While a dolphin is being held, its vocalizations are recorded using a suction cup hydrophone placed directly on the head. A total of 398 recording sessions, most containing hundreds of whistles from an identified individual, have been obtained from 134 known individuals. Many of these dolphins were first recorded at two years of age or less and many have been recorded over spans of a decade or more. These wild dolphins have a stable and distinctive signature whistle (Sayigh et al. 1990), similar to that reported by Caldwell et al. (1990). Whistles recorded when the same individuals are free-ranging confirm that the whistles recorded in the capture-release context are similar to those recorded in natural conditions (Sayigh 1992).

SOCIAL CONTEXTS OF WHISTLE PRODUCTION AND INDIVIDUAL RECOGNITION

Results from long term studies of identified individual dolphins allow us to relate the acoustic communication of bottlenose dolphins to the problems posed by their patterns of social behavior. Bottlenose dolphins live in fission-fusion societies in which group composition may change on a minute by minute basis (Smolker et al. 1992, Wells et al. 1987). Within these fluid groups, however, bottlenose dolphins will preferentially associate with particular individuals, depending particularly upon kinship for mother-calf pairs, reproductive state for adult females, and past history of interaction for adult males. Certain individuals may have particularly strong and stable relationships. For example, pairs or trios of adult males may be consistently sighted together for many years (Connor et al. 1992). The mother-calf bond is also strong. A bottlenose dolphin calf will typically stay with its mother until just before she gives birth to a new calf. This period typically ranges from approximately three to five years (full range from one to fourteen years; Wells et al. 1987). Concurrent visual and acoustic observations of captive dolphins suggest that whistles function to maintain contact, particularly between mother and young (McBride and Kritzler 1951).

Bottlenose dolphins thus appear to rely upon different individual-specific social relationships at different stages through the lifetime. For an animal to be able to form individual-specific relationships, it must be able to recognize individually distinctive signature signals (Beecher 1989). Terrestrial mammals typically achieve individual recognition using visual, olfactory or voice cues. The sensory options for individual recognition are limited for marine mammals, which must rely upon acoustic signals for rapid communication over ranges more than a few body lengths. Caldwell and Caldwell (1965) proposed that signature whistles were just this kind of acoustic signal used to broadcast the identity and location of a dolphin to associates. For example, signature whistles might allow individuals to keep track of one another when a group of dolphins disperse to feed or when a dolphin approaches a group.

The hypothesis that whistles are signature signals requires that dolphins can use acoustic features of whistles to recognize different individuals. Both captive and wild dolphins have been shown to be able to discriminate whistles from different individuals. Caldwell et al. (1969) showed that a captive bottlenose dolphin was able to discriminate signature whistles from up to eight different individuals with a high degree of accuracy. Experimental playbacks have also shown that wild bottlenose dolphins respond more strongly to the signature whistles of animals with whom they have had a strong social bond (Sayigh 1992). The tendency to respond to closely bonded animals suggests that these wild dolphins also learn to associate each signature whistle with the appropriate individual. However, it has not been demonstrated that dolphins can use a signature whistle to recognize a particular individual.

Quantitative acoustic analyses of signature whistles also demonstrates that they are sufficiently distinctive to distinguish individuals. Buck and Tyack (1993) developed a computer algorithm to compare similarity in the fundamental frequency of whistles while allowing timing to vary. The algorithm was run on a sample of three randomly chosen whistles from each of ten dolphins. Of the 30 whistles in the sample, 29 were correctly matched.

Signature whistles may be of critical importance for a dependent calf to maintain contact with its mother. Dolphin calves can swim well at birth, and even very young calves often become separated by tens of meters from their mothers, on whom they are completely dependent. When a wild mother is temporarily separated from her young calf during the capture-release project, both mother and calf whistle at high rates (Sayigh et al. 1990). Smolker et al. (1993) report lower rates of whistling during voluntary separations in the wild. However, during these voluntary separations, the calf often whistles as it returns to the mother. The combination of early separations and prolonged dependence may put a premium on early development of individual recognition for mother and calf. This could be one-sided, involving recognition of a mother's signature whistle by the calf, but might also select for early development of a signature whistle by the calf. Dolphins may also need to maintain the ability to learn to recognize signature whistles throughout the lifespan if mothers must learn to recognize their calf's whistle or if dolphins of both sexes use signature whistles to mediate changing relationships as adults.

Acoustic structure of signature whistles

Signature whistles consist of both stereotyped and variable features. Some signature whistles show variation in the number of repetitive elements, called loops by Caldwell et al. (1990). Sayigh (1992) analyzed signature whistles from 81 wild Sarasota dolphins. She found that 73% had repeated loops, and the remaining 27% did not. Figure 1 illustrates variation in the number of loops in signature whistles from two different individuals, a juvenile male born in captivity and an adult female recorded in the wild. The whistles shown here have one introductory loop, from one to three repeated central loops, and one terminal loop. Most of the spectrograms in Figure 1 include several discrete whistle sounds separated by silence. Signature whistle segments are treated as one whistle if they occur in a repeated loop structure, just as discrete syllables of birdsong are typically treated as one song if they occur in a regular and predictable series. Signature whistles with the repeated loop structure are differentiated on the basis of the detailed structure of the loops, while allowing considerable variation in the number of loops (as in Figure 1) or deletions of segments of a signature whistle (e.g. Tyack 1986).

Non-repetitive whistles also show considerable variation in time and in frequency. Figure 2 shows four non-repetitive signature whistles from one wild adult female dolphin. While these whistles all share a basic pattern of frequency modulation, the variation among whistles should be obvious. For example, the central segment of relatively constant 5 kHz frequency in the whistle on the top right of

