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Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members

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Abstract Bottlenose dolphins are unusual among non-human mammals in their ability to learn new sounds. This study investigates the importance of vocal learning in the development of dolphin signature whistles and the influence of social interactions on that process. We used focal animal behavioral follows to observe six calves in Sarasota Bay, Fla., recording their social associations during their first summer, and their signature whistles during their second. The signature whistles of five calves were determined. Using dynamic time warping (DTW) of frequency contours, the calves' signature whistles were compared to the signature whistles of several sets of dolphins: their own associates, the other calves' associates, Tampa Bay dolphins, and captive dolphins. Whistles were considered similar if their DTW similarity score was greater than those of 95% of the whistle comparisons. Association was defined primarily in terms of time within 50 m of the mother/calf pair. On average, there were six dolphins with signature whistles similar to the signature

whistles of each of the calves. These were significantly more likely to be Sarasota Bay resident dolphins than non-Sarasota dolphins, and (though not significantly) more likely to be dolphins that were within 50 m of the mother and calf less than 5% of the time. These results suggest that calves may model their signature whistles on the signature whistles of members of their community, possibly community members with whom they associate only rarely.

Keywords Bottlenose dolphin · Vocal learning · Whistle development · Social influences on learning

Introduction

Although vocal learning is an essential part of the development of both human language and birdsong (Kroodsma and Baylis 1982), vocal learning is rarely important to the development of the natural vocalizations of non-human mammals (general review: Janik and Slater 1997; primate review: Seyfarth and Cheney 1997). Although some non-human primates learn what contexts are appropriate for each sound (Seyfarth and Cheney 1997), few non-human mammals actually learn how to produce the sounds in the first place (bats: Boughman 1998; tamarins: Hodun et al. 1981; review: Janik and Slater 1997). In species that do learn sound production, including humans, social interactions play an important role in the course of vocal development (Snowdon and Hausberger 1997). A complete understanding of vocal development therefore requires an investigation of both the potential for vocal learning and the social influences on the learning process.

Previous evidence suggests that the bottlenose dolphin (*Tursiops truncatus*) is a likely candidate for vocal learning in a non-human mammal (Richards et al. 1984; Tyack and Sayigh 1997). Adult and juvenile dolphins have repeatedly demonstrated an ability to imitate novel sounds (Caldwell and Caldwell 1972; Richards et al. 1984; Reiss and McCowan 1993). The imitation of novel sounds by

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adult bottlenose dolphins does not prove that infants of that species learn their natural vocalizations but suggests that infants might be capable of such learning.

Bottlenose dolphins produce individually specific whistles called signature whistles (Caldwell and Caldwell 1965; Caldwell et al. 1990) that appear to be used as cohesion calls (Janik and Slater 1998). Each individual's signature whistle has a unique frequency contour that is generally fully developed by 1 year of age and remains reasonably stable throughout the individual's lifetime (Caldwell et al. 1990; Sayigh et al. 1990; Sayigh 1992; see Smolker and Pepper 1999; Watwood 2003 on adult male signature whistle convergence). Because each signature whistle is unique, a calf's signature whistle never matches a single "model" whistle exactly. Instead, the calf's signature whistle will have some similarities to other whistles. Preliminary studies have reported on bottlenose dolphin calves that developed signature whistles that were similar to whistles in their environment, including the whistles of unrelated dolphins and man-made whistles (Caldwell and Caldwell 1979; Sayigh 1992; Tyack 1997; Miksis et al. 2002). Preliminary evidence also suggests that the early social environment influences which whistles are most similar to the calf's signature whistle (Sayigh 1992; Tyack and Sayigh 1997). However, none of these studies has been able to show conclusively that learning is an essential part of bottlenose dolphin signature whistle development.

The objective of this study is to address two issues: (1) do wild bottlenose dolphin calves model their signature whistles on whistles they hear? and (2) if so, what types of social interactions did the calves have with the animals they chose as models? To answer the first question, the calves' signature whistles must be compared to whistles they heard (i.e. the whistles produced by members of their community) and to whistles they did not hear (i.e. whistles produced by animals in other wild locations or in captivity). If the calves are using models, their signature

whistles should be similar to the whistles of community members and not similar to the whistles of dolphins from other locations. If this is the case, then the interactions between the calves and the animals they chose as models can be evaluated. The calves may select models from among the animals with whom they interacted frequently or they may select models from among animals they heard but with whom they interacted rarely.

To investigate these questions, wild-born calves in Sarasota Bay, Fla. were followed in their first 4 months of life, and their behavior and interactions were recorded. Their signature whistles were recorded the following year and compared to the signature whistles of (1) the dolphins with whom they interacted, (2) the dolphins in their community with whom they were not seen to interact, and (3) dolphins from other communities. The similarity between each calf's signature whistle and the signature whistle of each dolphin was then evaluated with respect to the calf's interactions with that dolphin.

