What's Occurring? Ultrasonic signature whistle use in Welsh bottlenose dolphins (*Tursiops truncatus*)

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Abstract

Animal communication signals are diverse. The type of sounds that animals' produce, and the way that information is encoded in those sounds, not only varies between species but can also vary geographically within a species. Therefore, an understanding of the vocal repertoire at the population level is important for providing insight into regional differences in vocal communication signals. One species whose vocal repertoire has received considerable attention is the bottlenose dolphin. This species is well known for its use of individually distinctive identity signals known as signature whistles. Bottlenose dolphins use their signature whistles to broadcast their identity and to maintain contact with social companions. Signature whistles are not innate but are learnt signals that develop within the first few months of an animal's life. It is therefore unsurprising that studies, which have characterised signature whistles in wild populations of bottlenose dolphins, have provided evidence of geographic variation in signature whistle structure. Here we describe the occurrence of signature whistles in a previously unexplored wild population of bottlenose dolphins in Cardigan Bay, Wales. We present the first occurrence of a signature whistle with an ultrasonic fundamental frequency component (> 30 kHz), a frequency band that was not thought to be utilised by this species for whistle communication. We also describe the occurrence of an ultrasonic non-signature whistle. Our findings highlight the importance of conducting regional studies in order to fully quantify a species' vocal repertoire, and call into question the efficacy of those studies that use restricted sampling rates.

Keywords: signature whistles, vocal learning, bottlenose dolphin, ultrasonic

Introduction

Animal communication studies have provided fundamental insight into the type of acoustic signals that animals use to share and transfer information with one another. By quantifying the vocal repertoire of a species we are in a better position to understand signal function, to standardise the terminology used to classify vocalisations (Leong et al. 2003), and to identify call types, which could be used as individual markers in conservation tools (Darden et al. 2003; Janik et al. 2013; Terry and Mcgregor 2002). This means that the quantification of a species vocal repertoire is particularly critical for acoustic population monitoring (Gridley et al. 2015; Boisseau 2005).

One species whose vocal repertoire has received considerable attention is the bottlenose dolphin (*Tursiops* spp.). Bottlenose dolphins are known for their use of signature whistles (Caldwell et al. 1990; Janik and Sayigh 2013). These are individually distinctive signals where the unique frequency modulation pattern of the whistle encodes the identity of the animal independently of general voice features (Janik et al. 2006). Animals therefore use their whistles to broadcast their identity (Sayigh et al. 1999; Janik et al. 2006) but also to maintain group cohesion (Janik and Slater 1998). Due to the strong link between signature whistle structure and animal identity, there is potential for signature whistles to be used as individual markers in mark-recapture studies as suggested by Janik et al. (2013) and Terry et al. (2005).

Signature whistle development is influenced by vocal learning where individual dolphins develop their own unique signature whistle within the first few months of life, and calves appear to model their signature whistle on other whistles they hear in their environment (Sayigh et al.1995; Fripp et al. 2005; Miksis et al.2002; Tyack and Sayigh 1997; Tyack 1997). Signature whistles have been documented in captive bottlenose dolphins (*Tursiops truncatus*) as well as a number of wild populations, including *Sarasota Bay, Florida* (Cook et al. 2004; Esch et al. 2009); *East coast of Scotland* (King and Janik, 2013; Quick and Janik, 2012; Gridley, 2011); *Namibia* (Kriesell et al. 2014); *South Western Sicily* (Papale et al. 2015) and *Sado estuary, Portugal* (Luis et al. 2015). They've also been documented in the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) using data from populations found in *South Africa*, *Japan* and *Australia* (Gridley et al. 2014). These studies have explored signature whistle diversity, both within and between populations, by investigating the variability in a number of whistle frequency and temporal parameter measurements. Signature whistles have been reported to range from 1 kHz up to approximately 30 kHz (Sayigh and Janik 2010; Janik and Sayigh 2013), in fact the maximum signature whistle frequency recorded so far is 27.3 kHz (Esch et al. 2009). Signature whistle durations have been recorded to range from 0.1 to 4 seconds (Buckstaff 2004). It is the maximum frequency of a species' call that should determine which sampling rate is used when making acoustic recordings of that species' vocal repertoire. However, some researchers continue to use a 48 kHz sampling rate when recording bottlenose dolphin vocalisations, effectively only recording whistles up to 24 kHz (e.g. Azevedo et al. 2007; dos Santos et al. 2005; Quick and Janik 2008). Using an insufficient sampling frequency can cause higher frequency components of whistles to be cut-off or missed entirely, which can have serious implications for repertoire classification (Boisseau 2005; May-Collado and Wartzok 2009), behavioural studies and acoustic monitoring programs.