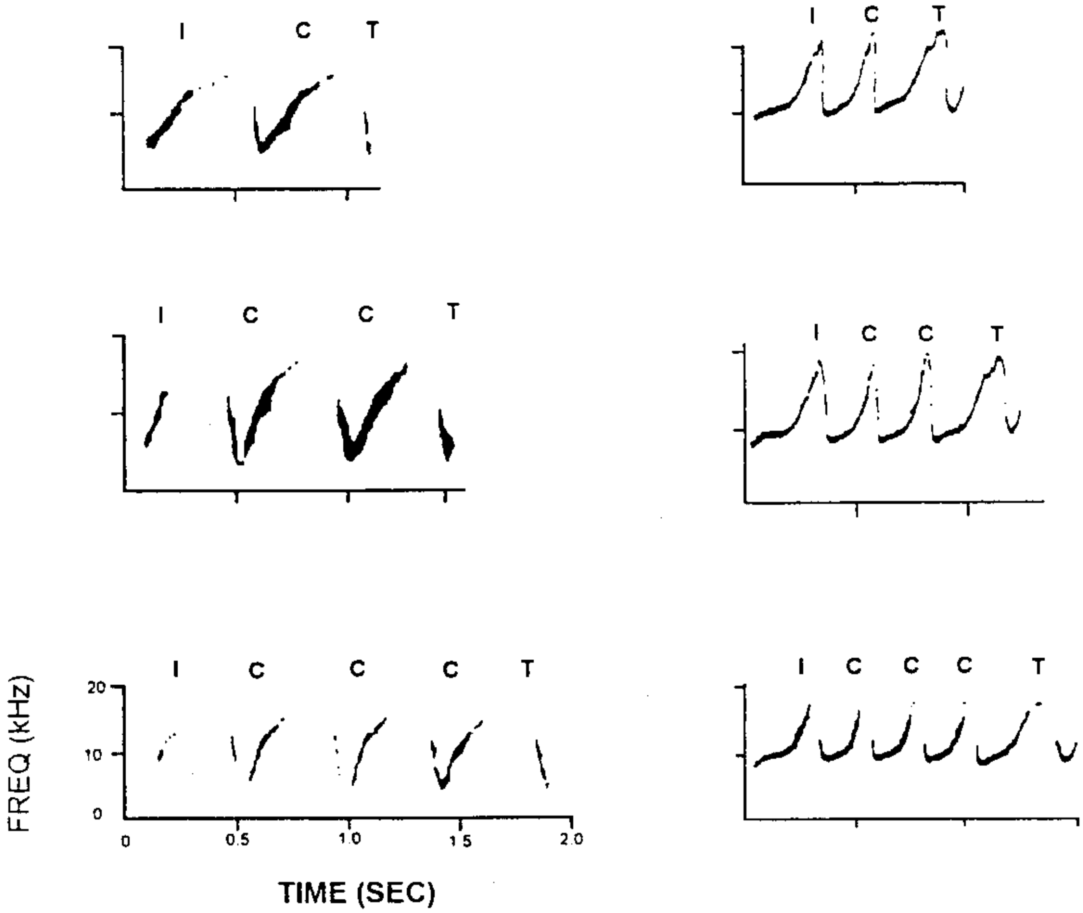

Figure 1. Examples of signature whistles with varying numbers of repetitive subunits called loops by Caldwell et al. (1990). These whistles are from two different individuals. The left column shows whistles from a juvenile male from captivity (from Figure 1 in Caldwell et al. 1990) and the right column shows whistles from an adult female from a wild population near Sarasota FL (from Figure 2.2 in Sayigh 1992). The initial subunit of each whistle is an introductory loop marked "I". One to three central loops then follow, marked "C." Each whistle ends with a terminal loop, marked "T." The x axis indicates time in seconds and the y axis indicates frequency in kHz.

Figure 2 has a longer duration than that on the top left, while the earlier and later segments of the whistle are much less elongated. The whistle on the upper left has sidebands at the start of the central 5 kHz section, while these are not visible on the other three whistles. While the signature whistle hypothesis proposes that signature whistles contain sufficient information to allow individual recognition, the Caldwells never suggested that this was the only information broadcast in whistles. Slight variations in signature whistles are thought to communicate factors such as the animal's motivational state (Caldwell et al. 1990; Janik et al. 1994).

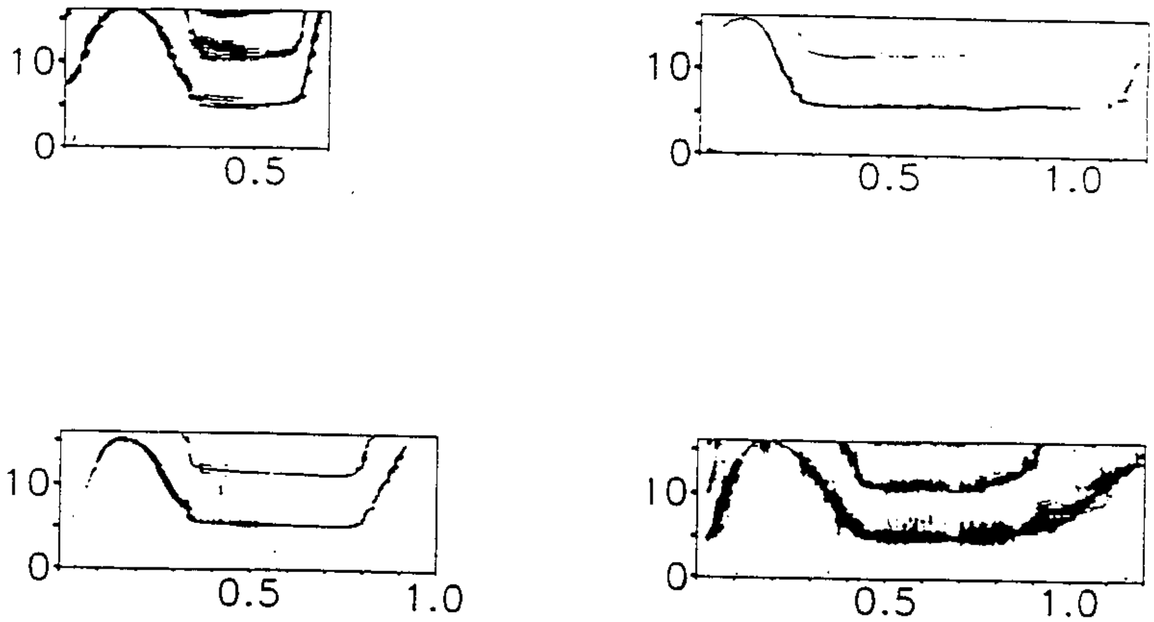

Figure 2. Four examples of a signature whistle without repetitive loops (from Figure 1 Sayigh et al. 1990). These spectrograms show the range of variability in duration and frequency of one adult female's signature whistle. They were recorded from a wild dolphin of the Sarasota community during a capture-release project. Spectrograms were made with a 90 Hz filter and a frequency range of 160–16000 Hz. The x axis indicates time in seconds and the y axis indicates frequency in kHz.

Parent-offspring comparisons in captive dolphins

In species with parental care, most infants both inherit their genotype from their parents and hear the sounds they produce. If the young develop vocalizations like those of their parents, this similarity makes it difficult to compare the effects of genetic factors versus auditory experience on vocal development. However, parent-offspring comparisons of dolphin whistles provide evidence against simple inheritance of call structure. Most dolphin calves appear to develop signature whistles that are quite different from those of their parents. In their longitudinal study of whistle development among 14 infant dolphins born in captivity, Caldwell and Caldwell (1979) reported that only one infant produced a signature whistle similar to those of its parents. This one calf, which rapidly developed a whistle similar to its mother's, was the only calf raised alone with its mother (except for a brief period with an adult male white-sided dolphin). Sayigh (1992) and Tyack et al. (in revision), compared whistles from nine dolphins born in a large community pool at the Miami Seaquarium to those of their parents. Signature whistles recorded from all of the calves and their known parents are shown in Figure 3. Of the five male and four