Methods

Study site: Sarasota Bay, Florida

This study was conducted with the community of wild bottlenose dolphins in Sarasota Bay, Fla. A long-term study of this community has generated a great deal of information on the social structure and whistles of wild dolphins (Wells 1991; 2003). The Sarasota community consists of approximately 140 resident bottlenose dolphins. The community encompasses "a 40-km stretch of coastline that includes a system of bays, protected by a series of barrier islands [off Sarasota, Florida], and the waters of the Gulf of Mexico up to about 1 km offshore of the islands" (Scott et al. 1990, p. 237). Since the early 1970s, a research program has studied the life history, community parameters, communication, and behavior of

Table 1 Summary of follows for all six calves during 2000 and 2001. Six calves born in Sarasota Bay, Fla. were observed by focal samples as young-of-the-year in 2000 and yearlings in 2001. Follows lasted up to 2 h (120 min)

Focal calf	First follow	Sex ^a	Year 1 (2000)			Year 2 (2001)			Source of signature whistle
			No. of follows	Total hours	Average duration (min)	No. of follows	Total hours	Average duration (min)	
1493	26 May 2000 ^b	Unknown	3	5.73	114.7	5	4.30	51.6	2001 Follows
C932	6 June 2000	Unknown	10	9.88	59.3	1	1.00	60.0	Not determined
1573	9 June 2000	F	10	13.72	82.3	8	11.58	86.9	2002 Capture–releases ^c
C011	19 June 2000	F	10	10.65	63.9	11	14.08	76.8	2003 Capture–releases
C545	10 July 2000	F	9	10.70	71.3	8	8.55	64.1	2002 Capture–releases ^c
C992	20 July 2000	Unknown	8	10.65	79.9	10	9.35	56.1	2001 Follows
Total			50	61.33	–	43	48.87	–	
Average			8.3	10.22	78.6	7	8.14	68.2	

^a Sex was determined during capture–release efforts. The genders of the three calves that have not been found are therefore not yet known.

^b The data from this follow were not used. The first usable follow on this calf was 28 June 2000

^c Similar signature whistles were recorded from these calves during the 2001 follows (1573 $S=3.81$; C545 $S=4.08$; $S>3.55$ was considered similar).

this community (Scott et al. 1990; Wells 2003). As part of the Sarasota project, dolphins are temporarily captured from time to time to assess age, genetic relatedness, reproductive state, health, environmental contaminant burdens, and vocal behavior, as well as to perform sound playback experiments (Wells 1991; 2003; Sayigh 1992). The signature whistles of most adults in the community have been recorded during these operations (Sayigh et al. 1990). The combination of data from temporarily captured animals and observations of free-ranging animals has provided a wealth of background information on this community, which enables even more detailed studies to be performed. Past patterns of association are known for most of the dolphins in the community, allowing the social structure of the community to be well understood (Wells 1991; 2003). Most of the matrilineal relationships of the animals are also known, as are the birth dates of most calves born into the community since 1980 (Wells 1991; 2003).

Focal follows

Six calves were born into the Sarasota community in the spring of 2000. These six calves were our focal animals. Each one was identified through association with a distinctive adult female, who was presumed to be the mother. They were followed as young-of-the-year from 1 June–15 September, 2000 and as yearlings from 1 June–20 August, 2001 (Table 1). The dolphins were observed from a 6.7-m Grady White Fisherman center console vessel with a 225 hp 2-stroke Yamaha outboard engine. In 2001, an additional 9.9 hp 4-stroke engine was added for use during follows. This smaller, quieter engine solved a serious problem we had in 2000 with engine noise interfering with the acoustic recordings. Dolphin behaviors were observed visually from a 2.3-m tower in the center of the boat. The boat's crew consisted of two observers, two to three interns, and one equipment coordinator.

Year 1 association patterns

The primary goal of the 2000 follows was to determine association patterns. Focal animal behavioral samples (Altmann 1974) were taken on the calves and their mothers using a point-sample protocol, recording association patterns and social interactions between animals. The mothers' association patterns were recorded at 3-min time points. At the mother's first surfacing following the time point, an observer in the tower recorded all animals within 50 m of the focal mother, and the mother's nearest neighbor (NN), defined as the dolphin nearest to the mother by distance. If no surfacing occurred within 2 min after the time point, the time point was considered missed. The calf's association patterns were recorded at 1-min time points. At the calf's first surfacing following the time point, the observer recorded all animals within 5 m of the

focal calf, and the calf's NN. The time point was considered missed if the calf did not surface before the next time point. The observer reported these data to interns on the deck of the boat who then recorded them on paper data-sheets, which were later transcribed into Microsoft Excel. Follows lasted up to 2 h.

Four behavioral measures were calculated from each focal follow for each interacting animal: (1) the percentage of 3-min time points within 50 m of the mother, (2) the percentage of 1-min time points within 5 m of the calf, (3) time as the mother's NN corrected for time within 50 m, and (4) time as the calf's NN corrected for time within 5 m. Time as the mother's NN was corrected by taking the number of 3-min time points where an animal was the mother's NN as a percentage of the 3-min time points that animal was within 50 m of the mother. Time as the calf's NN was similarly corrected for time within 5 m of the calf, using the 1-min time points. The percentage of 3-min time points that the mother and calf had no other associates (% alone with mother) was also calculated. All these measures were calculated for each follow and then averaged over all follows for each calf. Averaging the associations over all the follows allows us to more accurately represent transient associations, which is important because each calf was only followed for a small number of hours (Table 1). In addition, the total number of different associates (individual animals within 50 m at any point during any of the follows) was determined for each mother-calf pair over the course of the season.

