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# Pre- and Post-Partum Observations of Signature Whistle Characteristics of the Bottlenose Dolphin (Tursiops truncatus)

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# Pre- and Post-Partum Observations of Signature Whistle Characteristics of the Bottlenose Dolphin (*Tursiops truncatus*)

Ву

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Submitted in partial fulfillment
of the requirements for the degree of
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#### Abstract

This study represents an in-depth analysis of pre- and post-partum whistle usage in an Atlantic bottlenose dolphin (*Tursiops truncatus*). Findings show that the mother, Bonnie, produces two predominant whistle contours, which had been previously suggested as two possible signature whistles, which is uncommon in the literature. The frequency of these whistles was found to peak during particularly stressful events post-partum, as conferred by the behavioral context. Apparent congruities between the two whistle contours were compared and it was found that the type 1 contour bears some structural similarity to the rising first component of the type 2 contour, indicating combinatorial whistle construction. Type 3 whistles did not show any structural similarity to the falling component of the type 2 contour. Further studies of maternal whistle production and contextual use in the pre-partum and post-partum periods will be important to enable us to shed light on more subtle variations in whistle use, and whether discrete elements of specific contours may be combined into a continuous call.

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#### Introduction

The study of bottlenose dolphin (Tursiops truncatus) vocal communication represents an important area of research within the animal communication field, largely since this species is one of a handful of mammals which exhibits vocal learning. Vocal learning refers to the modification of vocalizations as a direct result of interactions with other individuals, as opposed to the innate communication abilities seen in most other animals (Janik & Slater, 1997). In fact, despite the breadth of the animal kingdom, only eight groups have been found to have this rare trait: the cetaceans, an order of animals which includes both whales and dolphins, songbirds, parrots, hummingbirds, bats, elephants, pinnipeds, which include seals and sea lions, and of course humans. Learning about the mechanisms underlying dolphin communication may help further elucidate how human speech is biologically encoded (Lattenkamp & Vernes, 2018) and provide a comparative view between the vocal learning mechanisms in humans, avian species, and dolphins. Additionally, dolphins are notable for their capacities for vocal mimicry: they can spontaneously imitate both species-specific whistles (Tyack, 1986) and computergenerated novel whistles (Reiss and McCowan, 1993). They can also be trained to imitate computergenerated sounds as part of an artificially created acoustic language (Herman et al. 1984), and match the number of 'sonic bursts' of human speech (Lilly et al. 1968) and other aspects of human vocalizations as well (Lilly, 1965). However, despite literature dating back over 50 years, there are still questions yet to be fully explored concerning acoustic structure and coding.

A major area of research, discussion and contention within the dolphin communication field is the nature of the 'signature whistle'. Dolphins can produce a variety of sounds including broadband clicks used for navigation, detection and orientation, a wide range of broadband burst-pulsed sounds, and frequency-modulated narrowband whistles (Tyack & Clark, 2000). Dolphins use this variety of whistles, as well as burst pulse signals and echolocation, during social interactions. Whistle subtypes include chirps, moans, squeaks, and squeals, which are categorized based on duration, frequency, repetition rate and/or

intensity (Jones *et al.* 2019). Herzing (2000) in fact showed that low-frequency, shorter duration vocalizations tend to be associated with aggression and/or fear related behaviors, while high-frequency, longer vocalizations are associated with affiliative behaviors. In a seminal paper, Caldwell & Caldwell (1965) observed that when isolated from their group, individual dolphins consistently produced distinct whistle contours. A signature whistle thus typically refers to a single or repeated stereotyped and individually distinct whistle contour produced by an individual dolphin. Furthermore, it was been defined as the most common whistle type an individual uses when in isolation, and in fact, signature whistles have been observed in more than 300 individual bottlenose dolphins (*Tursiops truncatus*) in both captivity and the wild (Sayigh & Janik, 2009). They have further been distinguished by Janik *et al.* (2013), who found that during free swimming signature whistles are produced in bouts with 1.0-10.0 seconds in between each whistle, whereas non-signature whistles typically occur in intervals either less than or greater than the aforementioned range.

Additional work determined that although there may be some differences within the signature whistles produced by an individual in terms of acoustic parameters like duration, the general contour or overall shape, the whistle remains consistent (Tyack, 1968; Sayigh et al. 1990). The individual calls are thought by many researchers to be related to individual-level identification, as seen in a number of playback experiments (Sayigh *et al.* 1999; Janik *et al.* 2006), where dolphins responded more strongly to whistles of related versus nonrelated (but familiar) individuals. Furthermore, when using artificial stimuli that replicated the contours of the calls, the same findings were seen, meaning that dolphin can recognize contour shape (Sayigh *et al.* 1999). This suggested that not only can these signature whistles be used for intraspecies identification, but there may further be familiarity or relatedness encoded as well. Context-related information may also be transmitted through signature whistles. Janik *et al.* 1994 showed differences in whistle rate that appeared to reflect changes in motivational state, illustrated by differences in whistle production following a discrimination task when the dolphin was in isolation versus in a group,

as well as whether the dolphin was rewarded or not after completion of the task. Marler *et al.* (1992) similarly showed changes to whistle production that reflected information on external referenda.

Existing literature has ascribed signature whistles as accounting for 70-95% of all whistles produced by an individual (Tyack, 1986). Tyack however, reporting on two cohoused captive dolphins, found that although both favored different primary whistle types, they also both produced the others' signature whistle as their next most common vocalization. He suggested that the signature whistle hypothesis could still hold in cases of such mimicry, "if the mimicked whistles occur significantly less often than those produced by the 'appropriate' animal, or if the mimicked whistles have a similar contour but include some acoustic features that are different from those produced by the 'appropriate' animal," both of which were true in these subjects. This mimicry of the signature whistle may serve as a referential tag to refer to a specific individual.

