

Whistle Stability and Variation in Captive Bottlenose Dolphins (*Tursiops truncatus*) Recorded in Isolation and Social Contexts

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Abstract

Common bottlenose dolphins (*Tursiops truncatus*) produce a range of underwater vocalizations, both pulsed (echolocation clicks and burst-pulses) and nonpulsed (whistles). Whistles may be emitted in stereotyped (signature) or variant patterns, and their production might be affected by sex, age, environmental, and social contexts. This study examined, non-intrusively, the whistle emissions of six captive bottlenose dolphins at Zoomarine in Algarve, Portugal, in two separate time sets and three different contexts: two of the animals in isolation in 2008, and all six in 2012, both segregated from their group and in social context. From a total of 1,681 whistles, 1,249 were analyzed from 32 samples in different contexts: seven samples in isolation in 2008, 18 in segregation in 2012, and seven in social context. Through visual inspection of spectrograms, whistles were classified into 12 different contour categories. Only one category was found in both time sets and could be considered a signature whistle by SIGID criteria (Janik et al., 2013). This contour was associated with the same animal in 2008 and 2012. Whistle emission rates were 7.8 times higher in isolation as compared with social context, and significant differences were also found in the end and maximum frequencies as well as number of inflections and loops. Multiloop whistles were more common in isolation than in social contexts. The variant (nonstereotyped) contours dominated the whistle production in segregated contexts (but not by isolated animals) as well as in social contexts. This study highlights the importance of examining the nonstereotyped portion of the bottlenose dolphin's whistle repertoire in different contexts as signature whistle production may not be a constant or universal phenomenon.

Key Words: common bottlenose dolphins, *Tursiops truncatus*, whistles, emission rates, isolation, social contexts, captivity

Introduction

Common bottlenose dolphins (*Tursiops truncatus*) produce a wide variety of underwater sounds (Lammers & Oswald, 2015), including pulsed emissions (i.e., echolocation clicks and burst-pulsed sounds) and nonpulsed signals (i.e., whistles). Whistles usually occur between 4 and 15 kHz and may have a social function such as individual identification (Caldwell et al., 1990; Janik, 2013). This type of vocalization often lasts less than 1 s but shows a range of frequency modulation contour shapes varying from concave to convex, upsweep to downsweep, and with intermediary forms between categories (Bazúa-Durán & Au, 2002; Dudzinski et al., 2009).

Bottlenose dolphin whistles may consist of one unit of sound (uniloop) or several units (multiloop), which may be repeated as a single multicontoured whistle (connected) or with short periods of silence (disconnected) (Caldwell et al., 1990; Sayigh et al., 1990, 1995; Janik & Slater, 1998; Esch et al., 2009a; King et al., 2013). Previous research has demonstrated that the number and duration of loops are affected by the behavioral context. Isolation or capture-release contexts revealed a higher number of loops of the same repetitive whistle (stereotyped) compared with undisturbed conditions (Esch et al., 2009b). These results suggest that alterations to whistle production may contain information about the emitter's motivational/emotional state and that the increase in number of loops might allow dolphins to convey additional information while also communicating identity (Weary & Fraser, 1995; Watts & Stookey, 2001; Barton, 2006; Esch et al., 2009b).

The fact that dolphins produce stereotyped whistles that are stable over long periods of time (Sayigh et al., 1990, 2007; Bruck, 2013; Luís et al., 2015) suggests that these acoustical signals may be involved in individual identification and position, thus, the notion of a signature whistle (Caldwell & Caldwell, 1965; Tyack 1986; Caldwell et al., 1990; Sayigh et al., 1990; dos Santos et al., 2005). Studies on ontogeny of signature whistles revealed that these whistle types are developed through vocal learning during the first year of a dolphin's life and may remain stable throughout an individual's lifetime (Caldwell & Caldwell, 1979; Caldwell et al., 1990; Sayigh et al., 1990; Janik & Sayigh, 2013). Furthermore, dolphin calves are known to model their signature whistles on sounds in their acoustic environments (Tyack & Sayigh, 1997; Fripp et al., 2005), including man-made whistles (Miksis et al., 2002). Male dolphin calves are more likely to produce whistles similar to those of their mothers, while females tend to produce more distinct signature whistles (Sayigh et al., 1990, 1995). While females seem to produce stable signature whistles throughout their life (Sayigh et al., 1990, 2007), males are more likely to change the modulation pattern of their signature whistles in the process of establishing alliances with other males (Smolker & Pepper, 1999; Connor et al., 2000; Watwood et al., 2004).

