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An Acoustic Play-Fight Signal in Bottlenose Dolphins (*Tursiops truncatus*) in Human Care

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Abstract

Play-fighting is common in many mammals, especially among juveniles and subadults, providing a safe opportunity to practice behaviours important in adult life. To prevent escalation into a potentially dangerous real fight, play-fighting often is accompanied by acoustic and/or visual appeasement behaviours. We studied aggressive and play-fight behaviours in bottlenose dolphins (*Tursiops truncatus*) at the Kolmården Djurpark. The results showed that play-fighting subadult dolphins emitted a characteristic sound, which was never observed in aggressive interactions. This was a short pulse burst followed by an FM-whistle. By plotting pulse repetition rate (PRR) vs. duration of the bursts, two main clusters were found. The bottom cluster had a mean PRR of 59 pulses per second (pps), and a mean duration of 154 msec. The top cluster had a mean PRR of 502 pps and a mean duration of 149 msec. These play-fight clusters were compared separately to corresponding adult aggressive pulse burst clusters. Taking both PRR and duration into consideration, no significant difference was found between the top clusters, or between the bottom clusters, in the two age groups. The trailing whistles were divided into five different frequency contour categories. These did not resemble the signature whistles of any of the play-fighting dolphins. The average start and end frequencies were 13.0 kHz and 10.1 kHz, respectively, and the maximum and minimum frequencies were 13.7 kHz and 7.0 kHz, respectively. The mean duration was 410 msec. Based on the fact that this sound occurred only in play-fights, we propose that it helps prevent a play-fight from escalating into a real fight and, hence, is analogous to the "laugh" and "chuckle" seen in apes.

Key Words: Bottlenose dolphin, *Tursiops truncatus*, play-fight, acoustic appeasement signal, pulse burst, whistle, Kolmårdens Djurpark

Introduction

Among marine mammals, behaviours categorised as play have been observed in Galapagos fur seals (*Arctocephalus galapagoensis*) (Arnold & Trillmich 1985), harbour seals (*Phoca vitulina*) (Renouf & Lawson 1986), common seal (*Phoca vitulina vitulina*) (Wilson 1974), Steller sea lions (*Eumetopias jubatus*) (Gentry 1974), killer whales (*Orcinus orca*) (Guinet 1991), and bottlenose dolphins (*Tursiops truncatus*) (e.g., Bel'kovich et al., 1970; Delfour & Aulagnier 1997; Essapian 1953). Play occurs both as a solitary and social activity (McDonnell & Poulin, 2002), and it is regarded as an important component of the ontogeny. It often is defined as an activity with no other immediate function to the animals other than providing a sense of pleasure, combined with elements of surprise (Pace, 2000); however, there is a wide range of indirect functions to play behaviour, which prepare young animals for adult life. Aiding the process of growth and development by enhancing general muscular-skeletal and cardiovascular fitness (McDonnell & Poulin, 2002), learning about the environment, practicing adult social activities, and establishing social relationships and communication skills (Pace, 2000) are examples of such probable indirect functions.

Play-fighting is common in mammals and may help train the young animal in predator-prey skills as well as in how to deal with social relations (Pellis & Pellis, 1987). It is usually distinguished from adult fighting by a more relaxed and often exaggerated behaviour pattern, often combined with specific visual and sometimes acoustic appeasement signals (McDonnell & Poulin, 2002).

Most aggressive behaviours can be characterised as threat behaviours (Huntingford & Turner, 1988; Norris, 1967; Overstrom, 1983) and make it possible to settle conflicts without actual fighting (deCarvalho et al., 2004; Jennings et al., 2004). If the conflict is not resolved by these means, it may escalate into a potentially dangerous and, in some species, lethal fight (deCarvalho et al., 2004; Jennings et al., 2004). Threat behaviours allow the adult animals to avoid physical confrontations and contact, whereas play-fighting in subadults is characterized by such.

A way to control intraspecific fighting is especially important in social carnivores and many primates that possess long and sharp canines and powerful jaws, which enable them to kill prey and defend themselves against predators, but also may cause them to seriously injure each other.

To avoid a play-fight escalating into a serious fight, playmates need to confirm their non-aggressive agreement through play signals (Bekoff, 1977, 1995; Pellis & Pellis, 1987, 1996). In apes, specific visual and acoustic signals are used for this: the smiling facial expression in combination with a soft "laughing" in the chimpanzee (*Pan troglodytes*) (Goodall, 1986) and the "chuckle" in gorillas (*Gorilla gorilla gorilla*) (Hoff et al., 1981; Maple & Hoff, 1982).