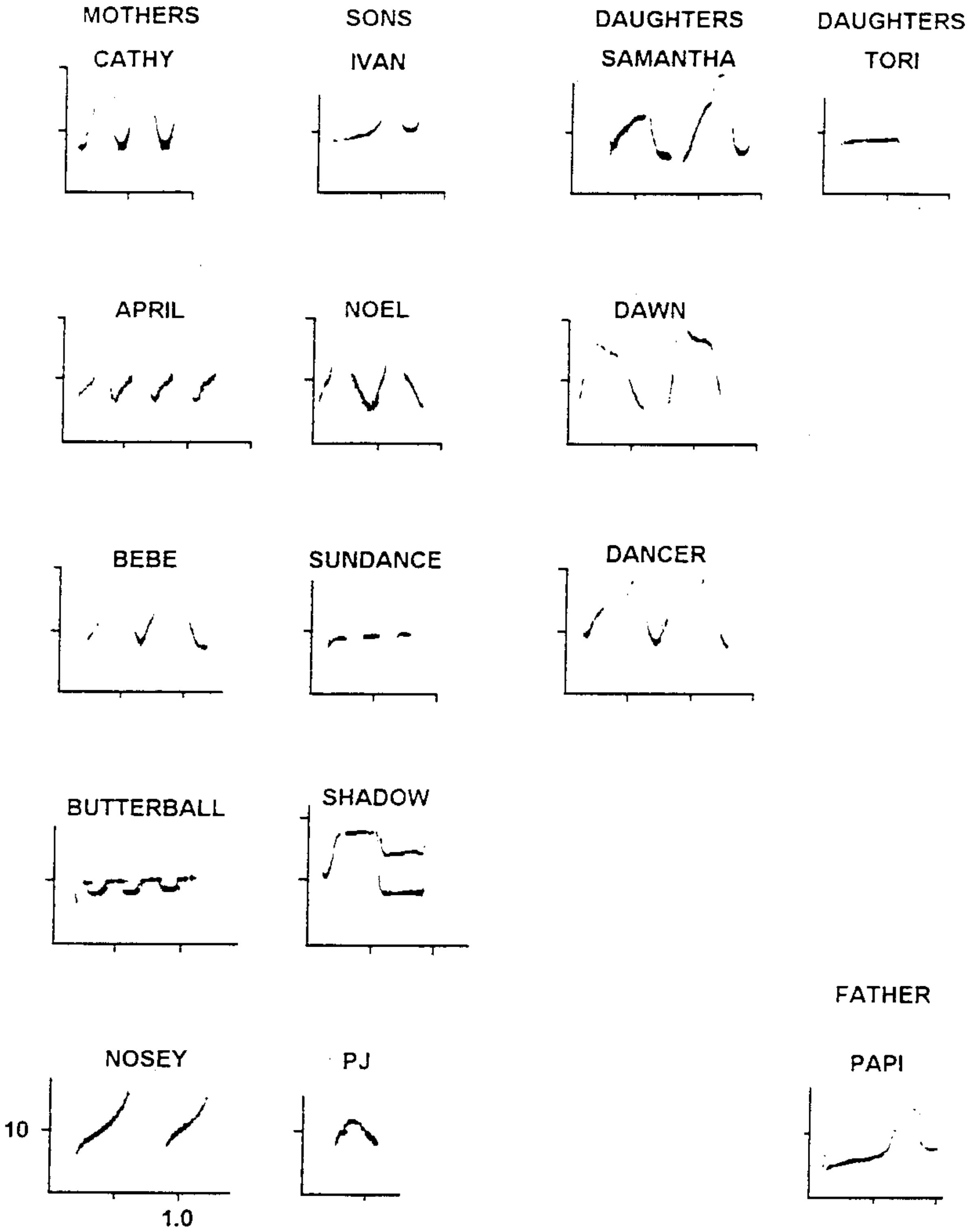

Figure 3. Parent-offspring comparisons of the signature whistles of nine dolphin calves (from Tyack and Sayigh 1997). All of these calves were born in captivity at the Miami Seaquarium. The left column shows the whistles from each mother. Calves' whistles are shown on the same row as the whistle of the mother. Papi was the father of all of the nine captive born calves except Dawn and Dancer. The signature whistle of Papi is illustrated in the lower right of the figure. Spectrograms were made with a sampling rate of 81,920 Hz, 256 point FFT and Hamming window. The x axis indicates time in seconds and the y axis indicates frequency in kH_3.

female calves, only Dancer developed a signature whistle somewhat similar to that of her mother Bebe. The father of all of the calves except Dawn and Dancer was named Papi. Ivan was the only calf with a signature whistle similar to that of his father, Papi.

Dolphin calves develop signature whistles that match acoustic models

While the captive dolphin calves just discussed did not produce whistles like those of their parents, their whistles were similar to other sounds common in their natal environment. For example, Tori and Sundance developed whistles very similar to the trainers' whistle, which is used to signal a dolphin that it has performed a requested task correctly (Figure 4). Another calf, named PJ, developed a whistle that was similar to the signature whistles of two subadults, Noel and Samantha, who were also raised together in the pool (Tyack et al. in revision; Figure 4). If verified with larger samples, matching of synthetic whistles would provide compelling evidence for vocal learning in development of signature whistles in bottlenose dolphins.

An important method for separating inheritance from experience in the study of development involves experiments in which the young are either isolated or cross-fostered with animals other than their relatives. For example, primates raised with foster mothers of a different species still produce species-typical vocalizations (Owren et al. 1993). Since signature whistles are individually distinctive, cross-fostering can be performed with captive conspecific dolphins to evaluate the role of vocal learning in signature whistle development. This kind of cross-fostering has been successful both with stranded wild dolphin infants and with captive-born infants whose mothers are not providing proper care. I will describe one successful cross-fostering of a stranded 1–2 month old *Tursiops* calf. The top row of Figure 5 shows the whistles of this calf, named April, as she arrived at the Gulfarium at Fort Walton Beach, FL. Since this calf did not strand with her biological mother, it is impossible to compare her original whistle to that of her mother. April was bottle-fed by humans, but for dolphin companionship was put in a pool with a nulliparous adult female named Cindy. Cindy was not lactating, but she rapidly took on most of the other roles of a dolphin mother to April. Cindy's signature whistle is indicated on the third row of Figure 5.[2] When April was 6–7 months old, her whistle was quite different from when first recorded. April's signature whistle (second row of Figure 5) had become more similar to the signature

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[2] Cindy also produced another stereotyped whistle that was rare. Caldwell et al. (1990) call this a secondary signature whistle. They report it for two out of 120 captive dolphins in their data set.