Signature whistles are individually distinctive, stereotyped, and the most commonly produced whistle type in isolation (Caldwell et al., 1990). While in isolation, signature whistles may represent 80 to 100% of whistles' emissions (Caldwell & Caldwell, 1965; Caldwell et al., 1990; Janik & Slater, 1998; Sayigh et al., 2007; Janik et al., 2013). Considering different contexts, however, signature whistles may not be the most abundant type (McCowan & Reiss, 1995, 2001; Cook et al., 2004; Watwood et al., 2005; Luís et al., 2015). For wild bottlenose dolphins, signature whistle production may be lower, accounting only for 32 to 52% of all whistles (Cook et al., 2004; Watwood

et al., 2005; Luís et al., 2015). Moreover, in captivity contexts, the emission of signature whistles may not even occur (McCowan & Reiss, 1995, 2001); hence, additional investigations of whistle production remain relevant.

Recently, Janik et al. (2013) proposed a useful approach to identify signature whistles based on their pattern of emission (the SIGNature IDentification [SIGID] criteria): if 75% or more of whistles of the same whistle type are emitted within 1 to 10 s of another whistle of the same type, this contour may be considered a signature whistle. In this study, the acoustic behavior of six captive bottlenose dolphins of various ages and both sexes was sampled in order to examine whistle stability and variation as well as the variability of emission rates and time-frequency characteristics of the whistles. This study focused on not only recording whistles in different social conditions, allowing a contextual comparison, but also on recording the same animals across 4 y, allowing an examination of the stability of the whistles.

Methods

Facility and Subjects

Recordings were conducted at Zoomarine, Algarve, Portugal, in two different periods: (1) between February and April 2008 and (2) between April and May 2012. The subjects of this study were two subadult males (coded AM4 and UM3) in 2008; and a male calf (PM9), two subadult females (AF6 and IF7), and three adult males (HM5, UM3, and AM4) in 2012 (Table 1). AM4 and UM3 were the focal animals of this study and were recorded in different life stages in 2008 and 2012.

AM4 and UM3 were together with other dolphins in Sam's Stadium in 2008. All subjects, with the exception of calf PM9, were together in the same pool, Blue Lagoon, for 5 mo prior to the 2012 recordings. These dolphins had already been part of a larger group in another pool, Enseada,

Table 1. Bottlenose dolphins (*Tursiops truncatus*) held at Zoomarine, Algarve, Portugal, which were involved in this study, along with their sex, year of birth, identity of mother (when known), and year of recording

Code name	Sex	Year of birth	Mother	Year recorded
HM5	M	1995	--	2012
UM3	M	2003	CF8	2008, 2012
AM4	M	2004	MF8	2008, 2012
AF6	F	2006	CF8	2012
IF7	F	2007	MF8	2012
PM9	M	2009	XF9	2012

with other adult male and female animals. PM9 was with his mother and other dolphins in a different pool, Sam's Stadium, prior to joining this social group in Blue Lagoon only 2 mo before the data collection.

This study was reviewed and approved by Zoomarine's Ethical and Animal Welfare Committee and followed careful procedures to minimize disturbance to the animals.

Data Collection

2008—Recordings were carried out at Sam's Stadium in a covered support pool (pool E), which is connected to other pools by channels that can be blocked by solid metal panels (Figure 1). During isolation sampling, the focal animal (either AM4 or UM3) was placed alone, with all passage panels closed and the other dolphins kept away by trainers in pool A.

2012—Recordings were carried out in the covered Blue Lagoon pool, which is divided by perforated fiberglass gates (Figure 2). Data collection was carried out in two contexts: (1) segregated (animal alone in one section of the pool but not acoustically isolated from the others) and (2) social group (one or two more animals in the pool with the focal animal) (Table 2).

Acoustic Recordings

In 2008, emissions were recorded using a Cetacean Research Technology SQ26-MT hydrophone, which has a frequency range of 0.020 to 50 kHz, a transducer sensitivity of -194 dB re $1\text{V}/\mu\text{Pa}$, and an effective sensitivity of -169 dB re $1\text{V}/\mu\text{Pa}$. For the 2012 recordings, the hydrophone used was a Cetacean Research Technology C55, which has a linear frequency range of ± 3 dB in the 0.016 to 44 kHz, a usable frequency range of $+3/-20$ dB in the 0.006 to 203 kHz band, a transducer sensitivity of -185 dB re $1\text{V}/\mu\text{Pa}$, and an effective sensitivity of -165 dB re $1\text{V}/1 \mu\text{Pa}$. Both hydrophones were connected to a Micro Track II recorder set to record .wav files with a 48-kHz sampling rate and a 24-bit resolution in a 2-GB CompactFlash card. During the data collection, human presence near the pools was kept to a minimum (one trainer and one data recorder).

For the data collected in 2008 at Sam's Stadium pool (Figure 1), a minimum habituation period of 10 min was established to prepare the set up and to allow the dolphin to adapt to the new context (isolation).