Here we contribute to our understanding of signature whistle use in free ranging bottlenose dolphins by describing the signature whistles used by the wild population of bottlenose dolphins (*Tursiops truncatus*) that inhabit Cardigan Bay, Wales, UK. In addition, by using a higher sampling rate of 96 kHz we also document the first case of an ultrasonic (> 30 kHz) signature whistle in this species.

Materials & Methods

Acoustic Recordings

Acoustic recordings of wild bottlenose dolphins were made in Cardigan Bay, off the west coast of Wales between New Quay and Fishguard, between the months of June to November in 2011 to 2014. These animals are members of a resident population of approximately 133 bottlenose dolphins that inhabit the Cardigan Bay SAC (Feingold and Evans 2014).

Recordings were either made from the 'Sulaire': a 33ft modern charter vessel (2011, 2012 and 2013) or the 'Anna Lloyd': a 33 ft modern catamaran (2013 and 2014). Both vessels are owned and run by Dolphin Survey Boat Trips with survey trips run in association with the Cardigan Bay Marine Wildlife Centre (CBMWC) in New Quay, Wales. Survey trips where acoustic recordings were made were conducted in Beaufort sea state three or less, and animals were photographed with either a Canon Digital 20D or 30D SLR camera with a Canon 75–300 mm, F4 zoom lens.

Acoustic recordings were made using two HTI-96 MIN hydrophones (frequency response: 0.002–30 kHz ± 1 dB) towed at 2-m depth and a Fujitsu Siemens Esprimo mobile Laptop with either an Edirol UA-25 sound card (2011) or Roland UA55 Quad capture sound card (2012-2014). The sampling rate for both cards was 96 kHz, and 16 bit. All recordings were made whilst the engine was running and whilst the boat was both stationary (engine in neutral) and moving. Recordings were carried out during a variety of behavioural contexts; these included, but were not restricted to, feeding, socialising, travelling and resting. During each recording the number of dolphins present, group composition, the behaviour of the dolphins and location in relation to the boat was recorded using *Ad libitum* sampling (Mann 1999).

Signature Whistle Identification

One observer (HH) analysed the acoustic recordings by inspecting the spectrograms (FFT length 1024, overlap 100%, Hanning window) in Adobe Audition v2.0 (Adobe Systems). Those recording segments in which engine noise exceeded 2 kHz were discarded from the analysis. Each whistle was visually graded from 1 to 3 based on signal to noise ratio using the following scale: 1: signal is faint and either start or end time are not discernable, 2: signal is clear and both start and end of the whistle are clear, 3: Signal is prominent and dominates. Only whistles graded 2 or 3, for which start and end times were visible and the overall shape of the whistle was clear. Thus, any whistles that were masked by boat noise were not used in the SIGID or parameter measurement analysis.

Whistles were then categorised into discrete whistle types by visual inspection of the contours. Visual classification has previously been shown to be a superior method to computerised categorisation (Janik 1999). Once categorised, the SIGID method was used to identify which whistles were signature whistles, based on their temporal patterning and stereotyped structure (Janik et al. 2013). We employed the SIGID sequential bout analysis, where a minimum of 75% of whistles of the same type (within a whistle bout) must occur within 1-10 seconds of at least one other in order for that whistle type to be classed as a signature whistle (Janik et al. 2013). Only whistle types that occurred at least four times in a recording were used in this analysis. This method has already been successfully applied in a number of studies of bottlenose dolphin signature whistles (Quick and Janik 2012; Kriesell et al. 2014; King and Janik 2013; Gridley et al. 2014).

Visual Classification

Visual classification was used on a sub-set of data to confirm that the initial classification of whistle types by the observer (HH) was correct. Four naïve human judges (blind to context and animal identity) were provided with a subset of the whistle data. A total of 114 whistle spectrograms from one recording were given to each of the judges to sort into categories. Judges were asked to focus on the fundamental frequency of the whistle and group whistles based on similarity. Judges were allowed to sort the whistles into as many categories they saw fit. The similarity ratings were compared between the 4 judges and the initial observer (HH) using the Fleiss' Kappa statistic (Siegel and Castellan 1988) to determine the inter-observer agreement.