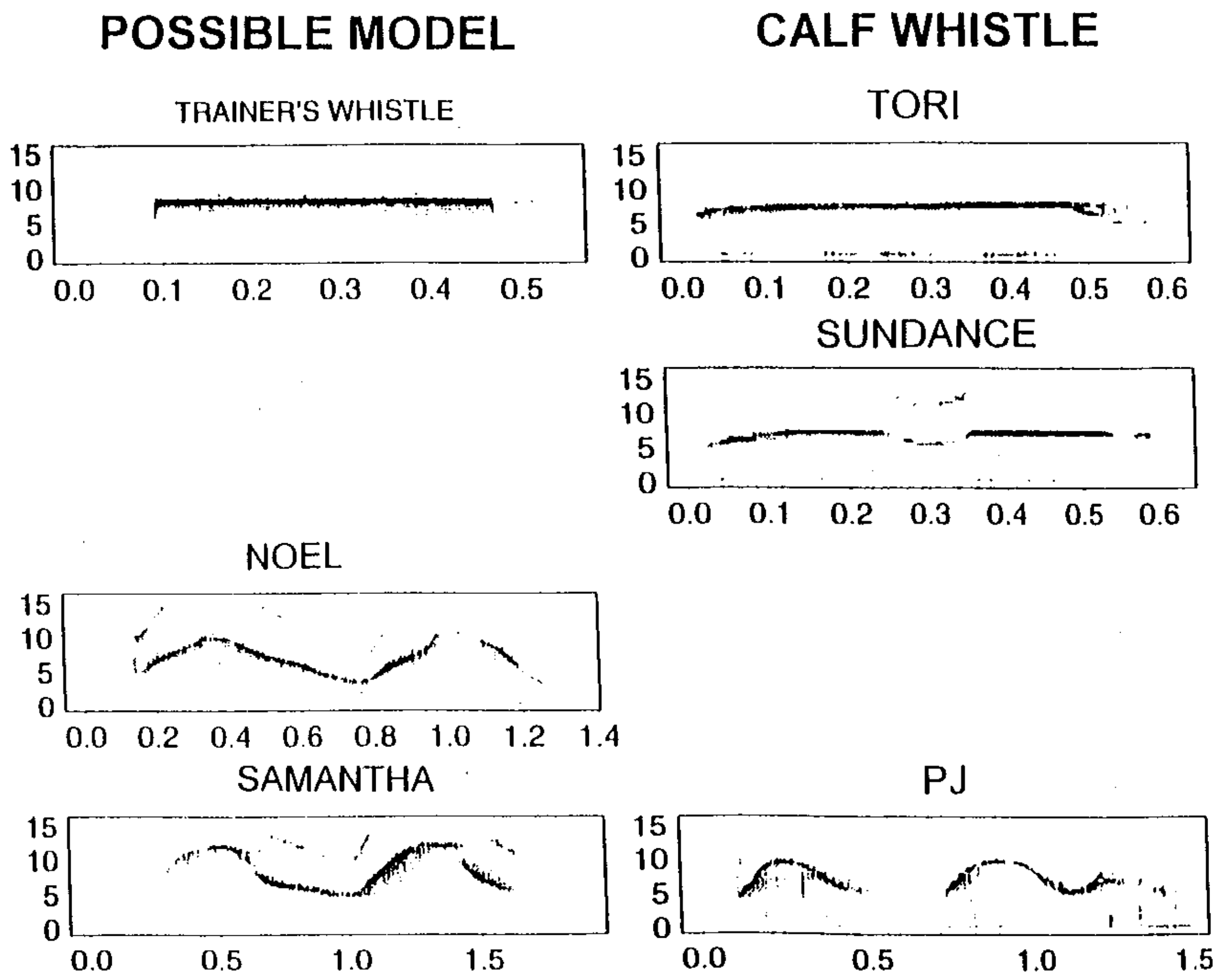

Figure 4. Comparisons of the signature whistles from three of the calves illustrated in Figure 3 to the most similar acoustic models present in the natal pool (adapted from Tyack and Sayigh 1997). These three calves, Tori, Sundance and PJ, were selected because they were born within a three month period in the same pool. Noel and Samantha were sub-adults during the period when Tori, Sundance and PJ were born, and their whistles were the most common in the pool at this time. Axes and spectrogram settings as in Figure 3.

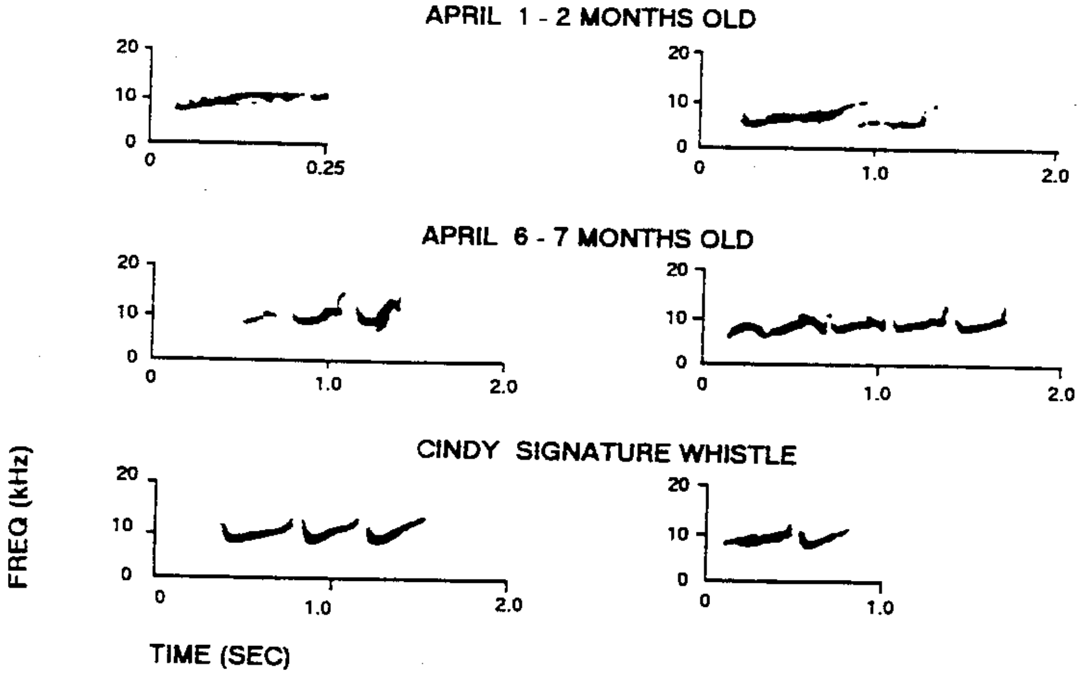

Figure 5. Spectrograms of signature whistles from a wild born calf (April) orphaned at 1–2 months of age and raised in captivity with a foster mother named Cindy (adapted from Tyack and Sayigh 1997). The first whistles recorded from April (top row) were not similar to Cindy's signature whistle (third row), but by 6–7 months of age, the calf April had developed a signature whistle (second row) similar to Cindy's signature whistle (third row). Axes and spectrogram settings as in Figure 3.

whistle of her foster mother. This suggests that exposure to the whistles of her foster mother modified the course of April's whistle development, causing her to develop a similar whistle. One case of possible cross-species matching was described by Caldwell and Caldwell (1979). One male *Tursiops* calf raised in a pool with seven *Tursiops* and two Pacific white-sided dolphins *Lagenorhynchus obliquidens* had a whistle that was different from the *Tursiops* but similar to one of the white-sided dolphins.

While isolation or cross-fostering experiments are more traditional ways experimentally to manipulate development, the tendency of dolphin calves to match whistles other than those of their mother as they develop their signature whistles presents an excellent alternative to separating the infant from its mother. There are potentially serious problems with the more traditional experiments. Not only may separation from the mother lead to generalized developmental deficits (see Mitchell 1968 for a primate example), but separation at birth does not guarantee that the calf was not exposed to the mother's calls. Dolphin calves hear well at birth, so prenatal exposure to sounds *in utero* may affect vocal development (see

DeCasper and Fifer 1980 for a human example). There is some indication in the data summarized above that calves raised in a pool with only one adult are more likely to develop whistles like that adult, whether or not it is the biological mother, while calves raised in community pools are less likely to develop whistles like their biological mother. Comparisons of whistle development for calves raised in a community pool, alone with a biological mother, or alone with a foster mother, may provide opportunities to control for auditory exposure in experiments on vocal learning and imitation in the development of dolphin whistles.

Variation in the timing of signature whistle development

The range of ages at which young dolphins in captivity acquire a stereotyped signature whistle is remarkably broad, from immediately after birth to over 17 months of age (Caldwell and Caldwell 1979). Dolphin infants whistle within a few days of birth, but Caldwell and Caldwell (1979) reported that it took between 1.5-2.5 months for most of the 14 captive infants in their study to develop a repeated stereotyped signature whistle. One dolphin in their study still had not developed a stereotyped signature whistle at 17 months of age. Once these calves developed a stereotyped signature whistle, it became a stable part of their vocal repertoire. The study of calves at the Miami Seaquarium suggests even earlier development of signature whistles. Tyack et al. (unpublished) studied whistles from three calves born within a three-month interval: Tori, Sundance and PJ. Two of these calves, Tori and Sundance, were recorded during the first week of life, at which time they already had relatively discriminatable whistles (Figure 6). These early whistles were similar to signature whistles recorded many months later. A sample of these whistles recorded during the first nine months of the calves' lives was analyzed by discriminant analysis. The overall rate of misclassified whistles was only 6%; only one of these misclassified whistles came from the first hundred days of life of the calves. This showed that the whistles of each calf were highly discriminatable, with no tendency for misclassified whistles to come from early recordings.