Collection of signature whistles

Focal calves

Calf signature whistles were collected during focal follows in 2001 and temporary capture-release efforts in 2002 and 2003 (Table 1). Acoustic recordings were made in 2001 simultaneously with the behavioral observations, following the same focal protocols as in 2000. A rigid, 2-m, linear array of 14 hydrophones was towed approximately 1 m off the port side of the boat and 1 m deep (Miller and Tyack 1998). A pair of TASCAM DA-88 8-channel digital audio recorders recorded all 14 channels of the array. The behavioral observations in 2001 were used to find sections of follows when only the mother and calf were present. Signature whistles were assigned to the calves from these sections when two stereotyped contours could be found, one of which was the mother's signature whistle and the other was unknown. Stereotypy was determined by eye when a contour was seen at least 10 times on a section of tape. Most stereotyped contours were seen 25–50 times in a 30-min section. Signature whistles were also collected from two calves during the capture-release efforts in 2002 and a third in 2003. During the capture-release efforts, temporarily restrained dolphins were recorded with a hydrophone in a suction cup attached to the dolphin's melon. Signature whistles were determined by eye as the most common contour recorded on the suction-cup

hydrophone. From the capture–release tapes, a contour had to be found at least 10 times to be considered a signature whistle. Most signature whistles were found more than 50 times in a 10-min section of capture–release recording. The gender of the calves was determined during the capture–release efforts as well. The signature whistles of the two calves recorded in 2002 had also been recorded during the 2001 follows. In both cases, the 2002 signature whistles matched the 2001 whistles (Table 1). Only the 2002 signature whistles were used in the analysis because the signal-to-noise ratio was better in the 2002 recordings.

Other Sarasota whistles

Signature whistles were collected from other members of the Sarasota community during temporary capture–release efforts from 1975–2002. Whistles were extracted by Laela Sayigh from some of the earlier tapes (Sayigh 1992). Whistles from later tapes were digitized using Cool Edit Pro (Syntrillium Software, San Jose, Calif.) and extracted using an automatic extraction procedure (Fripp 1999). Whistles were collected for as many of the dolphins that interacted with the calves as possible.

Non-Sarasota whistles

All Sarasota animals share a home range and therefore have the potential to be in acoustic contact with each other at one time or another, even if they do not interact frequently. Therefore, two sets of non-Sarasota signature whistles were used: (1) signature whistles of captive animals at the Miami Seaquarium in Fla., USA, and the Kolmårdens Djurpark in Sweden, and (2) signature

whistles of wild bottlenose dolphins from Tampa Bay, Fla. Three dolphins at the Miami Seaquarium were recorded by Janet McIntosh and their signature whistles extracted by Jennifer Miksis (Tyack and Sayigh 1997; Miksis et al. 2002). Inês Mello provided signature whistles from seven dolphins at the Kolmårdens Djurpark. The signature whistles of five dolphins from Tampa Bay had been collected during capture–release efforts in 1989 and 1990. These whistles were extracted using the same methods as the Sarasota capture–release whistles.

Comparison of signature whistles

Whistle sample

The calves' signature whistles were compared to the signature whistles of their mothers, the other Sarasota dolphins, and the two control groups. The complete whistle collection consisted of 5 focal calves (one calf's signature whistle was never determined), 6 focal mothers, 57 non-focal Sarasota dolphins, 5 Tampa Bay dolphins, and 10 captive dolphins. Two signature whistles were used for one Sarasota dolphin because this animal consistently produces two signature whistles.

Whistle comparison

To compare whistles, the frequency contour of each whistle's fundamental frequency was first extracted using an automatic contour extraction algorithm (Buck and Tyack 1993). These contours were visually checked to confirm that they were extracted properly. Contours were then compared using dynamic time warping (DTW), a

Table 2 Summary of signature whistle similarities. Similarity between two dolphins' signature whistles was determined using the dynamic time warping (DTW) algorithm described in Buck and Tyack (1993). Similarity is defined here as median $[-\log_{10}(\text{DTW})]$ for the comparisons between all the whistles of the two dolphins. All measures exclude similarities of 0 (defined when

whistles differ in duration by more than a factor of 2 and are therefore not comparable by the DTW algorithm). Sample sizes (n) listed are number of comparisons (not including self except for the overall self-similarity) where the similarity was not 0. The complete sample is 82 dolphins, including the calves and their mothers

Focal	Self-similarity	All similarities except self				No. (%) greater than 3.55
		25th percentile	Median	75th percentile	95th percentile	
1493 ($n=79$)	3.82	2.77	2.99	3.31	3.55	3 (4%)
1573 ($n=79$)	5.09	2.59	2.70	2.78	3.05	1 (1%)
C011 ($n=68$)	5.02	2.66	2.80	3.24	3.78	9 (11%)
C545 ($n=81$)	4.18	2.90	3.04	3.29	3.55	3 (4%)
C992 ($n=71$)	5.21	2.86	3.05	3.39	3.88	16 (20%)
All calves ($n=5$ calves, 378 pairs) ^a		2.71	2.91	3.22	3.64	32 (8%)
Overall self-similarity ($n=79$) ^b		3.43	3.98	4.91	6.17	54 (68%)
All dolphins ($n=6170$ pairs) ^c		2.68	2.87	3.10	3.55 ^d	293 (5%)

^a These samples do not include self-similarities or similarities of 0, but do include the calves' mothers.