For the data collected in 2012 at Blue Lagoon pool (Figure 2), a habituation period of 15 min was established to allow the animal to adapt to the session context (segregated from the other animals or in a social group) and to desensitize it to

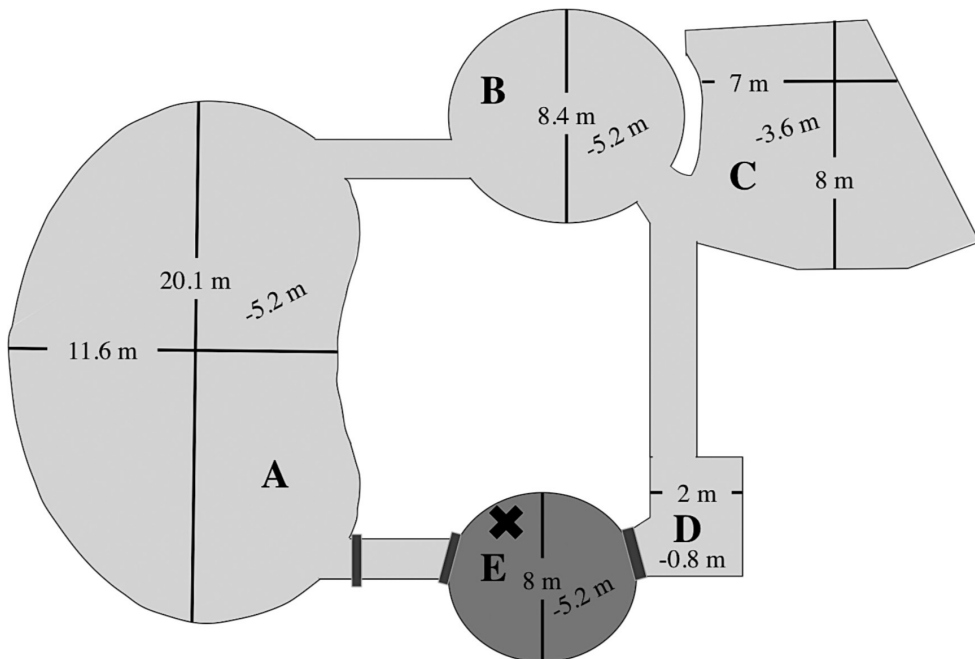


Figure 1. Pool dimensions of the Sam's Stadium sections, with the experimental pool for the isolation context in dark gray (E) and the closed metal panels in darker gray; the X represents the hydrophone position.

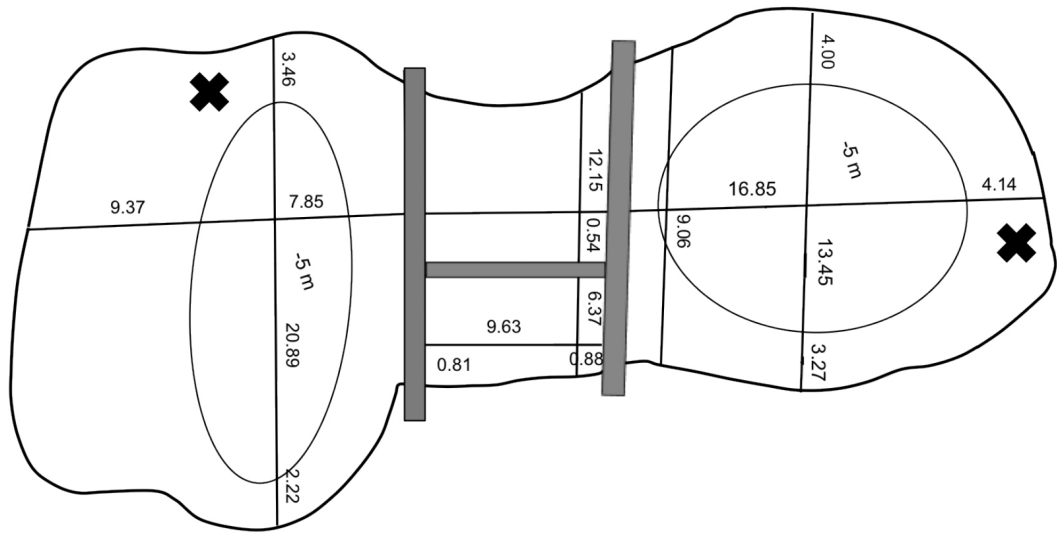


Figure 2. Pool dimensions of the Blue Lagoon sections with the Xs representing the hydrophone positions and the gray bars representing bridges and partitions connected with perforated fiberglass doors.

Table 2. Number of 15-min samples per focal dolphin and context of the acoustic recordings

	Condition	AM4	UM3	AF6	HM5	IF7	PM9
Feb-April 2008	Isolation	4	3	--	--	--	--
April 2012	Segregated in acoustic contact	3	3	3	3	3	3
April-May 2012	In social group (non-exclusive)	4	2	2	4	4	2

the presence of the hydrophone. In 2012, acoustic isolation was not logistically possible; thus, an alternative method was used to attribute whistles to emitters. Data collection included notation of intense acoustic emissions recorded when only one dolphin was under water near the hydrophone and at least partially oriented towards it, making this animal in those well-defined instances, with reasonable confidence, the *most-likely emitter*.