Stability of signature whistles

Signals used for individual recognition must remain stable over time. Stability of signature whistles can be assessed from longitudinal recordings of the same individual dolphin over many years. Hundreds of dolphins have been repeatedly recorded, both in captivity (Caldwell et al. 1990) and in the wild (Sayigh et al. 1990). Many individuals

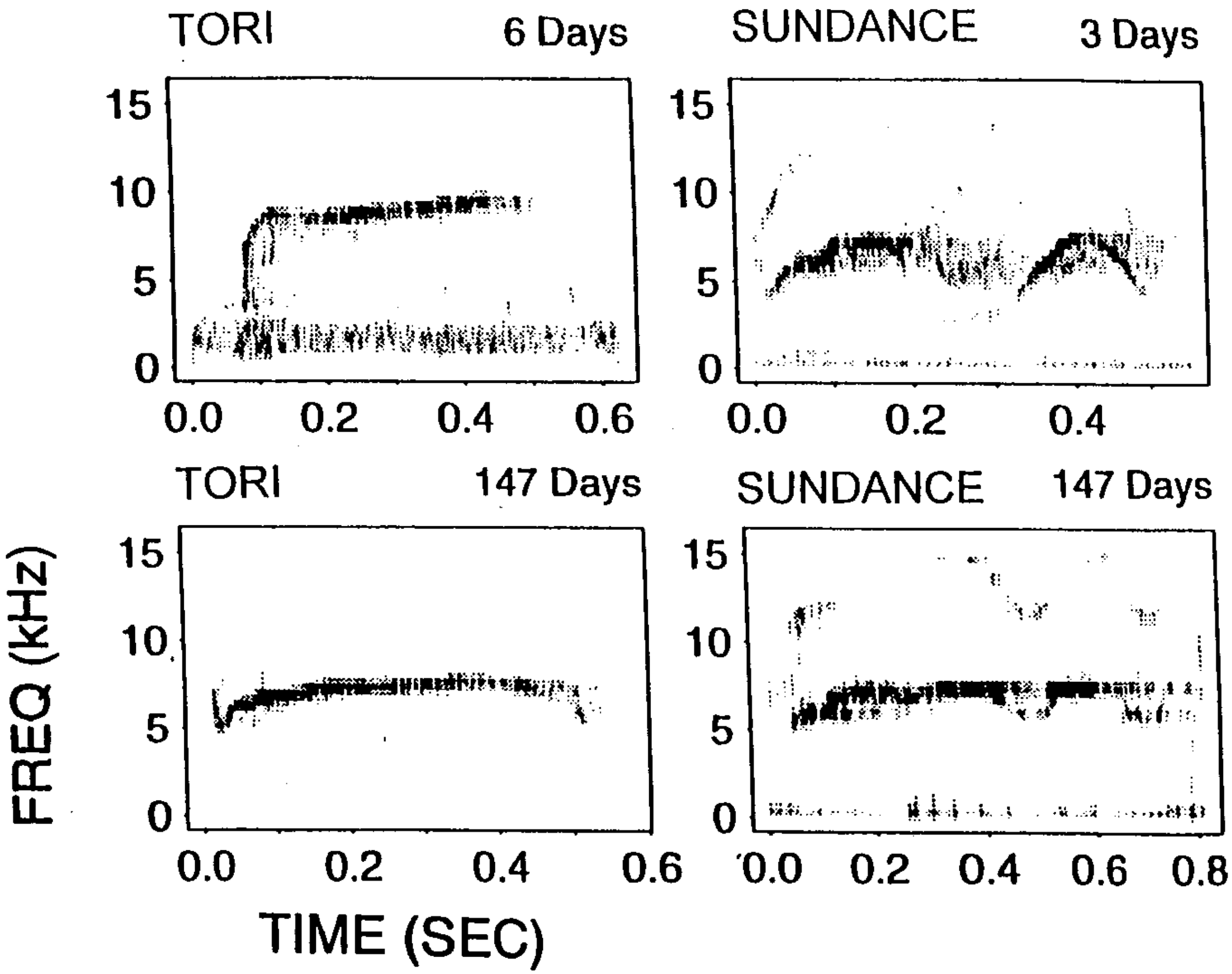

Figure 6. Spectrograms of signature whistles from two captive born calves recorded in the first week of life, with comparisons at 147 days of life (adapted from Tyack and Sayigh 1997). These were the only two of the nine calves illustrated in Figure 3 that were recorded during the first week of life. Axes and spectrogram settings as in Figure 3.

have been recorded for more than one decade. Visual comparison of spectrograms from whistles recorded from the same individuals over time demonstrates stability in signature whistles from one year of age through adulthood. These data suggest strongly that signature whistles, once developed, are stable throughout a dolphin's lifespan.

Parent-offspring comparisons in wild dolphins

The long term study of identified individual dolphins near Sarasota FL provides an opportunity to compare signature whistle development in the wild and in captivity. Figure 7 illustrates signature whistles recorded from an adult female over 11 years and a female calf at one and three years of age. Figure 8 illustrates the signature whistle of another adult female over 14 years, along with those of three male calves at ages of one to three years of age and a female calf at one year of age. Both of these adult females had whistles that were stable for over a decade.

Examination of Figures 7 and 8 suggests that among wild dolphins, daughters have whistles different from their mothers, while sons may have relatively similar whistles to their mother. In order to test whether sons have whistles more like their mothers than daughters do, Sayigh et al. (1995) compared the signature whistles of 42 wild dolphin calves, 21 sons and 21 daughters, to those of their mothers. Human judges compared spectrograms of pairs of whistles from mothers and offspring in order to rank their similarity. Many different judges ranked the same pairs of whistles to allow testing of the reliability of these similarity scores (reliability averaged 95%). Of the 42 calves, 31 (74%) produced signature whistles that were not judged similar to those of their mothers. There was a pronounced bias in the sex of the 11 calves rated as producing whistles very similar to their mothers. Nine of the 21 sons produced whistles rated very similar to those of their mothers, whereas only two of the 21 daughters had very similar whistles.

Social and acoustic factors affect signature whistle development

It is more difficult to attempt a longitudinal study of whistle development among wild dolphins than among captive ones. However, long term studies of identified individual dolphins make it possible to target a few focal mother-calf pairs. In the coastal waters near Sarasota FL, it is possible to find each target pair every week or so. This makes it possible to design a study of the factors influencing the timing and outcome of signature whistle development in the wild. Sayigh (1992)