^b These measures include only self-similarity measures for all dolphins (including calves). Four of the 67 dolphins only had one whistle in the sample so no self-comparison could be made.

^c These samples do not include self-similarities or similarities of 0, but do include the calves and their mothers.

^d This is the cut-off used to define similar whistles.

procedure that correlates the frequencies of two contours after allowing non-linear warping in time (but not in frequency) of one contour to fit the other (Buck and Tyack 1993). To make the numbers more manageable, the DTW correlations, which range up to 10^8 , were transformed by the logarithm base 10. Because DTW determines dissimilarity, not similarity, the transformed DTWs were converted to similarity by subtracting them from 10. The final measure of similarity between two whistles was therefore $10 - \log_{10}(\text{DTW})$. These similarities ranged from 1–6.5, but only 1.5% were greater than 4. The DTW algorithm could not calculate similarity for whistles that differed in duration by more than a factor of 2. These pairs were arbitrarily assigned a similarity score of 0. Because a 0 score indicates an inability to make a comparison, not a lack of similarity, the 0 scores were excluded for most of the analyses.

Signature whistle similarity

For each pair of dolphins, a median similarity, S , was defined to represent the overall similarity between the two dolphins' signature whistles. The whistle sample included up to ten examples of the signature whistle of each dolphin. The contours chosen were those with the fewest anomalies (jumps in frequency caused by poor signal to noise ratio in the recordings). The median similarity between two dolphins' signature whistles was the median of the similarity scores for all comparisons between their signature whistles, excluding measurements of 0. Measurements of 0 were excluded because these indicate that the two contours could not be compared because of differences in duration and do not reflect an accurate measure of similarity. If there were no similarities that were not 0, the median similarity was defined as 0. These median similarities ranged from 0–5.9 but again, only 1.25% were greater than 4. Two dolphins were considered to have similar whistles if the similarity between their whistles was greater than 3.55, which was the 95th percentile of all similarities excluding the 0s (see Table 2). This means that 95% of the median similarities were less than this cutoff, and whistles with median similarities greater than 3.55 were significantly more similar than random whistles at a criterion of $P < 0.05$.

Results

Focal follows

The focal animals were the six calves born in Sarasota Bay, Florida in 2000. All six calves were followed in both 2000 and 2001 (Table 1). A total of 50 follows were performed for 61 h in 2000, an average of 8 ± 3 follows and 10.2 ± 2.6 h per calf (Table 1). These follows averaged 79 ± 20 min in duration. The behavioral data from these follows were analyzed to determine the behavioral relationships between the calves and the other dolphins

during the calves' first 3 to 4 months, the period when their signature whistles were developing. In 2001, a total of 43 follows were performed over 49 h. This yielded an average of 7 ± 4 follows and 8.1 ± 4.8 h per calf, with an average follow time of 68 ± 34 min.

The primary goal of the 2001 follows was to determine the calves' signature whistles. The signature whistles of four of the six calves were determined during this season: 1493, 1573, C545, and C992. Calf C932 was only found once during the 2001 season and too many animals were present during the follow to determine the calf's signature whistle. Calf C011 did not appear to produce a stereotyped whistle in 2001. Calves 1573 and C545 were caught during temporary capture–release efforts in 2002. They were both determined to be female, and their signature whistles were recorded. The signature whistles recorded matched those found during the 2001 field season (1573: $S = 3.81$; C545: $S = 4.08$; $S > 3.55$ was considered similar). For the analysis of signature whistle similarities, only the 2002 signature whistles from these two calves were used. Calf C011's signature whistle was recorded during the 2003 capture–release and this calf was determined to be female as well.

Signature whistle similarities

The overall median of similarities between the calves' signature whistles and the other whistles in the sample was 2.91 (Table 2). Dolphins' signature whistles were considered similar to each other if the median similarity was greater than the 95th percentile of all non-self comparisons (3.55, Table 2). As 95% of the non-self comparisons were less than this cutoff, whistles with a similarity score greater than 3.55 were significantly more similar than random whistles from our sample at the $P < 0.05$ level. On average, there were 6.4 (8%) dolphins with signature whistles similar to each calf's (Table 2). This varied from calf 1573, who had 1 (1%), to calf C992, who had 16 (20%).