Other issues further complicate our understanding of signature whistles, including the role of contact calls, as well as differences in signature whistle production between captive and wild dolphins. One striking fact is that the nature of signature whistles as individually distinct calls is exceedingly rare in the animal kingdom. Most cases of distinctive calls in animals are not learned, and they are species-specific, rather than individual-specific (Boughman & Moss, 2003). These contact calls are shared within social groups, or even within the species as whole, and it is through subtle variation in acoustic parameters that members of the group can identify specific individuals (McCowan & Reiss, 1995a; Sayigh et al. 2007). Again, this is very different from the historical definition of signature whistles in dolphins, which are said to be individually distinctive. McCowan & Reiss (2001) found that across three different social groups across three different aquaria, 10 out of 12 dolphins were using a shared whistle type, despite never having been exposed to one another. Classification of the contact call revealed 14 subtle variations within that one type that could be responsible for identification, at least partially. This was further elaborated on using multiple observers who categorized the calls and were blind to the identity of the vocalizing

dolphin, and who ended up in agreement on classification. Of note is that a shared rise-type contour contact call has been shown in individuals both within and across social groups (McCowan & Reiss 1995a, b; 1997; 2001). This predominant yet shared call type was repeated and varied in the number of repetitions within sequences, consistent with the characteristics of signature whistles. The authors proposed that signature whistles may be influenced by the calls of other members of the social group and that there may be a convergence in the signature whistle contours used within a social group or even a species. Whether this is limited to captive populations who are more familiar with one another is still up for debate, as isolation of communication is much easier with these populations compared to wild dolphin pods.

The influence of stress on whistle characteristics is also an area of interest for research, as the ecological applications for both wild and captive populations are massive. Understanding how stress effects call structure and contours could serve as an acoustic indicator of well-being. For example, it could indicate if a wild population were suffering under negative anthropogenic impact, or if a dolphin in captivity was sick, and would help guide conservation interventions. Wild dolphins have been shown to produce greater whistle rates, higher numbers of loops, and higher frequency whistles during capture-release periods as opposed to undisturbed conditions (Esch *et al.* 2009). This indicates that at the very least, higher stress situations do result in changes to their whistle output. Boat traffic is also a major source of ecological concern for dolphins as they exhibit several behavioral responses including physical avoidance and decreased resting behavior (Constantine *et al.* 2004). Acoustic influences may be less obvious but nevertheless impactful. Sea ambient noise is significantly higher in areas of high boat traffic, which has been shown to change the whistle structure of nearby populations. For example, when a population of dolphins traveling and foraging in the Archipelago of Bocas del Toro in Panama were in the presence of high numbers of boats, they produced longer and more modulated whistles (May-Collado & Quiñones-Lebrón, 2014). Within another population in the Cres-Lošinj archipelago off Croatia,

researchers saw a shift towards higher frequency whistles because boats generally produce sounds in the low-frequency noise range (below 2 kHz). Conversely, when boat noise levels were elevated into the 2-20 kHz frequency range, dolphins produced whistles with reduced maximum, delta and start frequencies (Gospić & Picciulin, 2016). On the other hand, Heiler *et al.* (2016) reported that a population in Walvis Bay, Namibia exposed to boat traffic showed a general upward shift in whistle frequency by up to 2 kHz, there were no changes in frequency range, duration of whistles, or number of inflection points. This may be due to the number of boats overall, or possibly unknown population differences, but is somewhat unclear.

Pain or distress can also influence whistle structure and contour. A more specific contour-based "distress call" was first noted by Lilly (1963), and was described as a unique whistle pattern different from an alarm call, that was comprised of a pair of two whistles: "The first whistle starts at a relatively low fundamental frequency (3 to 5 kcy/sec) and rises to a relatively high fundamental frequency (8 to 20 kcy/sec). The second whistle of the pair starts at a relatively high fundamental frequency (8 to 20 kcy/sec) and falls to a relatively low fundamental frequency (3 to 5 kcy/ sec). This pair is emitted repeatedly with a delay of only a few tenths of a second between pairs for several seconds or several hours and stops when appropriate relief is obtained." The effects of pain and distress on captive dolphins appears more infrequently in the literature, but could be crucial as an indicator of animal welfare and health. This would be especially useful for aquariums and zoos where examining dolphins is an otherwise very strenuous process. An unpublished paper by Reiss (2011) reported the production and exchange of a rise-fall call similar to the distress call as described by Lilly (1963), in a mother-calf pair of bottlenose dolphins that were stranded and then rescued from the Shrewsbury River in New Jersey. The mother, succumbed to internal injuries upon rescue and the younger dolphin was moved to the National Aquarium in Baltimore, Maryland for care but also died several weeks later due to internal injuries. The calf, estimated to be about 1.5 years of age, continued to produce a predominant rise-fall call throughout the first weeks of rehabilitation. Her second most frequently produced call was a rise call, similar to the general type of rise contours reported as the predominant calls produced by bottlenose dolphins in previous studies (McCowan & Reiss, 1995a; McCowan & Reiss, 1995b; McCowan & Reiss, 1998; McCowan & Reiss, 2001). The use of both the rise-fall and rise calls in these injured dolphins has been suggested as further support of the distress call hypothesis (Reiss, 2011).

Further literature has also attempted to explain the relationship between distress and signature whistle output. Herzing (1996) found that both excitement and distress would elicit repeated emissions of a variation of a dolphin's signature whistle in which the signature whistle was accompanied by a burstpulse vocalization and a bubble stream. This increased production of the signature whistle was also seen in another wild dolphin, which interestingly was also correlated with the amount of support behaviors the distressed dolphin received from other conspecifics (Kuczaj et al. 2015). This notable event was captured by chance off the coast of Saudi Arabia in 2012, where researchers surveying sharks witnessed an apparently distressed dolphin who was in a vertical position calling out and was subsequently pushed and lifted up to the surface by other dolphins. The dolphin was heard emitting, with high frequency, a specific call accompanied by continuous bubble-stream emissions. The whistle duration was highly variable but the contour, that of a rise-fall call, remained consistent. The emission of this contour continued even after the supportive behaviors had been received. Given that the whistle emission from the conspecifics decreased during the distress event, the authors suggests that the distress call may suppress vocalizations not associated with distress or may simply allow the other individuals to better perceive the distressed individual's calls. Overall, this suggests a critical role of signature whistles in conspecific epimeletic behavior. These examples highlight the immense importance of understanding the role of signature whistles during distress, as comparing output during these events versus baseline could help us to understand when a dolphin is indicating it needs help or is sick before it is too late to help.