In both years, hydrophones were placed as far away from the other animals as possible (Figures 1 & 2) at a depth of 1 m. The duration of the recordings was 15 min, and all dolphins were familiar with every section of the pool since changing sections is part of their routines.

Acoustic Analysis

To identify, count, and classify whistle emissions, acoustic recordings were inspected and validated by two independent observers, visually and aurally,

using *Raven Pro 1.4* (Cornell Lab of Ornithology, Ithaca, NY, USA) with a Hann window of 512 points (2008 data) and a Hamming window of 512 points (2012 data), both with 50% overlap. Whistles were selected according to Bazúa-Dúran & Au (2002, 2004) and Baron et al. (2008), taking into account the following features: minimum of 300 ms duration, sharp and defined contours, no overlapping with other vocalizations, and good signal-to-noise ratio. Since absolute levels were not critical, no attempt was made to obtain calibrated pressure measurements. For the previously selected whistles, the following acoustic features were measured using *Raven Pro 1.4*: start, end, minimum, maximum, and peak frequencies; duration; number of inflection points; and number of loops.

Using visual categorization (Janik & Slater, 1998), stereotyped whistle contours were cross-compared for frequency modulation similarity and assigned to mutually exclusive groups,

regardless of the emitter. Each whistle category had to include at least five similar contours in the total recordings. Whistle contours with low representation were labeled *variant*.

Two experienced observers performed the initial contour classification task. Subsequently, a subset of 50 randomly selected whistles was used to test for interobserver reliability, using Kendall's W coefficient of concordance (Siegel & Castellan, 1988), to confirm the initial classification. Printed sheets (7 × 15 cm) with spectrograms of stereotyped whistles (repeatedly recognizable, stable contours) were presented, in random order, to two naïve observers. Each observer was asked to group the whistles into categories according to their graphical appearance.

Data Analysis

In order to identify signature whistles, the SIGID criteria (Janik et al., 2013) were used. This method proposes that a vocalization can be identified as a signature whistle if 75% of all whistles in a bout consist of the stereotyped whistle. Each bout has to be composed of sequences of the same contour in intervals of 1 to 10 s. These criteria were applied bidirectionally; thus, for a whistle to be counted as part of a bout, it had to be followed or preceded by another whistle of the same type inside the time interval.

To validate this approach, the whistles (*sensu* Caldwell & Caldwell, 1968) of AM4 and UM3 were extracted from the isolation recordings. Following Janik et al. (1994), the dominant whistle type emitted by each individual (i.e., the most frequently emitted whistle contour) could be considered its signature whistle. To assess

the differences between contexts of emission in whistle rates and characteristics, all the whistles that could be unambiguously assigned to AM4 and UM3 were selected. The Kruskal-Wallis test was used to examine differences in whistle emission rates according to the context (isolated, segregated, and social) for dolphins AM4 and UM3.

To study the effect of isolation, segregation, and social contexts on whistle characteristics, a full-factorial multivariate analysis of variance (MANOVA) with Games-Howell *post-hoc* test was performed for the acoustic features of the whistles assigned to the two dolphins that were present in all contexts (UM3 and AM4). All statistical analyses were performed using *SPSS Statistics 21* (IBM Inc., Armonk, NY, USA).

Results

A selection of 1,249 good-quality whistles (651 from 2008 and 598 from 2012) was extracted for analysis, representing 77.53% of the total whistle samples. Based on visual classification, a total of 466 stereotyped whistles from three categories (labelled with arbitrary codes LS, HOa, and HOB; Table 3 & Figure 3) and 185 nonstereotyped whistles (variant) were identified in the isolation context. From the 2012 dataset, a total of 464 whistles with variable contours were observed, and 134 whistles of nine stereotyped contours were identified (codes AR, BA, BG, ES, LC, LS, MN, PL, and VL; Figure 4). These categories were obtained with high concordance strength ($W = 0.846$, $p < 0.001$) when compared across observers.

When young males AM4 and UM3 were isolated (2008 dataset), they mostly emitted three

Table 3. Values represent percentages of stereotyped whistles occurring with intervals between 1 to 10 s (SIGID criteria). Those in bold refer to the contour qualifying as a signature whistle (> 75% occurrence). Double hyphens represent the categories of contours absent in the datasets.

Contour	SIGID % in isolation context	SIGID % in segregated/social context
AR	--	0
BA	--	0
BG	--	0
ES	--	0
HOa	56.94	--
HOb	56.25	--
LC	--	57.14
LS	93.65	88.89
MN	--	0
PL	--	14.29
VL	--	57.14

Table 4. Number of whistles attributed to their most-likely emitters (from the oldest to the youngest animal from left to right) in segregated and social contexts (2012); “Variants” refers to nonstereotyped whistles.