If the calves are forming their signature whistles by listening to the signature whistles in their environments, then the calves' signature whistles should be more similar to the signature whistles they heard than to those they did not hear. In other words, the whistles that are similar to the calves' whistles should be more likely to be whistles from Sarasota dolphins than from non-Sarasota dolphins. Because calves may model their signature whistles on the signature whistles of multiple dolphins, each pairwise comparison between a calf's signature whistle and the signature whistle of another dolphin is important. We therefore looked at all the pairwise comparisons to determine which had high similarities.

The dolphins with whistles similar to the calves' whistles were significantly more likely to be Sarasota dolphins than expected. Of the 410 pairwise comparisons, 32 were greater than 3.55 and were therefore classified as similar (Table 3). Of those 32, 30 (94%) were Sarasota dolphins and only 2 (6%) were non-Sarasota dolphins

(Table 3). However, Sarasota dolphins only comprised 82% of the total sample (Table 3). To test whether this difference was significant, the similarity scores were randomized with respect to the associations (Sarasota vs non-Sarasota), and the number of high similarity scores assigned to Sarasota dolphins was calculated. Out of 10,000 trials, less than 5% resulted in 30 or more of the high similarity scores being assigned to Sarasota dolphins (so $P < 0.05$). Although the Sarasota dolphins far outnumbered the non-Sarasota dolphins in our sample, the Sarasota dolphins were significantly more likely to have signature whistles similar to the calves' signature whistles than randomly expected.

Association patterns

To investigate the social factors that might affect the calves' choices of models, we examined the behavioral interactions between the calves and the dolphins in the sample. This analysis addressed the following question: what characterized the dolphins with whistles similar to the calves' whistles? During year 1 (2000), the first summer of the calves' lives, their mothers dominated their social relations. All of the calves were within 50 m of their mothers more than 99% of the time (Table 4). The mothers were within 5 m of their calves 76% of the time on average (Table 4). Time spent alone with their mothers varied greatly, from 15–59% (Table 4). The focal pairs had between 9 and 39 total associates over that first summer, averaging 28 (Table 4). Not surprisingly, time spent alone with the mothers and total number of associates were highly negatively correlated ($n=6$, $r=-0.87$, $P=0.05$).

For each focal pair, four measures were calculated for each associate: (1) percent time within 50 m of the mother, (2) percent time within 5 m of the calf, (3) time as the mother's NN, corrected for time within 50 m, and (4) time as the calf's NN, corrected for time within 5 m. As would be expected, time within 50 m and time within 5 m were highly correlated ($n=168$, $r=0.88$, $P < 0.0001$). Time as the mother's NN was correlated with both time within 50 m and time within 5 m (50 m: $n=168$, $r=0.44$, $P < 0.0001$; 5 m, $n=168$, $r=0.54$, $P < 0.001$). Time as the calf's NN was not significantly correlated with any of the other measures ($n=168$, all r 's between -0.3 and 0.3).

Table 3 Similarities to calf signature whistles by location. This table tests whether calves were more likely to have whistles similar to dolphins in the Sarasota community than dolphins from other communities. The total sample for comparison includes 82 dolphins/calf for 5 calves. The sample includes the calves and their mothers but does not include self-comparisons. Of the 82 dolphins, 67 were Sarasota dolphins and 15 were non-Sarasota dolphins, including 10 captive dolphins and 5 Tampa Bay dolphins

Similarity	Sarasota	Non-Sarasota	Total
Low (≤ 3.55)	305 (81%)	73 (19%)	378
High (> 3.55)	30 (94%)	2 (6%)	32
Total	335 (82%)	75 (18%)	410

The relationship between signature whistle similarity and behavioral association

Having established that the calves modeled their signature whistles on the whistles they heard from Sarasota dolphins, we next investigated who those models were. Of the 30 Sarasota dolphins with signature whistles similar to one of the focal calves, 18 (60%) were female, 11 (37%) were male, and 1 (3%) was of unknown gender. This breakdown was similar to the overall breakdown of the sample (53% female, 45% male, 2% unknown) and was not significantly different from random (by randomization test, 10,000 trials, $P=0.86$). Similarly, the similar signature whistles were randomly spread across the Sarasota dolphins by age (10,000 trial randomization, $P=0.8$).

The most notable pattern in similar Sarasota signature whistles was that they were more likely to be dolphins who spent only a small amount of time with the calves (Table 5). Of the 30 Sarasota dolphins with similar whistles, 27 (90%) were within 50 m of the focal pair less than 5% of the time. However, by a randomization test, this result was not statistically significant (10,000 trials, $P=0.1$). Figure 1 shows spectrograms of the calves' signature whistles and the signature whistles of some of their potential models. The figure includes spectrograms of each calf's mother's signature whistle, and that of the associate that spent the greatest amount of time within 50 m. With the exception of C011, whose signature whistle is similar to her mother's, none of the calves' signature whistles were similar to the signature whistles of their mothers or closest associates. Figure 1 also shows spectrograms of the two Sarasota dolphins with the most similar signature whistles to each calf's signature whistle. All of these potential models were Sarasota dolphins who were within 50 m of the focal pair less than 5% of the time. The "potential models" shown in this figure are only some of the dolphins with similar signature whistles. On average, each calf had six dolphins with similar signature whistles. The calves could have used any or all of these signature whistles as models from which to create their own unique signature whistles.