Additionally, there is the topic of mother-calf whistle behavior. Following birth, mother dolphins increase whistle production in breadth and frequency, with signature whistles calls being repeated the most frequently (Tavolga & Essapian, 1957; Gnone et al. 1996; Fripp & Tyack, 2008). Additionally, mothers and calves maintain a close association in the wild, on average from 3-6 years together (Sayigh et al. 1990). In terms of vocal ontogeny, McCowan & Reiss (1995a) recorded the vocalizations of eight infants and ten adult dolphins from three different social groups and found that the infants shared a portion of their whistle repertoires regardless of group. The predominant whistle used by the infants in their first months was a convex-rise contour that eventually changed into a concave-rise type call, one which closely resembled the contour of the signature call of their mothers. All the calves in this study were males, and so it remains unclear if female calves would show this same developmental pattern. Additionally, by the end of their first year, the infants and adults shared some other whistles types in common. The use of shared signature whistles and contact calls between mothers and calves has been well documented in the literature and suggests that these calls serve to establish and maintain contact and cohesion in social interactions between conspecifics.

There also appear to be sex-related effects on whistle learning, however the literature is limited and quite mixed on this matter. Sayigh  $et\ al$ . (1990, 1995) looked at whistle exchanges from 12 free ranging bottlenose dolphin mother-calf pairs over a period of over 14 years. They found that male calves consistently produced signature whistles closer to their mothers whereas female calves had significantly divergent whistles. Additionally, both the whistles of the mothers and calves remained stable and consistent for up to 3-12 years following initial observations. The authors hypothesize that males may retain their mothers' signature whistle in order to facilitate future kin recognition and to avoid inbreeding. Females, who tend to associate with their matrilineal groups into adulthood (Wells  $et\ al$ . 1987), therefore develop a distinctive whistle to enhance their individuality within the group. The stability of the males' whistle however was challenged by Smolker and Pepper (1999). They found that once males leave the

pod, they will form alliances with other males, and that within these groups there will be a convergence upon a shared whistle type. Conversely, Bebus & Herzing (2015) found that in free ranging Atlantic spotted dolphins (*Stenella frontalis*) the opposite was true, as female offspring produced signature whistles more like their mothers compared to two of the four males who produced more dissimilar calls. However, given their small sample size, neither sex could be categorized as more likely to produce signature whistles similar to their mothers. Given that these studies were done on free-ranging animals, understanding how signature calls are passed on in captivity, particularly between offspring of different sexes, would be useful in further developing the signature whistle discussion.

One aspect which is scarcely present in the current literature regarding signature whistles, is what may be unique behavior of a pre- and post-partum dolphin. Gestation for bottlenose dolphins is approximately 12 months, and along with many other behavior changes, marked differences in whistle production have been observed. Mello and Amundin (2005) found that whistle frequency increased significantly pre-partum and in the month prior to parturition showed an even sharper uptick in occurrence. One may reasonably assume that birth is an intensely stressful process, and so we see here the convergence of what role stress has on dolphin whistle structure.

Although as previously stated there exists literature focusing on post-partum whistle production by both mother and calf, in order to expound to what extent imprinting may play a role in dolphin development, pre-partum analysis of calls, particularly during the actual process of birth is rarer. Gnome & Moriconi (2009) conducted an analysis of the calls of between a mother and calf pair, Bonnie and Achilles, following delivery of the calf in 2002. They found that the mother emitted her signature whistle and its variants with increased frequency on the day of Achilles' birth, at a rate higher than her normal production. This was also seen by Gnome et al. (1997) during the birth of Bonnie's first calf Cleo in 1994.

The objective of this study was to shed light on the structure and contextual use of the whistles produced by the mother during the brief pre- and lengthy post-partum period to further elucidate the

relationship between signature whistles and distress or stress-related whistles. This was possible given the unique data set, a complete recording of Bonnie throughout the entire birth of her calf Cleo, as well as records of Bonnie's signature whistle prior to her pregnancy, and her second pregnancy and birth of calf Achilles in 2004. In this way, the following analysis can be considered a follow up to Gnome et al. (1997). One would expect to see Bonnie exhibit an overproduction of her signature whistle during the birthing process as well as production of a falling whistle during behavioral instances of high stress. Additionally, as Bonnie's signature whistle follows a rise-fall contour, we look to investigate whether evidence of combinatorial whistle structure exists, based on apparent acoustic parameter congruity between segmented whistles.

#### Methods

#### Subjects and Facilities

On September 5<sup>th</sup>, 1994, Bonnie, a 20-year-old bottlenose dolphin delivered a healthy female calf named Cleo at roughly 1:08 pm at the Acquario di Genova, in Genova, Italy, following approximately one hour of labor. Bonnie was housed inside a rectangular tank (23.5m by 8-10m, 5m deep, 1,104 m³) which was connected to two smaller tanks. The main tank consisted of three concrete walls, with the two shorter ones reproducing a cliff. The wall facing the visitor corridor consisted of 5 panels in acrylic glass allowing complete vision of the dolphin activity. The pool was illuminated at night with three 150 W amps (9.3 lux at the water surface). At the time of the birth, Bonnie was housed with a 10-year-old male dolphin named Micha. Both dolphins belonged to the Aquatic World Cattolica.