Contour	Most-likely emitters						Occurrences not attributed	Total of whistles by category
	HM5	UM3	AM4	AF6	IF7	PM9		
AR	0	3	1	1	1	1	3	10
BA	0	2	1	3	0	0	0	6
BG	0	0	0	1	3	2	3	9
ES	0	0	0	2	4	0	0	6
LC	0	0	1	0	0	0	13	14
LS	8	0	43	0	0	0	12	63
MN	0	1	0	0	4	0	0	5
PL	1	0	3	2	4	0	4	14
VL	0	1	0	0	0	0	6	7
Variants	24	40	58	65	69	54	154	464
Total of whistles by emitter	33	47	107	74	85	57	195	
Total								598

stereotyped whistles (LS, HOa, and HOb). For AM4, the dominant contour was LS, representing 79.04% of his total whistle emissions. For UM3, the dominant contour was HOa, representing 37.31% of his total emission, followed by HOb, representing 16.58% of his total emission.

In the 2012 sample of good quality whistles ($N = 599$), a total of 404 whistles could be attributed to their most-likely emitter based on the focal observations during segregated and social contexts. Of these attributed whistles, only 33.17% were stereotyped whistles ($n = 134$). Analyzing these stereotyped whistles and their most-likely emitters, the majority was the LS contour (68.25%) and was once again attributed to the dolphin AM4. Animal HM5 also produced the LS contour but at a lower percentage (12.70%). It should be noted that the contours BA, ES, and MN, despite their low number, all were attributed to a defined most-likely emitter. For example, the ES contour was only shared by females, and BA and MN are shared between dolphins that were together in the same pool when they were calves (Table 4).

The LS contour was the only whistle type observed in all contexts: in isolation (2008 dataset), segregation, and social contexts (2012 dataset) (Figure 3).

Using SIGID criteria, only LS qualified as a signature whistle (Figure 3) as 93.65% of the LS emissions occurred in isolation (by AM4) and

88.89% occurred in segregated and social contexts (Table 3). For HOa and HOb whistles (Figure 3), only 56.94 and 56.25% of the emissions (by UM3; see Table 3) occurred within 1 to 10 s of another whistle of the same type and, therefore, were not in agreement with SIGID conditions. For the segregated and social contexts, no other contour was identified as a signature whistle, with contours LC and VL emitted most frequently (both 57.14%; Table 3).

Emission Rates and Time-Frequency Parameters

The production rates and acoustic measurements of whistles were analyzed for the sessions involving dolphins AM4 and UM3 (in both years). The Kruskal-Wallis test revealed significant differences in the whistle emission rates between isolation and social context ($H(2) = 10.104, p = 0.006$) (Figure 5). During isolation, whistle emission rates were 7.8 times higher than in the social context. Although whistle rates were lower in the segregated context than in isolation and higher than in the social context, these differences were not significant.

Significant differences were found in the acoustic characteristics of whistles between contexts ($F(16, 1594) = 14.830, p < 0.001$). In particular, significant differences were obtained for end and maximum frequencies ($F = 38.125, p < 0.001$ and $F = 7.193, p = 0.001$, respectively), the number of inflection points ($F = 35.847, p < 0.001$), and the