Adult signature whistles by community

If calves model their signature whistles on the whistles of community members, the signature whistles of community members might be expected to be more similar to each other than to members of other communities. This is exactly what we saw. Of the 236 high similarity scores ($S > 3.55$, excluding self-similarities), 182 (77%) occurred between members of the same community (Table 6). To test whether this could have occurred randomly, the matrix of similarity scores between all adults was randomized, excluding self-similarities, and the number of high similarity scores that occurred between dolphins in the same community was calculated. Out of 10,000 trials, only 2% resulted in as many similar whistles within commu-

Table 4 Association patterns in year 1 (2000). Focal mother–calf pairs were observed in the calves’ first 3–4 months. Calves were identified through association with a presumed mother. Similarity is

Focal	Mother–calf distance		% Alone with mother ^a	Total associates ^a	Nearest neighbors		Associates present >5%		Similarity to mother’s whistle
	<50 m	<5 m			Mother	Calf	Within 50 m	Within 5 m	
1493	100%	65.6%	58.8%	9	1	2	3	0	2.98
C932	100%	79.5%	38.4%	32	19	11	17	3	N/A
1573	99.25%	76.1%	15.5%	39	9	11	18	2	2.49
C011	100%	74.7%	27.9%	29	12	10	16	8	3.65
C545	100%	81.7%	42.1%	32	7	6	15	4	3.16
C992	100%	80.7%	29.2%	27	14	1	14	4	3.04
Average	99.9%	76.4%	35.3%	28	10	8	14	4	3.06

^a Highly negatively correlated ($n=6$, $r=-0.87$, $P=0.05$).

Table 5 Similarity to Sarasota signature whistles by association. The similarity score of the Sarasota dolphins’ signature whistles to the calves’ signature whistles are shown here classified by each dolphin’s time within 50 m of the focal pair. Similarity scores are divided based on the similarity cutoff of 3.55, which was the 95th percentile of all similarities (see Table 2). $n=67$ animals/calf by 5 calves =335 comparisons

Similarity	Time within 50 m of focal pair		Total
	>5%	<5%	
Low (≤ 3.55)	64 (21%)	241 (79%)	305
High (> 3.55)	3 (10%)	27 (90%)	30
Total	67 (20%)	268 (80%)	335

nities as we observed ($P=0.02$). The whistles of each community therefore do appear to differ from each other.

Discussion

This study set out to answer two questions: (1) are the calves modeling their signature whistles on whistles in their acoustic environments? and (2) if so, what relationship do the calves have with the dolphins that produce their models? The results of this study indicate that bottlenose dolphin calves model their signature whistles on whistles they hear from community members, possibly from dolphins with whom they have few social interactions.

Table 6 Similar adult signature whistles by community. Adult whistles that were similar to each other are shown here classified by their community. Whistles were considered similar to each other if

Whistle community	Number of similar whistles (expected ^a)			Total similar whistles
	Sarasota	Captive	Tampa	
Sarasota	180 (154)	26 (24)	0 (12)	206
Captive	28 (24)	2 (4)	0 (2)	30
Tampa	0 (12)	0 (2)	0 (1)	0

^aExpected is based on a totally random distribution of similarity within the whistle sample, with the following breakdown: 81% (67 dolphins) Sarasota; 13% (10 dolphins) captive; 6% (5 dolphins) Tampa.

between the mother’s signature whistle and the calf’s. Whistles were considered similar if their similarity score was greater than 3.55 (see Table 2)

At the onset of this study, we had three hypotheses as to how calves could develop their unique signature whistle contours: (1) calves model their signature whistles on whistles they hear; (2) calves do not model their signature whistles but rather build signature whistles based on sounds they produce randomly; and (3) calves design their signature whistles to be different from the whistles they hear frequently. [Note that a fourth hypothesis, that signature whistles are determined genetically, has previously been discounted by Sayigh (1992; Sayigh et al. 1990; 1995).] These three hypotheses lead to different predictions about the similarity between the calves’ signature whistles and the other signature whistles in our sample. If calves model their signature whistles on whistles they hear (hypothesis 1), then their signature whistles should be significantly more similar to the signature whistles of other Sarasota dolphins than to non-Sarasota dolphins. If calves do not use models (hypothesis 2), then their signature whistles should be randomly similar to all the other signature whistles in the sample, irrespective of where those dolphins live. If calves anti-model, making their signature whistles different from the whistles they hear (hypothesis 3), then the calves’ signature whistles should be different from the whistles of their close associates but randomly similar to the rest of the whistles in the sample, regardless of where those dolphins live. Hypotheses 2 and 3 both predict that the calves’ signature whistles will be as likely to be similar to non-Sarasota whistles as to Sarasota whistles. In this study, the wild-born Sarasota calves were significantly more

their similarity score was greater than 3.55 (see Table 2). This analysis excludes self-similarities