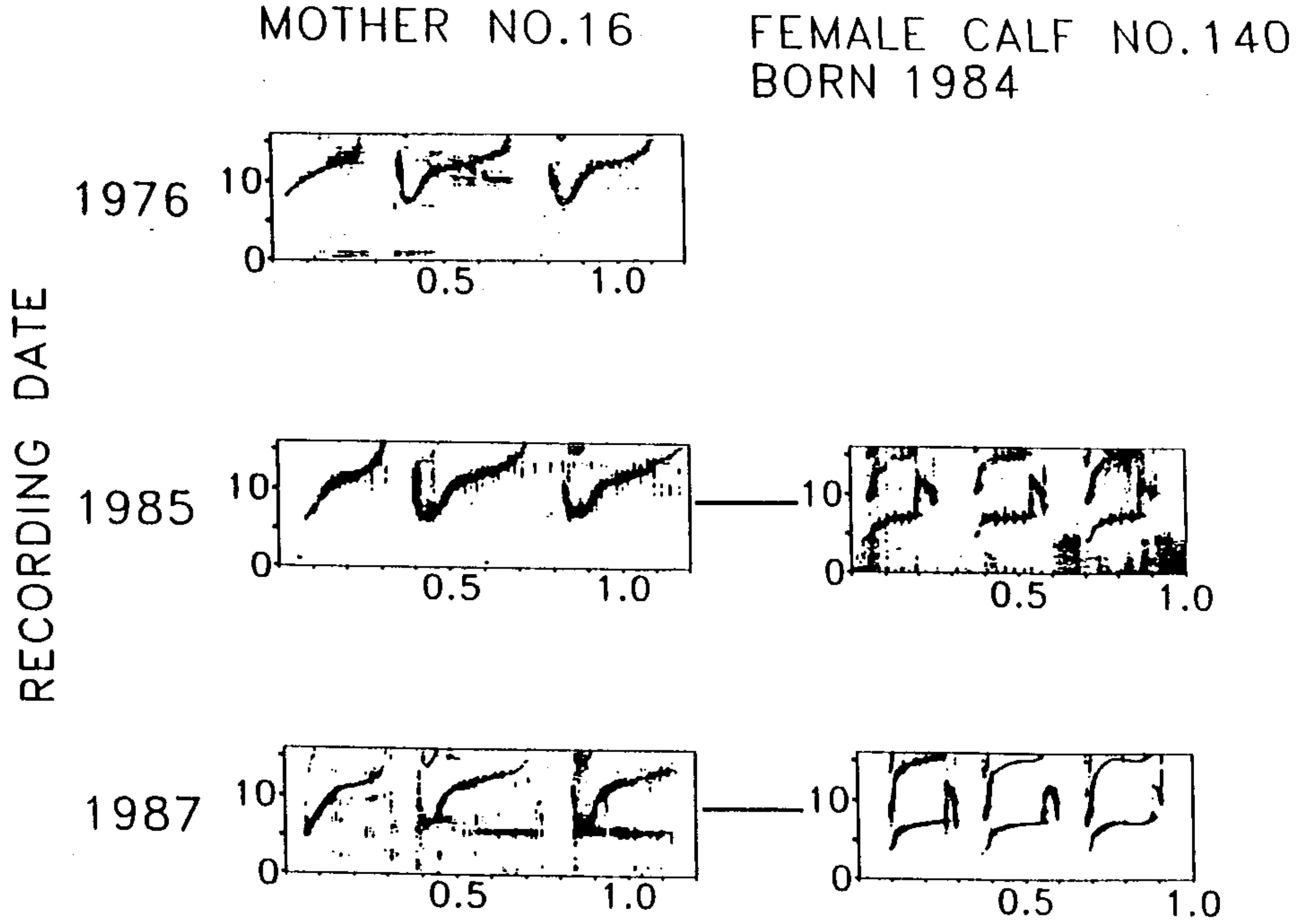

Figure 7. Spectrograms of signature whistles from one wild adult female recorded over a period of eleven years and of her daughter at one and three years of age (from Figure 2 Sayigh et al. 1990). Note the stability of both signature whistles. Axes and spectrogram settings as in Figure 2.

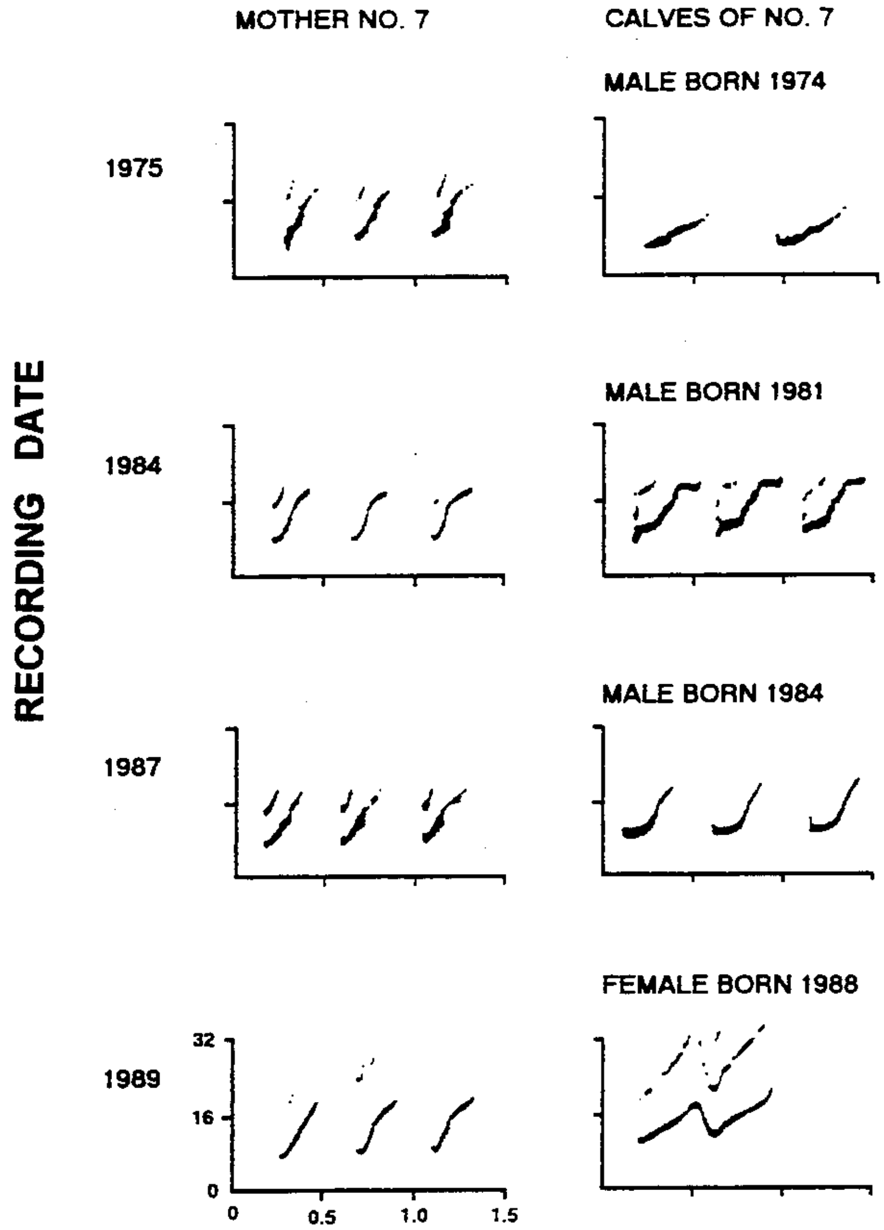

Figure 8. Spectrograms of signature whistles from one wild adult female recorded over a period of fourteen years, from three of her sons, and from her daughter (from Figure 4 Sayigh et al. 1995). Note the similarity of the signature whistles of mother and sons. Axes and spectrogram settings as in Figure 2.

conducted such a study involving focal observations of wild mothers and calves during the period of whistle development, along with simultaneous acoustic recordings using a method described in Sayigh et al. (1993). Sayigh's preliminary results from four calves indicate that there is considerable individual variability in both the speed with which a calf develops a stereotyped signature whistle and the factors affecting choice of whistle by a calf (Sayigh 1992). Two calves (one known to be male) exhibited relatively rapid (1–2 months) whistle development and produced contours that resembled those of their mothers, whereas two calves (one known to be female) exhibited more prolonged (3+ – 13+ months) whistle development and produced contours that did not resemble those of their mothers.

Some of the variability in signature whistle development appears to be correlated with the early social environment (Sayigh 1992). For example, the two calves that rapidly developed whistles similar to their mothers showed higher levels of synchronous surfacing with their mothers during the period of whistle development than did the other two calves (Sayigh 1992). The one calf in this sample known to be a male was one of these two calves. He spent a proportionately greater amount of time alone with his mother than the other calves, and he was sighted in smaller groups.

Sayigh (1992) also quantified the early acoustic environments of these four calves by measuring whistle rates and the proportion of whistles that were the mother's signature whistle. The two calves whose whistles were similar to their mothers were exposed to the lowest overall whistle rates (0.64 and 0.73 whistles per minute) and the greatest percentages of their mother's signature whistle (20% and 18%). Thus, the two calves that heard the fewest whistles and the greatest percentages of their mothers' signature whistle developed whistles resembling those of their mothers, and they had the most rapid whistle development. The only calf known to be a female exhibited the most prolonged (13+ months) and variable whistle development and developed a whistle highly distinct from her mother. She was exposed to the highest average whistle rate (0.91 whistles per minute) and the lowest percentage of her mother's signature whistle (6%). The acoustic environment of the other calf whose whistle differed from its mother fell somewhere in the middle: it was intermediate in the time it took to develop a stereotyped whistle (3–4 months), it was second to the female calf in overall whistle rates (0.79 whistles/min.), and it showed the second lowest percentage of signature whistles from the mother (14%).