#### Data Collection

The basis for this study comes from acoustic recordings and visual observations of the dolphin's concurrent behavior during the pre-natal, birth, and post-natal period. Six hours of recordings were made during this period. Observations were transcribed by on-site staff based on direct observation or from the visual recording that was taken via a video camera placed outside of the tank. The written transcript included notation of the time of day for each observation, a count of the time between events, and brief descriptions of the physical and auditory behavior of Bonnie, Cleo, and Micha. Audio recordings were made through the use of a spherical hydrophone (ITC-1089C, 1 Hz – 350 kHz) placed underwater, which was connected to both a S-VHS Hi-FI video recorder and a DAT recorder (SONY DTC-690), with sounds recorded in a frequency range from 100 Hz to 22 kHz (Gnone et al. 1996). The acoustic recording in total is about 6.2 hours in length: the first 12 minutes of which are Bonnie pre-birth during contractions, then the birth itself occurs, and the remaining 5 hours are spent with Bonnie and Cleo during free swimming and other affiliative behaviors. The original transcript written in Italian was translated accurately into English by a native Italian speaker for this study. Of note is that there is a period of approximately 50 minutes at the start of the fourth hour of the tape where, due to an unknown technical error, no whistles were recorded. Additionally, the behavioral transcript received from the Genoa research team concludes at the start of the fourth hour.

#### Data Compilation and Analysis

Audio recordings were analyzed with Raven Pro 1.5: Interactive Sound Analysis Software (Cornell Laboratory of Ornithology, Bioacoustics Research Program, 2014), and spectrograms of whistles were produced using a Hann window size of 250, with 50% overlap and 125 hop size. Whistles were only included if they had a good-signal-to-noise ratio, meaning clearly visible spectral contours, as well as clear start and end frequencies. Overlapping whistle contours were excluded if more than two whistles were present at a single time stamp to reduce complexity.

As Bonnie was the main subject of this study, and the goal was to isolate only her whistles for analysis. This involved several visual scrub-throughs in Raven of the complete audio file. All whistles were initially graded visually based on their signal-to-noise ratio, with grade 1 signals being faint, grade 2 being clear and unambiguous, and grade 3 being prominent and dominant, a criterion laid out by Marley *et al.* (2017). Grade 1 calls were of low quality and thus excluded from analysis because of their difficulty in being measured, which grade 2 and 3 calls were retained. These low-quality calls may have come from other animals in adjacent tanks, or even from Bonnie or Micha, but because of their position from the hydrophone, the call was distorted.

Once all qualified whistles were selected and their acoustic parameters measured via the Raven selection tool, a qualitative system for categorizing them into types of calls was utilized. This involved another review and visual assessment of all the calls based on whistle contour (McCowan and Reiss, 1995a). This resulted in a possible seven (7) call types that each subsequent whistle could be categorized as: convex, concave, sinusoidal, rise, fall, flat, and a stereotypical rise-fall contour. Whistles were separated into individual units if inter-whistle interval exceeded 0.1 s or more. As for the acoustic whistle parameters, those measured were: start and end frequency (Hz), minimum and maximum frequency (Hz), delta frequency (Hz), and delta time or duration (s). These parameters are consistent with acoustic analysis seen in similar studies (Kaplan and Reiss, 2017).

All type 1 and 2 whistles were attributed to Bonnie as they had been previously identified as two signature whistles she produced (Gnome & Moriconi, 2009). Micha's signature whistle was also previously identified as sinusoidal in nature (Gnome & Moriconi, 2009) and therefore not included in the analysis. Whistles from dolphins in other tanks were unlikely to be of high quality, and although some whistles may be attributable to Micha or these other dolphins, all non-sinusoidal whistles were attributed to Bonnie. This was done as the majority of whistle types consisted of her signature whistle, as well as rise and fall type contours which had visual congruity as segmented forms of her signature. The calf, Cleo, reportedly

did not vocalize until she was three days old, and thus attributing whistles to her was not a source of possible error (Gnone *et al.* 1996). Additionally, new-born calf whistles are highly tremulous in nature, and so identification versus adult whistles would be very noticeable. (Reiss, 1988).

#### Results

#### Whistle Types

A subset of 1267 out of 1663 total whistles from 372 minutes of recordings from Cleo's birth day were included in the analysis of Bonnie's calls based on their-signal-to-noise ratio. The whistle contour produced most frequently was a stereotyped rise-fall contour, whistle type 2 (Fig. 1), comprising 41.6% of the calls (n = 517). The second most frequent contour was a rise contour, whistle type 1 (n = 309, 23%). The third most frequency produced call was a concave contour (n = 279, 21%). A falling contour whistle (n = 117, 1%) was also produced and included in the analysis because it resembled the first element of whistle type 1. Both flat (n = 18) and convex (n = 27) type calls in total accounted for less than 0.04% of the total call production, and thus were not included in the statistical analysis. The rise and rise-fall call are termed type 1 and type 2 respectively. For sake of consistency, falling whistles will hereafter be termed type 3, concave whistles type 4, convex whistles type 5, and flat whistles type 6 (Figure 2).