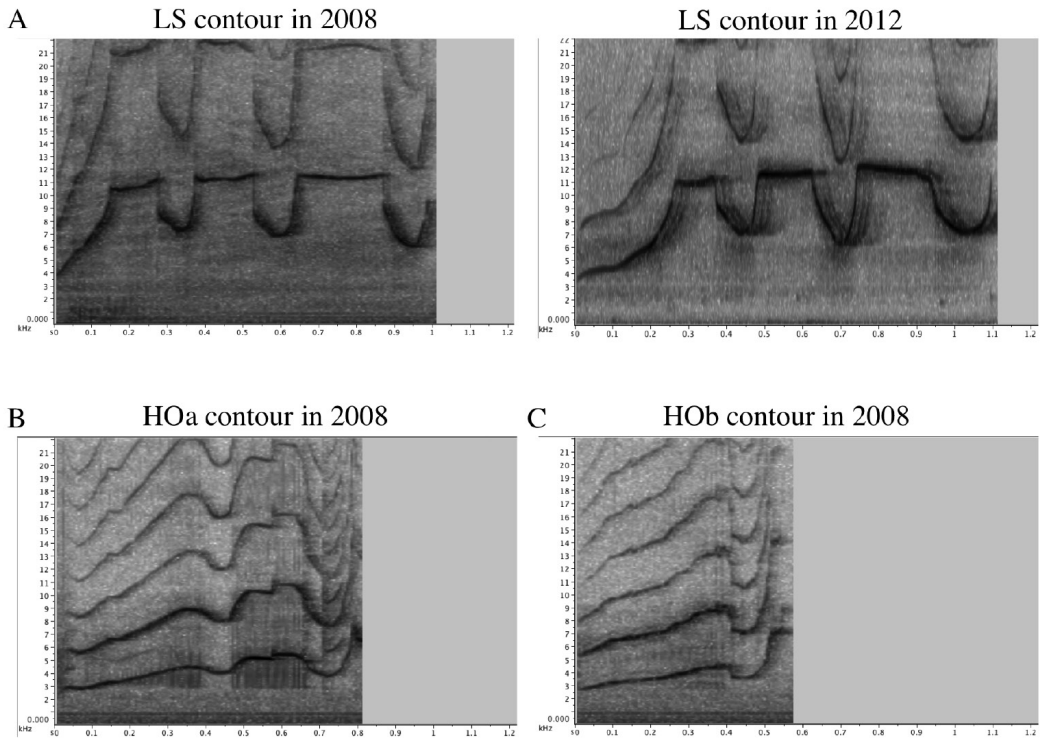


Figure 3. (A) LS contour observed in all contexts (2008 and 2012); (B) HOa contour observed only in isolation (2008); and (C) HOB contour observed only in isolation (2008).

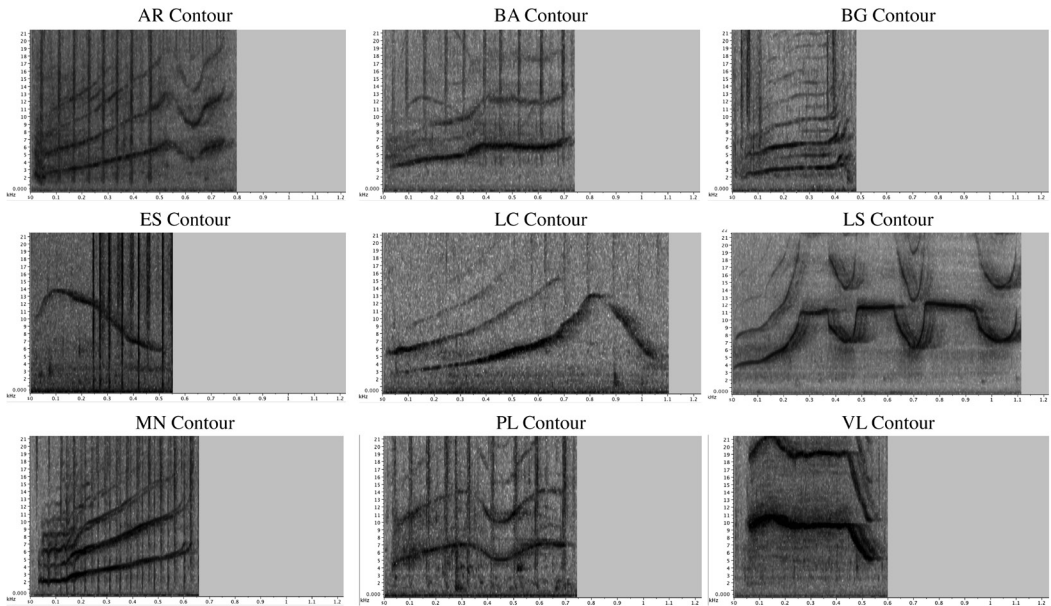


Figure 4. Whistle contours observed in 2012 for segregated and social contexts

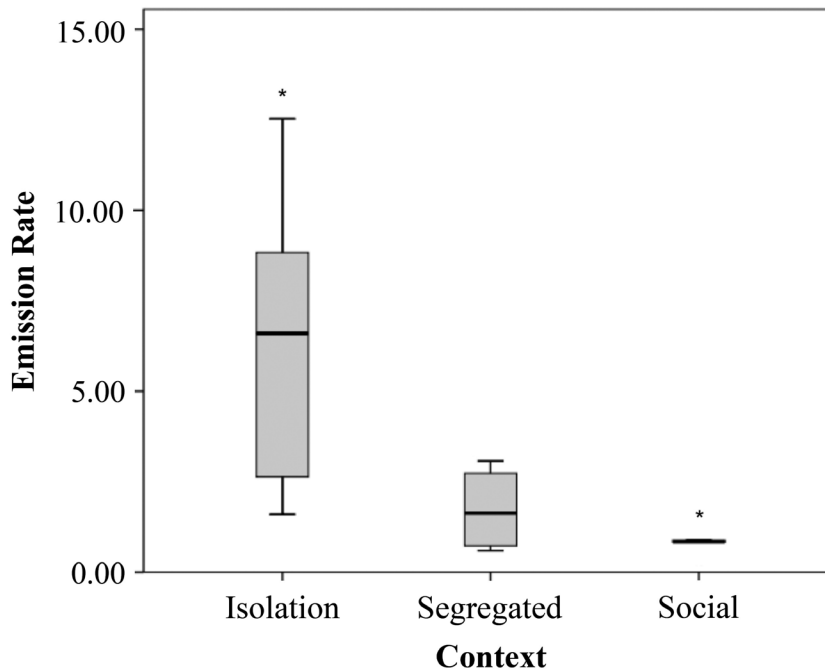


Figure 5. Whistle rate (number of whistles per minute per dolphin) in the different contexts; * represents significant differences in the whistle's emission rate between isolation and social conditions for sessions involving bottlenose dolphins AM4 and UM3 ($p = 0.006$).