Frequency Parameters

Signature whistle contours from each spectrogram (FFT size 2048, frame length 512, 87.5% overlap and Hanning window) were extracted in MATLAB v 7.0.4 using a supervised peak algorithm which detects and traces the peak frequency of contours (Deecke and Janik 2006). Whistle contours were saved at a 5 ms time resolution. Using a custom written script in MATLAB the following frequency and time parameters were extracted from the whistle contours; start frequency, end frequency, minimum frequency, maximum frequency, mean frequency (average of all frequency points making up the contour at 5ms resolution) and duration (Gridley et al. 2012).

Results

A total of 2,340 whistles were recorded in 16.7 hours from 43 encounters conducted between 2011 and 2014. Acoustic recordings were carried out for the entire length of the focal group photo ID follow, with an average recording length of 24 minutes (range: 1 to 62). The number of recordings per day ranged from 1 to 9. Only 1104 whistles had a signal to noise ration of 2 or more, and were therefore used in the SIGID analysis. Of those whistles, 83 fell into the category of signature whistles with 10 signature whistle types being identified using SIGID (Janik et al. 2013), from 6 different recordings (varying from 34 to 54 mins in length) across 5 different days. The number of individual animals identified across these 6 encounters was 67 including 3 calves. The average group size was 13 (range: 4 to 19), and individual re-sightings were relatively low, with 12% (8 animals) sighted twice across the 6 encounters, and the remaining 88% (59 animals) only sighted once. In all 6 encounters the animals were predominantly travelling, with occasional bouts of socialising, and in 5 out of the 6 encounters animals were bow-riding.

Of the 10 signature whistle types identified, three (signatures 1, 2 and 5) were included in the whistles provided to the human judges. The 5 judges showed significant agreement on the categorisation of these three signature whistle types (Kappa statistic; $k=0.94$, $Z=13$, $p<0.001$). All 10 signature whistle types are presented in Figure 1.

Frequency and temporal parameter measurements of the 10 signature whistle types are provided in Table 1. The mean start frequency for the 10 signature whistle types ranged from 4.6 kHz up to 15.3 kHz, with a population mean of 8.2 kHz (SD ± 3.9) for all whistle types combined. Mean end frequency fell within a similar range from 3 kHz up to 12.3 kHz, with a population mean of 8.1 kHz (SD ± 2.8). Interestingly maximum frequency proved to be exceptionally high in the population with mean maximum frequency ranging from 12.1 kHz up to 38.8 kHz with a population mean of 18.6 kHz (SD ± 7.4). We present one signature whistle type (Signature 10) with a mean maximum frequency of 38.8 kHz, which is the first case of signature whistle being produced in the ultrasonic frequency range (>30 kHz) that we know of. In total there were 13 examples of the Signature 10 whistle, but only 6 of those were full contours containing a high fundamental frequency component. The remaining 7 were partial contours where the high fundamental frequency component was missing. The full contour of the ultrasonic signature whistle (Signature 10) is shown in Figure 1 & 2.

In contrast, mean minimum frequency had the smallest range from 2.9 kHz to 7.7 kHz, with a population mean of 5.5 kHz (SD ± 1.5). The mean frequency range of whistles spanned 6.1 kHz to 33.3 kHz, with a population mean of 13 kHz (SD ± 8). The averaged mean whistle frequencies ranged from 7.8 kHz to 17.8 kHz, with a population mean of 12.1 kHz (SD ± 3.3). Finally, mean duration for each whistle type varied from 0.55 seconds to 1.48 seconds, with a population mean duration of 1.06 seconds (SD ± 0.29). The median/quartile ranges of each of the frequency and temporal parameters discussed above are shown in Figure 3.

High Frequency Whistles

There is some evidence that the whistles recorded from the Cardigan Bay bottlenose dolphin population appear to be characterised by high frequencies. As well as one signature whistle with part of its whistle contour in the ultrasonic range, we found evidence of a non-signature whistle type also produced at frequencies of 22-40 kHz (Figure 4).