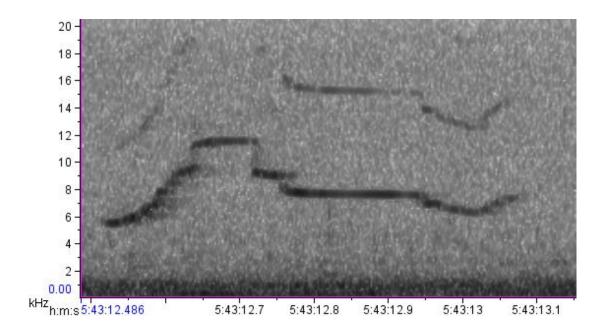


Fig. 1 Spectrogram of Bonnie's whistle type 2

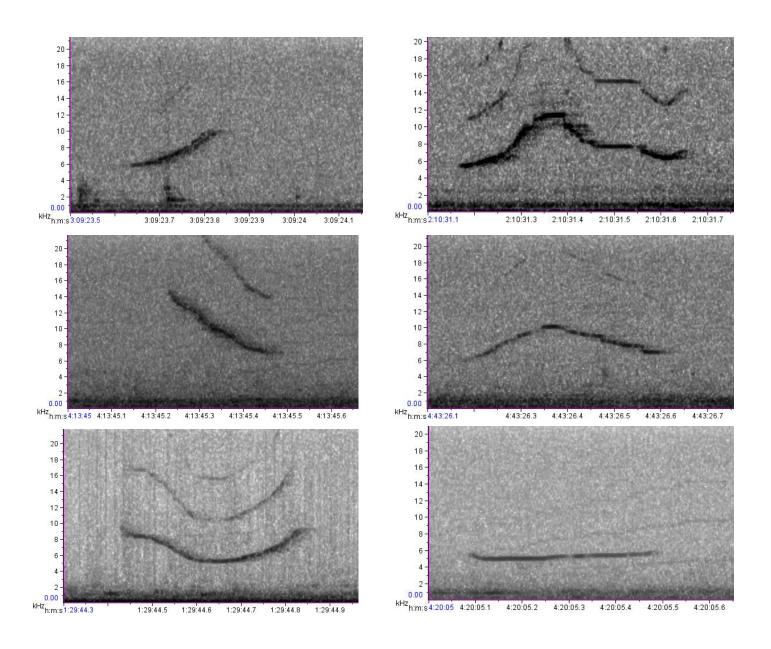


Fig. 2 Examples of Bonnie's (6) main whistle contour types

#### Contextual Use and Timeline

The broad outline of the behavioral events in the tank on the date of Cleo's birth are as follows: Bonnie is swimming around the perimeter of the pool with Micha following her. Several unusual whistles are heard (see appendix), immediately preceding Cleo's birth. After that, there is an increase in the frequency of production of whistle type 1 and 2, as well as sinusoidal whistles.

Bonnie swims alongside Cleo on her right side, directing her away from obstacles. Micha also swims alongside following them. Micha occasionally gets more aggressive and swims very close to the pair, which results in subsequent aggression on Bonnie's part. There is a feeding session for the dolphins at the end of the first hour of observation.

In the following hours, Bonnie continues directing Cleo around the tank, away from the sides and bottom, while Micha follows them on and off. If Micha gets too close there would be an increase in whistles from both him and Bonnie. Bonnie and Cleo remained as a pair, swimming around the tank, and at one point in the third hour when Bonnie loses track of Cleo for a few seconds there is an increase in vocalizations. During the fourth hour, Cleo begins her first attempts at breastfeeding and Bonnie expels the placenta.

The frequency and distribution of call types was not equal across the 6-hour recording period. Type 1 calls were produced at a rate of 8 calls per 10 minutes on average, although this peaked threefold during the fourth hour. Type 2 whistles were produced at a rate of roughly 14 calls per 10 minutes, however, rate of production was near zero during the first two hours of recording. Type 2 and type 1 whistle production both peaked during the third hour, with another smaller increase in production during the fifth hour. Type 3 calls were very rare for the majority of the post-partum period but increased at the end of the fourth hour (Figure 3).

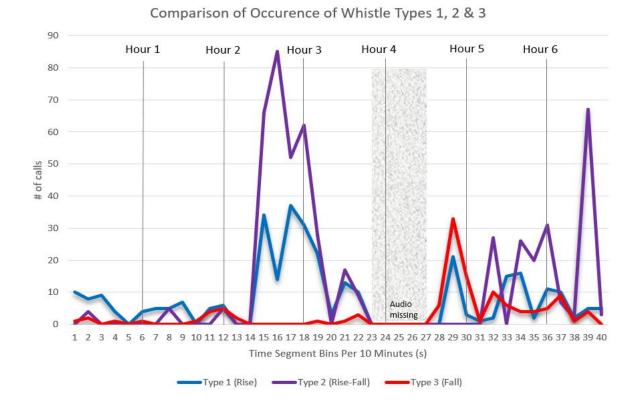


Fig 3. Frequency of Production of Bonnie's Whistle Types 1, 2 and 3 over Time

Whistle type 1 and type 2 both increased in frequency simultaneously. Type 3 calls decreased as type 2 calls increased during time bins 14-18 and inversely, type 3 calls increased as type 2 calls decreased in time bins 23-25. Type 5 and 6 calls are too rare to contextualize in the timeline, however, type 4 calls are quite interesting. They also show their own peaks in production at the same points as type 1 and 2 calls. This may suggest that type 4 calls are a kind of generalized type 2 call, simply lacking the specific stereotyped contour modifications that mark it as the signature whistle.

#### Acoustic Parameters and Analysis

#### Parametric Summary

For all whistles, six main acoustic parameters were measured using the Raven software, namely: start and end frequency, minimum and maximum frequency, delta frequency and duration (or delta time). The means and standard deviations for these are reported in table 1. Type 3 calls had the highest mean starting frequency while type 1 had the highest mean ending frequency. Type 2 calls had the mean lowest minimum frequencies and the second mean highest maximum frequencies, after type 3, compared to all the other calls. Type 3 calls had the greatest mean delta frequency, the greatest change in call frequency over time. Type 1 calls were the shortest in duration with an average length of 0.15 s, while type 2 calls the longest in duration, on average about 0.48 s in length.

Whistle Type		Start Freq	End Freq	Min Freq	Max Freq	Delta Freq	Delta Time
Type 1 (Rise)	Mean	5824.70	8978.79	5145.23	10884.01	5738.78	.15
	SD	2157.52	3089.75	1567.35	3243.37	2782.56	.09
Type 2 (Rise-Fall)	Mean	5401.71	6750.35	4859.66	12157.00	7297.34	.48
	SD	839.33	828.09	432.29	1251.29	1275.51	.06
Type 3 (Fall)	Mean	12166.08	7837.05	6615.84	14320.42	7704.58	.35
	SD	4152.27	2622.12	1847.89	3599.26	3322.40	.16
Type 4 (Concave)	Mean	6372.59	7257.70	4977.60	12113.67	7136.07	.45
	SD	2711.27	2574.31	1662.74	3683.88	3337.66	.22
Type 5 (Convex)	Mean	8791.93	7851.18	6000.43	10674.61	4674.18	.23
	SD	2700.50	3930.26	1664.21	3170.19	2530.49	.18
Type 6 (Flat)	Mean	6311.62	5897.03	5266.56	7375.68	2109.12	.38
	SD	2770.28	2855.04	1748.92	3327.73	2453.73	.47