The source of the signature whistle is obvious for the calves that developed signature whistles like those of their mothers. What about the calves whose whistles were different from their mothers? Two possible sources are suggested for each of the two calves with whistles different from their mother's signature whistle: learning from another individual present in the community, and production of a distinctive whistle by the mother that was different from her own signature whistle. The mother of the known female calf apparently repeated a whistle quite different from her own signature during her calf's first few months of life. The calf appeared to have imitated this whistle by one month of age and this whistle resembled the eventual signature whistle of the calf (Sayigh 1992). With regard to whistles of dolphins other than the mother, the signature whistles of both calves were similar to whistles of young females present in the Sarasota community. There are over 100 Sarasota dolphins for which signature whistles can be compared. Given this large number of comparisons, it is possible that the similarities might be due to chance. Association patterns may help one to evaluate whether the calves might have learned their signature whistles from these females. For example, allomaternal care is often reported for dolphins, and a calf might be exposed to many whistles of a highly vocal allomother compared to a relatively silent mother. The signature whistle of the known female calf was similar to that of a female who was present in five out of the 17 observation sessions. The other calf produced a whistle similar to that of a female with which it never was observed to associate. However, each calf was only followed for a small percentage of the time, and this other calf could have associated with animals such as this female when not under observation by Sayigh. The limited sample size of these longitudinal studies of wild calves provides only a tantalizing glimpse into the factors that may affect whistle development. However, they demonstrate the power of methods currently available for studying the early social and acoustic environments of dolphin calves in the wild. Further study using these techniques is clearly warranted.

Dolphins can continue to learn and produce new whistles throughout their lifetime

While bottlenose dolphins develop a stable signature whistle early in life, captive studies have shown that dolphins maintain the ability to imitate sounds throughout their lifespan (e.g. Evans 1967, Richards et al. 1984, Sigurdson 1993). Captive bottlenose dolphins of both sexes are highly skilled at imitating synthetic pulses and frequency modulated tones (Caldwell and Caldwell 1972, Herman 1980). Once a dolphin learns to imitate a sound, the novel sound can become incorporated into its vocal repertoire, and the dolphin can produce the sound even without the model as a stimulus (Richards et al. 1984).

Why should dolphins maintain the ability to imitate throughout their lifespan if their signature whistle is developed early in life? One factor may involve the role of imitation of signature whistles in the natural communication system of adult dolphins. Tyack (1986) found that two captive dolphins imitated each others' signature whistles at rates of about 25% (i.e. of all occurrences of each signature whistle, 25% were imitations). These two dolphins were caught in the wild and first housed together at about 5 years of age; they therefore must have learned to imitate one another after this age. Captive dolphins in separate pools that can hear one another through an acoustic link have also been reported to imitate each others' signature whistles at rates of near 1% (Burdin et al. 1975, Gish 1979). Once a dolphin learns to imitate the signature whistle of a partner, the imitated whistle appears to become incorporated into the dolphin's own whistle repertoire, and is not just produced immediately after the partner makes its own signature whistle.

As described two paragraphs above, captive dolphins have long been known to imitate synthetic whistle sounds. This raises the question whether imitation of signature whistles by adults is an artifact of captivity or whether it plays a functional role in the wild. This question can be addressed by analyzing recordings of known individual dolphins made during the temporary capture and release projects in Sarasota FL. Imitation of signature whistles has been recorded in whistle exchanges between pairs of wild dolphins that were caught together and that share strong social bonds. For example, some pairs of adult males in Sarasota are consistently sighted together (Wells et al. 1987). Signature whistles from a pair of males sighted together 75% of the time in Sarasota surveys are shown in Figure 9 along with imitations of the partner's whistle. Coalitions of 2–3 adult males are also reported from western Australia (Connor et al. 1992). Smolker (1993) reports convergence of whistles among three adult males over two years as they formed a coalition. One whistle was initially only recorded from one member of the coalition, but it gradually became the most common whistle for all three males.

Age and sex differences in the proportion of signature whistles

Most terrestrial non-human mammals develop a stereotyped repertoire of species-specific vocalizations. Vocal development has been characterized for many species as a progressive narrowing from a large and variable repertoire in the young to a more fixed repertoire in mature animals. Dolphin whistles show a very different developmental pattern. Dolphin calves can whistle at birth and produce a variable whistle repertoire. Within a few months to a year, the variability of their whistles is reduced as they develop a stereotyped signature whistle. While this signature whistle appears to be stable for the rest of the dolphin's lifetime, it is accompanied by an increase in the production of highly variable calls with age. Whistling dolphins combine the capability to develop a highly stable stereotyped call with a lifelong ability to imitate sounds and an increasing proportion of variable sounds with age.

Caldwell et al. (1990) reported that in addition to signature whistles, bottlenose dolphins produce an extremely variable array of whistles which are not individually distinctive. Whistles other than the signature whistle will be called variant whistles in this paper. Variant whistles made up only about 6% of the whistles reported by Caldwell