Discussion

We provide the first evidence of signature whistles in the Cardigan Bay bottlenose dolphin population. This brings the total number of wild populations of bottlenose dolphins (*Tursiops truncatus*) where signature whistles have been identified up to 6; *Sarasota Bay, Florida* (Cook et al. 2004; Esch et al. 2009); *East coast of Scotland* (King and Janik, 2013; Quick and Janik, 2012); *Namibia* (Kriesell et al. 2014); *South western Sicily* (Papale et al. 2015) and *Sado estuary, Portugal* (Luis et al. 2015). In addition, we present evidence that bottlenose dolphins produce signature whistles and other communicative whistle types in the ultrasonic frequency range i.e. at frequencies > 30 kHz. It was previously believed bottlenose dolphins did not exploit the 30 to 40 kHz frequency band. The frequency range for Signature 10 ranged from 29 to 36 kHz, and was considerably higher than most of the other signature whistle types identified, which ranged from 3.5 to 21 kHz. Minimum frequency for the 10 signature whistle types identified ranged from 1.4 kHz to 9.4 kHz, in line with previously published values (Caldwell et al. 1990; Esch et al. 2009; Kriesell et al. 2014). Signature whistle duration ranged from 0.4 seconds to 2.9 seconds, again, in line with the aforementioned studies. However, the duration of Signature 10 was relatively short (mean: 0.55 range: 0.4 to 0.6), and was shorter than the nine other signature whistle types. If producing high frequencies is energetically expensive then reducing the duration of the call may help offset this cost (Wiley and Richards, 1978). This may also explain why not all the Signature 10 whistles contained a high fundamental frequency component.

Both our study, and other studies, which have used an adequate sampling rate (e.g. Gridley et al. 2012, King and Janik, 2013, Esch et al. 2009) suggest that high frequency components (>30 kHz) are rare both within this population and other populations of bottlenose dolphins. Although high frequency whistles may not propagate as far underwater as those in the 5 to 20 kHz band, some animals nevertheless favour them. High frequency whistles have been described in other delphinid species; such as the Amazon river dolphin (*Inia geoffrensis geoffrensis*), which produces whistles up to 48 kHz (May-Collado and Wartzok 2007). Interestingly, these whistles were also very short in duration (0.002–0.080 seconds). It has also been shown that killer whales (*Orcinus orca*) can produce ultrasonic whistles ranging from 28 kHz to 75 kHz, with most of their whistles having an entirely ultrasonic fundamental frequency contour and being very short in duration (Samarra et al. 2010). The aforementioned study showed that whistle frequency also varied substantially across killer whale populations, highlighting the importance of sampling many different populations to fully explore whistle frequency parameters (Samarra et al. 2010).

To date signature whistles had only been recorded up to a maximum frequency of 27.3 kHz in Sarasota Bay, Florida (Esch et al. 2009). Although any frequency over 20 to 22 kHz may be considered ultrasonic, the occurrence of bottlenose dolphin signature whistles in > 30 kHz frequency range had yet to be documented. Although one previous study hinted that bottlenose dolphin whistles might be produced in the 40 kHz range, it appears the author was referring to the whistle harmonics (Boisseau 2005). The highest fundamental frequency reached for Signature 10 in this study was 41.8 kHz, which is over 10 kHz higher than previously reported maximum fundamental frequencies for signature whistles in this species (*Tursiops sp.*). Maximum fundamental frequencies for the other nine signature whistles types identified for this population ranged from 12.6 kHz to 23.2 kHz (Table 1). In addition to the signature whistle with ultrasonic frequency components, a non-signature whistle was also recorded whose entire fundamental frequency contour was ultrasonic (Figure 4).

Our findings therefore have significant implications for the management and conservation of regional populations. The quantification of the vocal repertoire of local populations is particularly imperative for effective acoustic monitoring programs. For example, through long-term acoustic monitoring the identification of signature whistle types in wild bottlenose dolphins can be used in mark-recapture studies to explore habitat use and ranging patterns of specific individuals, or can be used to estimate population size (Janik et al. 2013). In order to use this approach it is important that the repertoire of the population has been correctly classified, and the correct recording system is employed. During this study, we were only able to identify the signature whistles of 10 individuals, approximately 15% of the animals present during the recordings. The SIGID method is known to be conservative, where only 50% of signature whistles are likely to be identified, yet a 15% identification rate can be considered relatively low. The low detection rates of signature whistles in this study may be a result of recording context, with animals frequently travelling and/or bow-riding during recordings. Further acoustic sampling across a broader range of contexts is therefore required in order to improve the detection rate of signature whistle types in this population.