**Table 1.** Acoustic parameters of Bonnie's (6) main whistle types. Frequencies are in Hz and time in seconds (s).

#### Whistle Components

In order to further investigate whistle structure, and the possibility that the type 2 rise-fall contour might be composed of the type 1 rise whistle and the type 3 falling contour, we compared the acoustic parameters of these whistles. Specifically, the acoustic parameters of the rise and fall portions of the type 2 contour were measured, with the bounds of these selections being determined by start and end frequencies as well as the inflection point of the signals. The means and standard deviations of these rise and fall units are listed in table 2.

Acoustic Parameter	Mean	Std. Deviation
Start Freq Rise Comp.	5355.13	708.79
End Freq Rise Comp.	10948.42	1777.15
Low Freq Rise Comp.	4983.42	471.75
High Freq Rise Comp.	11652.72	1348.46
Delta Freq Rise Comp.	6669.31	1432.38
Delta Time Rise Comp.	.14	.03
Low Freq Fall Comp.	5874.06	1138.90
High Freq Fall Comp.	11610.83	1799.38
Delta Freq Fall Comp.	5736.77	1888.94
Delta Time Fall Comp.	.26	.11
Start Freq Fall Comp.	10759.96	1966.25
End Freq Fall Comp.	6663.80	1229.22

**Table 2.** Mean and standard deviations for acoustic parameters of the rise and fall components of Bonnie's type 2 whistle

#### Statistical Analysis

Mann-Whitney U tests were used as the data was not parametric in nature and was done to compare the acoustic parameters of the rise and fall components of type 2 calls against these same parameters for both type 1 and 3 calls. Statistical analysis was done via SPSS, Version 26.

Type 2 rise components were not statistically significantly different compared to type 1 calls in regards to the start frequency (Z = -1.197, p = 0.231), minimum frequency (Z = -0.989, p = 0.323) and duration (Z = -2.166, p = 0.060), however, were significantly different in regards to maximum frequency (Z = -6.913, p < 0.01) and delta frequency (Z = -8.047, p < 0.01). Type 2 fall components were statistically significantly different when compared to type 3 calls for across all four acoustic parameters. Full resulted are described below (table 3).

Type 2 Rise Component vs Type 1 Rise<sup>a</sup>

	Start Freq	End Freq	Low Freq	High Freq	Delta Freq	Delta Time
Mann-Whitney U	78135.500	40562.500	78834.500	54627.500	52431.500	74847.500
Wilcoxon W	219913.500	88457.500	126729.500	102522.500	100326.500	122742.500
Z	-1.197	-12.261	989	-8.117	-8.763	-2.166
Asymp. Sig. (2-tailed)	.231	.000	.323	.000	.000	.060

a. Grouping Variable: WhistleType

Type 2 Fall Component vs Type 3 Falla

	Start Freq	End Freq	Min Freq	Max Freq	Delta Freq	Delta Time
Mann-Whitney U	23213.000	18744.500	18247.000	14294.000	18442.500	19205.000
Wilcoxon W	164991.000	160522.500	160025.000	156072.000	160220.500	160983.000
Z	-4.308	-6.745	-7.013	-9.165	-6.905	-6.496
Asymp. Sig. (2-tailed)	.000	.000	.000	.000	.000	.000

a. Grouping Variable: WhistleType

**Table 3.** Comparison of mean acoustic parameters between rise and fall components of whistle type 2 versus whistle type 1 and type 3 respectively

#### Discussion

#### Frequency and Contextual Use of Whistles

The most prominent whistle produced by Bonnie through the labor and post-partum experience was the type 2 rise-fall whistle, a whistle previously seen and identified by researchers as her signature whistle (Gnone *et al.* 1996). This is consistent with the literature, as many studies have shown that mother dolphins will increase their signature whistle output both in the weeks prior to and after following birth,

at production levels that are actually greater than when not pregnant or having recently given birth (Mello and Amundin, 2005). Gnome & Moriconi (2009), when reviewing the same dolphin, Bonnie, giving birth again in 2002 to a calf named Achilles, noted the increased production of her signature whistle, and suggested this is likely a form of acoustic imprinting. Although pre-partum whistle production is not very well studied, several authors have suggested that there may be in utero learning taking place. Ames (2016), for example, found pre-partum production of a mother's signature whistle increase greatly, whilst signature whistle production by other members of the social group actually decreased. Interestingly however, in this case Bonnie emitted predominantly whistle type 1 during the pre-partum period.

The highest peak in type 2 production occurred between hours two and three. During this time the observer transcript mentions several items of interest: 'Cleo loses contact with Bonnie for a few seconds', 'Bonnie pushes Cleo away from the bottom [of the tank] with some difficulty', and 'noise of a very close airplane'. Although giving birth is obviously a stressful event for a dolphin, these aforementioned occurrences seem as they may be particularly highly stressful for Bonnie. This would lend more credence to the theory that signature whistle increases may be an indication of stress or distress in dolphins.

#### Combinatorial Calls

When examining the possible role of combinatorial whistle structure, we see some interesting results. The rising component of Bonnie's type 2 signature whistle is somewhat similar, in at least 3 out of 6 acoustic parameters, to her type 1 whistle, which is the rising contour. This may suggest that structurally, the rise portion of whistle type 2 is comparable to whistle type 1 – and that contour production is consistent across these two whistle types.