Table 5. Mean values of whistle acoustic parameters of AM4 and UM3 for each context; only parameters that revealed significant differences in the MANOVA test were included in the table.

Context	Whistle parameters			
	End freq. (kHz)	Max. freq. (kHz)	Inflection points	Number of loops
Isolation	9.06 ^{ab}	11.39 ^{ab}	5.59 ^{ab}	2.08 ^{ab}
Segregated	7.20 ^a	10.57 ^a	3.25 ^a	1.89 ^{ac}
Social	7.37 ^b	9.19 ^b	2.67 ^b	1.20 ^{bc}

Note: The letters “a,” “b,” and “c” indicate pairs with significant differences in the pairwise comparisons; significance level = 0.05.

number of loops ($F = 7.337$, $p = 0.001$) (Table 5). End and maximum frequencies and number of inflection points were higher in isolation. The percentage of uniloop whistles was 38.86% in isolation, 50.71% in the segregated condition, and 80% in social contexts.

Discussion

The production of whistles by bottlenose dolphins in captive groups has been the focus of several studies with divergent results. While some authors consider signature whistles the most common whistle type produced by an individual, regardless

of the context of emission (Tyack, 1986; Caldwell et al., 1990; Janik et al., 1994), others emphasize the shared nature of some whistle types (McCowan & Reiss, 1995, 2001). In this study, relevant patterns of whistle production varied according to context, and some common stereotyped contours were only produced in isolation.

The studies of Caldwell et al. (1990) and Sayigh et al. (2007) found the whistle repertoire of isolated dolphins was represented mainly by signature whistles, which were more than 90% of the total whistle emissions. According to the results presented here, that may not always be the case for all individuals. In the same isolation conditions,

two subadult males demonstrated distinct acoustic behaviors: AM4 did emit one dominant whistle type (LS represented 79.04% of his whistle production), whereas almost half of UM3's whistle production was made of variant contours, and the most frequently occurring whistle represented just 37.31% of the emissions. Janik & Slater (1998) highlight the importance of habituation when it comes to signature whistle production—dolphins accustomed to captivity often need longer isolation periods before they emit signature whistles. In fact, the habituation/novelty factor seems to be a general issue in whistle production as initially observed by Tyack (1986), presenting higher whistle rates during novel events. Another relevant factor refers to dolphins' identities and individually specific behavior. Personality traits in nonhuman animals may stay consistent over time (e.g., Capitanio, 1999; Carere et al., 2005; Highfill & Kuczaj, 2007, 2010; Hill et al., 2007), and it is likely that whistling behavior in dolphins depends on personality.

Using SIGID criteria, the LS contour was identified as AM4's signature whistle (93.65% of the vocalizations in isolation and 88.89% in other contexts were produced in bouts with inter-whistle intervals between 1 and 10 s, thereby fulfilling the criteria). On the contrary, no signature whistle could be identified in UM3's emissions in isolation. Interestingly, UM3 emitted HOa and HOb in intercalated bouts, thus hindering the identification of both contours as signature whistles. Janik et al. (2013) have suggested that whistle categories with low emission counts might introduce errors in the conservative SIGID method, especially when using it with a small group of animals.

Another possible explanation for the absence of a signature whistle in the recordings of UM3 in isolation could be his fearful behavior profile, recently reported by Neto et al. (2016). The emission of his most common whistles in 2008 (HOa and HOb) was recorded only during his first encounter with the hydrophone, in a repetitive way. Considering that this animal seemed to be more afraid of new things compared with other dolphins in the park, this pattern of emission may indicate that these stereotyped whistles may not necessarily be identity calls but, rather, signals related to fear of novel stimuli. The 2012 recordings show that this dolphin does not seem to prefer any stereotyped whistle, at least not in social contexts.

Comparing the two datasets, only one of the contours, LS, was observed in both years, showing a stability already reported by other authors (Sayigh et al., 1990; dos Santos et al., 2005; Luís et al., 2015) who have observed the same contours lasting for more than a decade.

The overall low occurrence of stereotyped contours and the small group size may have hindered further identification of signature whistles. As to the scarce emission of these contours, it may be a consequence of the artificial environment: the animals are together in the same pool, at close range, and with good visibility conditions, so the emission of identity signals may not be important. As noted by Sayigh et al. (2007), when bottlenose dolphins are in visual contact, signature whistle emission might be suppressed.