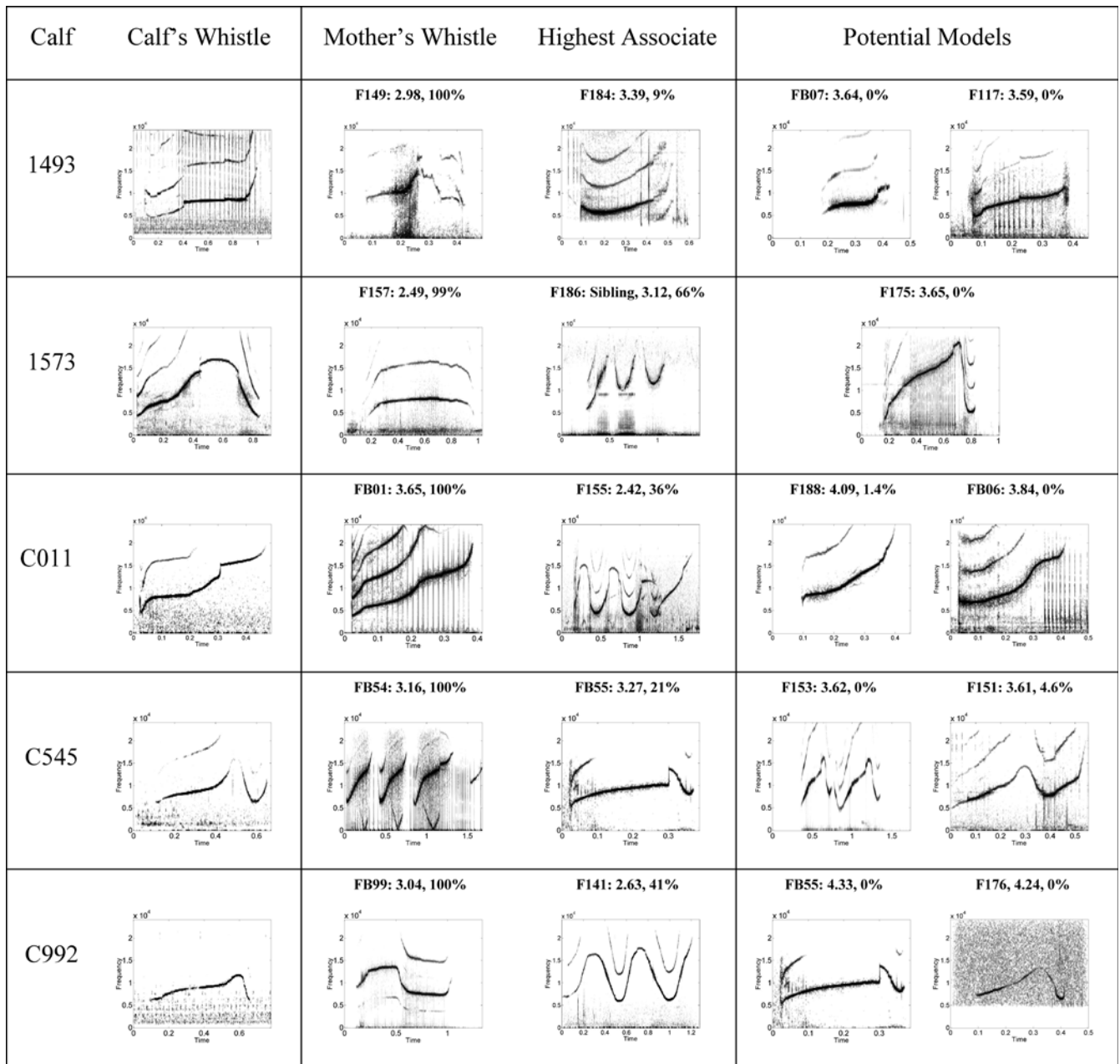


Fig. 1 Signature whistles of the calves and some of their potential models. The figure presents the signature whistles of the calves, their mothers, their highest associates (the dolphin with the most time within 50 m of the pair), and two of their potential models. The potential models are the two Sarasota whistles with the highest similarities, of those whose similarity to the calf's signature whistle is greater than 3.55 (see Table 2). The spectrograms are labeled with

the similarity score and the percent time within 50 m. For the mothers, the percent time is the time the calf was within 50 m of the mother. The frequency axes (in Hz) of all the spectrograms are the same but the time axes (in s) are different. Note that the DTW comparison algorithm warps contours in time, so minor differences in time do not affect the comparison

likely to have signature whistles similar to the signature whistles of other Sarasota dolphins than to those of non-Sarasota dolphins. Thus, the calves must have modeled their signature whistles on whistles they heard, and only hypothesis 1 can be correct.