Consider that Bonnie's type 1 call is a rising whistle, and thus may represent a possible contact call or signature whistle call as described previously for bottlenose dolphins (McCowan & Reiss, 1995a;

1995b; 1997; 2011, McCowan et al. 1998). Interestingly, the matching of rising calls has also been reported in wild dolphins (Janik, 2000). Notably, Gnome & Moriconi (2009) reported that Bonnie produced two signature whistles – defined as her two most predominant calls. This could explain its over production during the pre- and post-partum periods. As the type 1 call was frequently used in conjunction with the type 2, contour similarity would suggest a duality of patterning, or at the very least the use of combinatorial calls in which this discrete rising contour is used again in combination with another component, thus resulting in the type 2 whistle contour. There is evidence for combinatorial calls in dolphins and a few other species. In a previous study young bottlenose dolphins were exposed to novel and discrete computer-generated whistles, and it was reported that they showed spontaneous and continued production and behaviorally appropriate use of combination whistles, that is one continuous whistle composed of two discrete whistles (Reiss & McCowan, 1993). Pardo et al. (2019) found that 3 different species of elephants, all with ecological and geographic differences between, would combine broadband calls into the same 3 combination call types. These combinatorial calls however were produced at different frequencies among the groups and was found to be dependent on behavioral context.

The 3 acoustic parameters which were statistically significantly different between the type 1 rise component and type 2 whistles were end frequency, maximum frequency, and delta frequency. In the rising component, end and max frequency function as the same parameter, and it also follows that delta frequency would be statistically different if max frequency is, because delta frequency represents the difference between the minimum and maximum frequencies. The reason for this may suggest an influence of coarticulation, which would follow if dolphins indeed use combinational whistles. Coarticulation describes the phenomena by which a conceptually isolation sound is influenced when preceded or followed by another sound. In other words, the falling component of the type 2 whistle causes some changes in the ending acoustic parameters of the rising component.

Conversely, a comparison of the acoustic parameters of the falling component of Bonnie's type 2 whistle and the type 3 whistle indicated that they were statistically different. While at first this may seem to weaken the combinatorial unit argument, the difference may be due to the nature of distress calls. Bonnie's signature whistle had been known and reported for many years prior to this study, always matching the contour of the type 2 call. Falling whistles on the other hand, as discussed previously, have been suggested as a type of distress call. Considering the post-partum experience of guiding Cleo around the tank and trying to aid her in avoiding both obstacles as well as Micha's aggressive behaviors, it is very likely that Bonnie was experiencing stress during this time. If this was the case, and her type 3 call was indeed a distress signal, then it may not match her regular whistle contours because it is not a part of her normal whistle repertoire.

Overall, this unique data set represents a rare look into the bottlenose dolphin birthing process from an acoustic perspective and helps shed some light on whistle output during stressful experiences. There seems to be some evidence of combinatorial whistle construction, although this was a first level analysis and a more rigorous analysis comparing visual components on a more fine-tune scale will be done in the future. Overall, further research on both more individual dolphins and over longer periods of time is needed, specifically looking at how the discrete elements of certain contours can be used to further elucidate if and how combinatorial whistles are used.

Appendix:
Behavioral Transcript During Bonnie's Birthing Event

CASSETTA N.		Delivery - 2 + 5, Sept 5,1994	RECORD CARD# <b>1</b>
ORA	COUNT	BEHAVIOR	
12:56 pm	0:00:00	The tail is extended and it is already almost entirely out.	
		B swims clockwise around the perimeter of the pool. M	is following
12:57	0:01:10	Dry and short sounds - no idea where they came from	
	0:02:21	Same as above	
	0:05:52	B keeps swimming clockwise around the perimeter of th	ne pool. No whistles.
		M is following	
	0:07:03	I heard a "beat from the mouth" (??), but B is hidden. Th	nen, a series of vocalizations.
		B does' move holding the rostrum on the bottom.	
	0:07:39	Whistles: before sinusoidal. After, the usual ones. Then,	again sinusoidal
		with other vocalizations and "beats"(??).	
	0:08:16	Very "deformed" whistles and vocalizations.	
	0:08:25	Interesting whistle (M does not move from the back righ	nt corner of the pool).
	0:09:08	Still many very pronounced sinusoidal whistles and voca	alizations.
	0:09:43	Usual whistle and then croaking. M is following	
	0:10.43	Usual whistles mixed with many vocalizations and sinusc	oidal whistles.
		M is following	
	0:12:06	Same as above	
BIRTH	0:12:20	C comes out. Series of usual whistles. Then a lot of voca	lizations, sinusoidal and
		usual whistles.	
		C is behind, right side	
	0:18:30	Interesting whistle, continuing sinusoidal and usual whis	stles.
SUBJECT	DELIVERY:	- 2 + 05 <mark>(??)</mark>	RECORD CARD # 2
ORA	COUNT	BEHAVIOR	

13:22	pm 0:25:35	The sinusoidal whistles and the usual whistles continue.
		Often B drives C away from obstacles, C always behind on the right side.
13:25	0:28:49	Interesting whistle
13:26	0:30:06	Still dry and short sounds, similar to an isolated click. The whistles continue.
13:31	0:34:47	Sound that could come from Cleo.
13:36	0:39:54	The usual whistles continue. C always swims at the right side of B.
		M is also at the right side of B
13:41	0:44:41	Same as above. The sinusoidal whistles seem diminished, while the usual whistles
		continue.
13:43	0:46:37	C occurs to be outside for a few seconds. Many vocalizations and whistles
13:44	0:48:10	B points the rostrum against the acrylic and emits vocalizations associated with (??)
		Then, again whistles.
13:45	0:48:34	Series of "aberrant" (??) whistles. There is agitation. Maybe M gets too close or too
		wild. B speeds up the swimming
L3:46	0:49:56	Same as above. M approaches C and B by swimming fast on the surface.
L3:49	0:53:24	B speeds up the swim. I think there could be a feeding time.
		During the feeding time a long series of sinusoidal whistles.
13:54	0:58:14	A short series of usual whistles starts again
13:59	1:02:36	It seems that B enters between C and (continuing in the following Record Card #3)
SUBJECT	DELIVERY:	- 2 + 05 (??) RECORD CARD # <b>3</b>