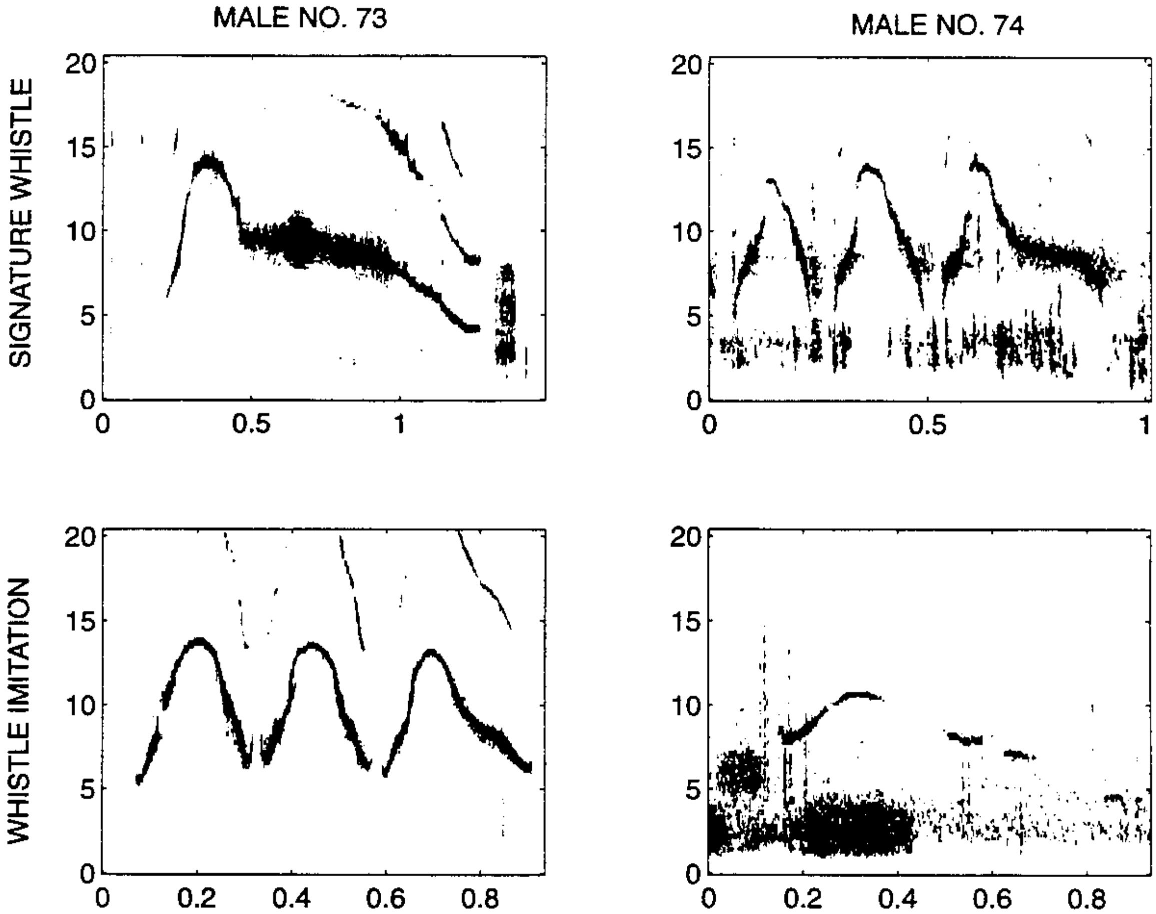

Figure 9. Spectrograms of signature whistles produced by two adult males from the wild population near Sarasota FL which were usually sighted together (from Figure 4.16 Sayigh 1992). Each male also repeated whistles that were similar to the signature of the partner, and these are interpreted as imitations of the partner's signature whistle. Axes and spectrogram settings as in Figure 3.

et al. (1990), but as high as 23% of the smaller whistle sample reported by Tyack (1986). Each individual dolphin produces a diverse array of variant whistles. Some variants do not appear to be repeated, and may share no obvious similarities to any other variant. Other whistles classed as variants may repeat in the repertoire of one individual, and variants from different individuals can be quite similar. Tyack (1986) and Janik et al. (1994) defined several categories such as simple upsweeps, downsweeps and sinusoidal patterns of frequency modulation that differed from the signature whistle but were repeated. Other whistles classed as variants in the Caldwell et al. (1990) study may have included what Tyack (1986) describes as imitation of signature whistles.

Caldwell et al. (1990) reviewed data on the percentage of variant whistles from 126 captive dolphins from both sexes and a wide range of ages. This sample included 5 female and 8 male infants (up to one year of age), 12 female and 25 male juveniles, 25 female and 22 male subadults, and 18 female and 7 male adults. At each age, male dolphins produced a larger proportion of variant whistles than females. There was a large whistle sample for the infant dolphins, with an average of nearly 600 whistles analyzed per individual. All of the infants appeared to have already developed their signature whistles before they were recorded for this sample except for two small males. The female infants had between 0–1% variant whistles, while the male infants ranged from 0–18% variant whistles. For each sex, there was an increase in percentage of variant whistles as a function of increasing age in these captive dolphins. Caldwell et al. (1990) report that this effect of sex and age class had a significant effect on the proportion of variant whistles ($p < 0.001$).

Sayigh et al. (1990) report the same sex difference in wild dolphins. Male calves had a higher proportion of variant whistles than did female calves. As young male calves matured, they also produced a higher proportion of variant whistles. This increasing repertoire of variant whistles occurred as the males broadened their network of social relationships. A productive area for future work will be tracing the connection between development of a social relationship with a new partner and imitation of the partner's signature whistle or convergence of signature whistles as described by Smolker (1993).

Social functions of shared whistles among dolphins

No studies have identified a function for imitation of signature whistles in the natural communication system of dolphins. However, work on other species capable of vocal learning suggest several hypotheses. The first hypothesis suggests a referential role for imitation. There are several indications that animals which learn one another's individually distinctive calls may imitate the call of another in order to initiate an interaction with that particular individual. For example, Gwinner and Kneutgen (1962) and Thorpe and North (1966) describe interactions in which one bird imitates the song of the absent partner, after which the absent partner "would return as quickly as possible as if called by name" (Thorpe and North 1966). Tyack (1993) describes a similar interaction in wild bottlenose dolphins in which two adult females synchronize their whistles only when one of the females imitates the signature whistle of the other one.

Experiments with synthetic signals have demonstrated that dolphins have the cognitive abilities required to perform this kind of vocal labelling (Richards et al. 1984). For the first stage of these experiments, a dolphin was trained to imitate synthetic whistle sounds upon command. When the trainers commanded the dolphin to imitate a sound, they would simultaneously play the synthetic whistle and hold up an arbitrary object. For example, they might show a ball when they played an upsweep and a plastic pipe when they played a warble. After the dolphin learned this task, the trainers started occasionally to show the object but not to play the whistle. In order to respond correctly, the dolphin had to remember how to reproduce the whistle that had been associated with the object. After sufficient training, the dolphin succeeded in learning to label each arbitrary object with an arbitrary whistle.

Research on both birds and humans has suggested that learning to produce a signal may improve an animal's ability to recognize the signal (Liberman et al. 1967, Williams and Nottebohm 1985). This kind of motor theory for vocal perception may be a factor in imitation of signature whistles. However, if dolphins imitate a signature whistle in order to memorize it, one might predict more imitation when one dolphin meets another for the first time. Current results suggest imitation is most common among dolphins with a long history of a close relationship. Another hypothesis concerning the function of imitation emphasizes its role as an affiliative signal (Bavelas et al. 1987). Vocal convergence of speech sounds is reported among adult humans, and this has been interpreted as an affiliative signal (Locke 1993). The convergence of whistles during formation of a coalition of dolphins reported by Smolker (1993) may have a similar affiliative component. In human mother-infant interaction, imitation is thought to play a critical role in matching or regulating affective states (Stern 1985). This raises questions about differences in mother-calf relationships in dolphins with similar or different signature whistles as reported by Sayigh et al. (1995).

More detailed study is required to determine the functions of variant whistles and of imitation of signature whistles. Janik et al. (1994) found that variant whistles were produced more often in a training context and signature whistles were more common when a captive dolphin was isolated. More work needs to be done on more naturalistic behavioral contexts in which variants are produced, and on possible responses of dolphins to variants. Detailed behavioral observations also need to be conducted on the contexts and consequences of vocal mimicry in order to test the predicted links with functional reference or naming, with using imitation to learn a whistle, and with affiliative behavior and affect. The referential, perceptual and affiliative roles of imitation are not mutually exclusive and may reinforce each other.

The evolution of vocal learning in dolphins

The evolution of vocal learning in cetaceans may be related to problems of individual recognition for animals that dive at sea. Many mammals can easily identify conspecifics using olfactory cues from scents or visual cues for face recognition. These cues are unlikely to be important for individual recognition in cetaceans. Among mammal species using acoustic cues, many rely upon involuntary voice cues to recognize one another. These voice cues derive from slight differences in the vocal tracts of individuals. Diving mammals may not be able to rely upon involuntary voice cues, because the slight differences in gas-filled vocal tracts may be trivial compared to modifications produced by the compression of these structures during diving (Tyack 1991). Instead, if diving mammals are to rely upon individually distinctive vocalizations while underwater, they may need to use vocal learning to produce distinctive signals under voluntary control. It would be useful to test whether and how dolphins can stabilize their whistles against these changes induced by diving. These can be tested by recording dolphins at different depths or by having subjects in the laboratory breathe gas mixtures of different densities.

In many animal species, patterns of communication and vocal development are strongly affected by patterns of social interaction. Individual-specific social relationships are important to bottlenose dolphins of both sexes and all ages. Signature whistles appear to play an important role in maintaining these relationships. If dolphins use imitation of signature whistles to mediate individual relationships that change throughout the lifespan, then this may be one reason both for the increasing diversity of whistles with age and for the maintenance of imitative skills into adulthood. The need to maintain individual-specific relationships with a variety of individuals may have been an important selection pressure in the evolution of vocal learning in these animals.

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