Additionally, a clear link between the distinct whistle contour category and their most-likely emitter could only be established for the LS contour in segregated and social contexts, with 68.25% of the emissions attributed to AM4. The LS whistle was also emitted by HM5 in a high percentage of its repertoire. This dolphin had a low number of attributed whistles (only 7.98%). It could be that HM5 was copying the LS contour produced by AM4. As suggested by several authors, some signature whistles can be incorporated in other animals' repertoires as a result of copying, even though rarely used, and may be emitted as a label for that particular individual when copied by others (Tyack, 1986; Janik, 2000; King & Janik, 2013; King et al., 2013). Acoustic and play behavior copying is mainly observed between animals with high associations, especially peers with similar age, and is likely to be a type of affiliation display (Kuczaj & Yeater, 2006; King et al., 2013). Dolphins AM4 and HM5 have shared the habitat since the end of 2008; thus, the emission of LS contour by HM5 could be a case of copying in a close association.

In this study, different individuals likely produced several stereotyped whistles, but they could not be confidently attributed to any individual animal. AF6 and IF7, the only female subjects in the study, seemed to share one whistle contour, ES, which is not present in the repertoire of any other dolphin. These emissions may indicate another close affiliation and should be investigated further.

Another interesting case is the BA contour that was emitted by UM3, AF6, and AM4. These individuals were pool companions during their first years of life, and UM3 and AF6 are siblings. As previous studies suggested (Caldwell & Caldwell, 1972; Richards et al., 1984; Janik & Slater, 1998), a dolphin's acoustic repertoire is built through vocal learning and through imitation of sounds that the animals may hear early in life. This could be the case for the BA contour, a whistle type that might have been present in the pool they shared when young, perhaps produced by another individual such as their mother.

PM9's whistle emissions also highlight the importance of an environmental model in

whistle production. This calf produced mainly variant contours, and 40.74% of its whistles were upsweeps. As previously reported (Miksis et al., 2002), artificial stimuli presented during whistle development, such as trainers' whistles, may be used as models and that could be the case for this young dolphin.

The low number of stereotyped whistles drastically contrasted with the high number of variant contours. These results are in line with what has been described for wild populations, where variant contours represent around 70% of the emissions (dos Santos et al., 2005; Hawkins & Gartside, 2009; Luís et al., 2015). Throughout the analysis, a high number of incomplete vocalizations were observed. The presence of these short emissions, reminiscent of abbreviations (e.g., resembled start or end of known stereotyped whistle), may be a result of captivity and the stable social context as these animals are together during most of the year, changing to other pools only when strictly necessary. Tyack (1998) also reported a case of abbreviated whistles in an isolated bottlenose dolphin, noting that the animal devoted less effort to communication and vocalized less frequently.

Emission Rates and Time-Frequency Parameters

The whistle emission rate was 7.82 times higher in isolation compared with social contexts. This higher emission rate in isolation is a common response when individuals are separated from their conspecifics (Caldwell et al., 1990; Janik & Slater, 1998; Sayigh et al., 2007). The lower emission rates observed in the segregated and social contexts suggest that once at close range and in visual and acoustic contact with other dolphins from the same group, whistle emissions might have secondary relevance in the transmission of information. Considering the acoustic and visual environment in a shallow, limited space such as these pools, it is possible that communication might occur preferentially through visual displays. Future studies should compare the emission rates throughout the day and night to assess variation with light conditions.

Whistles emitted in isolation had significantly higher values for maximum and end frequencies. Similar results have been reported for other mammals in stressful situations and in response to separation, handling, and pain (Weary et al., 1997). Although these individuals are used to being separated and handled, the isolation context may trigger stress responses such as the emission of higher frequency whistles.

The higher number of inflection points and loops in isolation also appears to be a common phenomenon. The number of loops was also found to be greater during capture-release events

vs undisturbed conditions (Esch et al., 2009b). These findings suggest that multilooped whistles may contain information about the signaler's motivational state as is the case with social signals of other species (Caldwell et al., 1990; Weary & Fraser, 1995; Watts & Stookey, 2001; Esch et al., 2009a, 2009b). Despite some studies that relate low-frequency modulation whistles to periods of stress in captivity (Lilly & Miller, 1961; Caldwell et al., 1970), this increase may actually represent a higher motivation to communicate rather than an increase in stress level (Esch et al., 2009b).

In our study, 38.86% of the whistles produced in isolation were multilooped, strengthening the idea of continuous information for the other animals. On the contrary, in social context, it was observed that only 20% of whistles were multilooped, agreeing with the idea that, in social contexts and in captivity, dolphins may not need to emit redundant signals.

In conclusion, this study shows that in a group of captive dolphins, only a single stable signature whistle type was recorded (both in 2008 and 2012) and was emitted mostly by the same dolphin, suggesting that the occurrence of signature whistles may not be a constant or universal phenomenon. Variant contours dominated the whistle production in segregated (but not isolated) and social contexts, possibly because signature calls are less relevant in such situations. Whistle production was much more frequent in isolation, with a higher proportion of multiloop contours supporting the social cohesion function of these signals. However, this study also highlights the importance of examining the nonstereotyped portion of the bottlenose dolphins' whistle repertoire in different contexts as signature whistle production may not be a constant or universal phenomenon.

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