SUBJECT		DELIVERY:	- 2 + 05 (??) RECORD CARD # <b>3</b>	3
ORA		COUNT	BEHAVIOR	
			M who came too close. Many vocalizations and usual sinusoidal whistles.	
14:01	pm	1:05:06	C goes ahead of B. Usual sinusoidal whistles mixed with vocalizations	
14:01		1:05:26	Vocalizations never heard before, very harmonious.	
			In the last few minutes it seems that M became more insistent in wanting to get close	r
			to C and B	
14:03		1:07:10	Usual whistles	
14:04		1:08:30	Usual whistles mixed with vocalizations, same as TIME 14:01	

14:06		1:08:36	Strange whistles and vocalizations with few usual whistles	S.	
14:06		1:10:28	Many clicks, vocalizations and whistles. M is quite agitate	d, and B makes dry soun	ds
			preceded by vocalizations. Occasionally, the usual whistle	es.	
14:07		1:11:15	M swims fast around B and C. It shows aggressive behavio	or.	
			Many sinusoidal different whistles. Several usual whistles		
14:09		1:12:45	The atmosphere seems to be quiet. Usual whistles, then s	still many vocalizations a	nd
			whistles with convulsive swimming of all. Sometimes it se	ems that Bonnie struggle	es to
			follow C.		
			Tail blows away from the obstacles and curiosity of M. Dr	y sounds.	
14:10		1:14:30	Usual and other sounds		
14:11		1:15:00	END		
SUBJECT		QT - 1 + S	(5/09 - 14.15)	RECORD CARD #	<b>1</b> a
ORA		COUNT	BEHAVIOR		
14:16	pm	0:02:39	Bonnie: usual whistles. B swims with Cleo side by side. M	follows	
14:17		0:03:53	B moves C away from the acrylic. Series of vocalizations +	sinusoidal whistle.	
14.17		0:04:51	The usual whistles of B. C is stuck side by side at the right	side.	
14:18		0:05:19	Particular whistle		
14:19		0:06:24	Darkness		
14:20		0:06:36	Video Signal		
14:20		0:06:54	The usual whistles of B. C is stuck on the right side.		
14:22		0:08:37	B pushes C away from the acrylic. Series of vocalizations + s	sinusoidal whistle.	
			B continues with usual whistles.		
14:25		0:11:35	B continues with usual whistles.  Series of very weak whistles. From whom?		

B pushes C away from the back wall. Series of vocalizations + sinusoidal whistle.

New period: C swims always attached to B's right side. M follows them.

C swims always attached to B's right side. M follows them.

0:13:37

0:15:00

0:15:19

Again with the usual whistles.

14:27

14:28

15:00

15:05	0:20:11	Same as above
15:05	0:20:51	B and C continue to turn in pairs. M stops on the surface near the "skimmer" (??)
15:06	0:21:33	M continues to follow B and C
15:08	0:24:03	C loses contact with B for a few seconds. Series of vocalizations.
15:09	0:24:41	Same as above + B's usual whistles
15:10	0:25:27	Still series of vocalizations following the getting away of C.
		Follow the usual whistles of B
SUBJECT	QT - 1 + S	(??) RECORD CARD # 2a
ORA	COUNT	BEHAVIOR
15:11	0:26:36	B pushes C away from the bottom with some difficulty
		Series of vocalizations and sinusoidal whistles.
		Noise of a very close airplane.
15:12	0:27:21	M stops following B and C
15:13	0:28:13	M begins again to follow B and C with some interest. Faster swimming. Vocalizations
15:14	0:29:52	END
16:00		NEW CYCLE. B's usual whistle. C always swims to the right side of B. M follows them.
		Slow swimming.
16:02	0:32:43	Still B's usual whistles
16:05	0:35:40	B's usual whistle. C always swims to the right side of B. M follows them.
16:08	0:38:36	M approaches B and C. Series of vocalizations and sinusoidal whistle.
16:09	0:39:13	B hints at the usual whistle. Strange sounds similar to the first cries of C.
16:10	0:40:10	M approaches C and B. Series of vocalizations and sinusoidal whistles.
16:10	0:40:57	Still series of vocalizations and whistles, while M approaches C and B.
16:11	0:41:18	It looks like a deformed B whistle. B and C swim alone fast.  Many vocalizations.
16:11	0:41:54	I still hear and see what seems a whistle very "deformed" (??) of B.  M starts again to follow B and C
		Faster swimming, many vocalizations and sinusoidal whistles
16:12	0:24:33	Still vocalizations and sinusoidal whistles

SUBJECT	QT - 1 + S	(??) RECORD CARD # <b>3a</b>
ORA	COUNT	BEHAVIOR
16:12	0:42:45	M stops following B and C. Swimming is slower
16:14	0:44:10	M starts following B and C. Swimming is faster. vocalizations
16:15	0:45:09	END
16:59	0:45:12	NEW CYCLE - C swims attached to the right side of B.
		M follows them closely. Slow swimming
16:59	0:45:32	C accelerates and B follows it by pointing the rostrum to "FG" (??). Vocalizations
17:00	0:45:46	B and C are again side by side. B's usual whistles. M following
17:01	0:46:43	A cry? C begins the first attempts at breastfeeding
17:02	0:47:52	B appears to lose control of C for a few seconds. Vocalizations, sinusoidal whistle and
		immediately the usual whistles. Breastfeeding attempts continue. M is following.
17:03	0:49:10	Still B's usual whistles and other vocalizations Very short and weak (??: by the Ital. analyst).
		B keeps C away from the rocks and the bottom. Vocalizations and whistles.
17:07	0:52:53	C always swims attached to the B's right side. Breastfeeding attempts continue.
		M is following.
17:07	0:53:11	M walks away
17:08	0:54:35	Whistles (maybe B) and (??) of bubbles by C. Breastfeeding attempts continue.
		M starts to follow again
17:10	0:56:01	B expels the placenta. Series of vocalizations and whistles

Addendum: Notation of "(??)" indicate words or phrases that the translator was unable to parse

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