Some of the Sarasota dolphins considered to be models based upon whistle similarity were never recorded associating with the calves, but this observation does not change our conclusion. All the Sarasota dolphins in this

sample associated with at least one of the focal calves. Since all of the focal calves were found in the same general area, they were likely to have heard the signature whistles of all the Sarasota dolphins in the sample, even if they were not sighted together in our samples. Unfortunately, we were only able to follow each calf for a small fraction of its first months, an average of 10 h each. In such a limited sample, we must be concerned that the associations we saw might not be representative of the

dolphins' actual association patterns. However, we can prevent rare association from appearing more common than they are by calculating the association for each follow and then averaging them over all follows for each calf, as we did. In addition, while it is likely that some common associations were missed, it is unlikely that common associations with acoustic models were missed preferentially. If common associations with models and non-models were missed randomly, such mistakes should not affect the randomization statistics. In fact, if common associates are less likely to be models, missed associations should only serve to dilute the statistics. Therefore, the probability that we missed some common associations does not negate the possible pattern we saw toward calves using rare associates as models.

The idea that some animals may prefer less abundant vocal models has been suggested before: Tchernichovski et al. (1997) found that the less often juvenile zebra finches heard a model song, the more completely they imitated it. They suggested that "the 'too much' factor might have to be considered as one of the variables that affects vocal learning," and that "model overexposure may trigger processes of active winnowing" (Tchernichovski et al. 1997, p 12904). Similar processes may be occurring in the dolphin calves. Overexposure to certain signature whistles may winnow those whistles from the calf's possible model pool, as it does for zebra finches.

Our results are consistent with previous data on signature whistle development in wild bottlenose dolphins. Sayigh (1992) reported on two calves from the Sarasota community (out of four in her study) whose signature whistles were most similar to unrelated females in the Sarasota community. In both cases, the adult "model" spent little (11%) or no (0%) time with the calves during the focal follows. Sayigh (1992) was unable to determine whether the similarity of the calves' signature whistles to the signature whistles of those particular adults was random or based on the probability that, as members of the same community, the models were part of the calves' acoustic environments. Our results show that the similarity is not random. Interestingly, one of these calves was female and the other of unknown gender (Sayigh 1992). Since all the calves of known gender in the current study were female, all the wild calves that have been shown to use this type of model have been either female or of unknown gender. Sayigh (1992) reported on two other Sarasota calves, whose signature whistles were similar to their mothers' signature whistles. One of those calves was male and the other of unknown gender. Sayigh et al. (1995) compared the whistles of 21 male calves and 21 female calves to their mothers' whistles, and confirmed that sons are much more likely than daughters to produce whistles similar to their mothers'. The whistles of adult males are also less stable than those of adult females. Pairs of male dolphins who share a strong social bond modify their signature whistles as adults when they form their alliance, developing signature whistles that are similar to each other (Smolker and Pepper 1999; Watwood 2003). These results suggest that males and females may use their

signature whistles differently as adults and may follow different rules when selecting models as calves. Further research is needed to investigate this possibility.

Previous data from captive-born calves also indicate that calves imitate acoustic models in their environments when developing their signature whistles. When calves are raised alone with their mother or a foster-mother, and therefore have only one acoustic model, they develop a signature whistle similar to the mother's signature whistle, regardless of their gender (Caldwell and Caldwell 1979; Tyack and Sayigh 1997). Calves in captivity sometimes choose a whistle that is common in their acoustic environment as a model (Caldwell and Caldwell 1979; Tyack and Sayigh 1997). Caldwell and Caldwell (1979) reported on one male calf whose signature whistle was somewhat similar to the whistles of an extremely vocal Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) in the pool. Tyack and Sayigh (1997) discuss a male bottlenose dolphin calf whose signature whistle was most similar to the signature whistles of two particularly vocal subadults in his community. In both cases, the interactions between the calf and his model were unknown. Other captive calves have chosen rarer whistles as their models. Two calves born at the Miami Seaquarium, one male and one female, developed signature whistles that most closely resembled the whistles used by their human trainers (Tyack and Sayigh 1997). At the Miami Seaquarium, the trainers' whistles represented fewer than 4% of the whistles heard in the pool. In fact, captive-born dolphins are significantly more likely to have signature whistles resembling the trainers' whistle than wild-born dolphins (Miksis et al. 2002). This indicates that captive-born calves, like their wild-born counterparts, are using acoustic models in their environments to create their unique signature whistles.

An interesting side effect of using community members as acoustic models could be to make the whistles of the members of the community more similar to each other. Wang et al. (1995) found differences in whistle structure between communities of bottlenose dolphins but could not determine whether the differences were learned or the result of genetic differences between communities. Our results, particularly calves imitating the whistles of unrelated dolphins, indicate that some of those differences are learned. In our study, the signature whistles of adults were more likely to be similar to the signature whistles of community members than expected. However, of the non-self comparisons between adult dolphins in our study, only 4% of the signature whistles were similar to each other. Therefore, although the similar signature whistles were more likely to be dolphins in the same community, it is unlikely that there are enough of these similarities for these individually specific calls to function well for community recognition.

In conclusion, bottlenose dolphins have evolved the ability to learn new sounds as adults and calves, and are among the few species of mammals that use this ability in the development of their natural vocalizations (bats: Boughman 1998; tamarins: Hodun et al. 1981; review:

Janik and Slater 1997). Dolphin calves learn their signature whistles by imitating acoustic features of the signature whistles of community members. To make their signature whistles distinguishable from the dolphins with whom they associate, dolphin calves may select their models from dolphins with whom they spend only a small amount of time.

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