To summarise, free ranging bottlenose dolphins in Cardigan Bay, Wales, produce signature whistles whose frequency and temporal parameters are mostly in line with previous studies on signature whistle production in other populations. Maximum fundamental frequency of signature whistles is higher in this population than has previously been reported, with at least one animal exploiting the 30 to 40 kHz frequency band. We are yet to determine how often this, or other populations use ultrasonic frequencies, but our results certainly add weight to the argument that higher sampling rates should be used in dolphin communication studies and acoustic monitoring programs in order to fully quantify this species acoustic repertoire.

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Tables

Table 1. Frequency and temporal parameter measurements (mean ± SD) of signature whistle types (n=10) recorded from the bottlenose dolphin population that inhabits Cardigan Bay, Wales.

Figures

Figure 1. Spectrograms of the 10 signature whistle types identified in Cardigan Bay, Wales; sampling rate is 96 kHz, FFT length 1024, Hanning window function. Signature 10 is the ultrasonic signature whistle.

Figure 2. Spectrogram of an ultrasonic signature whistle type (Signature 10) identified in Cardigan Bay, Wales; sampling rate is 96 kHz, FFT length 1024, Hanning window function.

Figure 3. Boxplots of standard frequency parameter measurements for the 10 signature whistle types recorded in Cardigan Bay, Wales.

Figure 4. Spectrogram of a high frequency non-signature whistle identified in Cardigan Bay, Wales; sampling rate is 96 kHz, FFT length 256, Hanning window function.

Table 1.

	N	Start Freq. (kHz)	End Freq. (kHz)	Maximum Freq. (kHz)	Minimum Freq. (kHz)	Frequency Range (kHz)	Mean Freq. (kHz)	Duration (seconds)
		Mean ± SD	***Mean ± SD***	***Mean ± SD***	***Mean ± SD***	***Mean ± SD***	***Mean ± SD***	***Mean ± SD***
SW 1	10	5.89 ± 0.84	10.58 ±1.43	17.04 ± 1.43	5.7 ± 0.57	11.34 ± 1.41	10.77 ± 0.24	0.92 ± 0.11
SW 2	6	6.25 ± 1.16	12.34 ± 1.28	23.17 ± 0.8	6.25 ± 1.16	16.92 ± 1.08	16.52 ± 0.67	0.97 ± 0.09
SW 3	6	9.81 ± 2.39	7.06 ± 2.04	12.48 ± 1.06	6.41 ± 1.43	6.07 ± 1.57	10.24 ± 0.3	0.92 ± 0.1
SW 4	11	15.32 ± 0.74	2.98 ±0.72	15.32 ± 0.73	2.91 ± 0.71	12.41 ± 1.12	7.76 ± 0.33	1.37 ± 0.08
SW 5	5	10.24 ± 2.71	8.66 ± 1.82	20.66 ± 1.01	7.69 ± 1.34	12.97 ± 1.69	15.1 ± 0.61	1.17 ± 0.17
SW 6	10	6.93 ± 1.09	8.66 ± 1.44	14.59 ± 1.24	6.35 ± 0.71	8.25 ± 1.13	10.57 ± 0.85	1.48 ± 0.07
SW 7	10	4.59 ±0.99	6.76 ± 1.59	12.08 ± 0.41	4.51 ± 0.85	7.57 ± 0.8	10.17 ± 0.34	1.40 ± 0.04
SW 8	8	5.26 ± 0.77	11.63 ± 7.2	19.56 ± 2.5	5.19 ± 0.8	14.37 ± 2.95	11.86 ± 1.31	0.83 ± 0.02
SW 9	10	3.76 ± 2.04	7.01 ± 1.34	13.91 ± 1.9	6.96 ± 1.29	6.96 ± 2.36	9.97 ± 0.69	0.97 ± 0.05
SW 10*	6	3.86 ± 1.13	5.63 ± 0.31	38.81 ± 3.94	3.5 ± 1.1	33.31 ± 3.15	17.84 ± 0.94	0.55 ± 0.01

* An additional 7 partial signature whistles were identified for signature whistle type 10, but the high frequency part of the contour was missing. Therefore only 6 full contours were used when extracting the frequency parameter measurements.