Dolphins have very sensitive skin and sharp teeth, and they are also capable of inflicting severe injuries to each other (Connor & Smolker, 1996; McBride & Herb, 1948; McCowan & Reiss, 1995; Norris, 1967; Östman, 1991). Contrary to animals like canids, felids, and primates, they lack the ability to express fine-tuned emotions by means of facial expressions, erecting fur, wagging tail, or elaborate body postures those terrestrial animals use to communicate (Goodall, 1986). In contrast, they have a rich repertoire of sounds (Bazúa-Durán, 2004; Caldwell & Caldwell, 1968; Coscia et al., 1991; Harrington, 1987; Popper, 1980; Robbins, 2000; Tooze et al., 1990). Hence, it would be reasonable to expect that if dolphins have developed a signal to control play-fighting, it would be in the acoustical domain. We studied this behaviour in juveniles and subadults in a group of bottlenose dolphins (*Tursiops truncatus*) in human care and compared it to serious aggression between adults in the same group.

Materials and Methods

Facility

Underwater recordings were made in 1996 and between 2001 and 2002 at the Kolmården Djurpark in Sweden. The pool complex contains two large public display pools, connected via two channels and with a holding pool system, and has a total water volume of 6,400 m^3, and a total water surface area of ca. 2,000 m^2. One of the display pools, which has a 900 m^2 and 3 to 6 m deep "Lagoon," is fitted with large underwater transparent acrylic panels at two levels, which offer underwater viewing to the visitors. The other display pool has an 800 m^2 water surface area and is 4 m deep. The behaviour observations were conducted in these two pools.

Dolphins

At the end of this study, the Kolmården Djurpark housed 16 dolphins: one adult male, two subadult males (Lotus, 6 years old, and Dino, 5 years old), two juvenile males (Max and Fenix, both 1 year old), seven adult females, two subadult females (Daphne, 7 years old, and Ariel, 5 years old), and two juvenile females (Lyra, 2 years old, and Luna, 1 year old). All subadults and juveniles were born at the facility, with the adult male being the father to all of them.

Data Collection

Different recording setups were used in the two study periods: (1) direct observations of play-fighting in 2001-2002, supplemented with audioband DAT (Digital Audio Tape) recordings of the concurrent acoustic activity in the pool; and (2) video recordings, with concurrent audioband recordings of aggressive interactions in 1996.

Online Observations in 2001-2002—The 1-h sessions of live observations were conducted using a Toshiba laptop computer, operating the computer software *The Observer*®, *Version 3.0* (Noldus Information Technology, Wageningen, The Netherlands). This software is designed for ethological studies, with a predefined computer keystroke or a series of keystrokes designated to represent different behaviours and subjects. The software provides a timestamp to each observation and facilitates the logging process as well as the subsequent statistical analysis. The ethogram was designed for a signature whistle development study and, therefore, no detailed quantitative behavioural description of play-fight activity was obtained. The play-fight behaviour could only be described qualitatively.

The concurrent acoustic activity within the audioband (< 22 kHz) in the pool was picked up using a HS/70 25-mm ball hydrophone (Sonar Research and Development, Ltd, Beverley, East Yorkshire, UK) and recorded on a Sony TCD-D8 DAT recorder. This system's frequency response was flat from 100 Hz to 22 kHz (±2 dB). During these recordings, all animals (juveniles and adults) were present in the same pool, but they had the option of leaving the study pool (Lagoon) to go into adjacent pools. Sounds were attributed to juveniles/subadults during play-fights by their vigorous visual behavioural displays.

Video Recordings in 1996—Recordings obtained in 1996 by Blomqvist (2004) focused on the aggressive interactions between two adult females that had been separated from the rest of the group and placed into the display pool "lagoon" with their calves in an attempt to improve their nursing conditions. Sounds within the audioband were picked up by a 25-mm HS/70 Sonar Products ball 188 hydrophone by Blomqvist et al. (now Sonar Research and Development, Ltd, Beverley, East Yorkshire, UK) and recorded together with the video images of the concurrent visual behaviours on a VHS VCR (Panasonic NV-FS 1 HQ). From these recordings, 25 representative aggressive interactions were selected, based on the picture quality (i.e., short distance to the camera and clear water) (for a detailed description, see Blomqvist, 2004).

Acoustic and Statistical Analysis

Measurement of sound duration and frequency analysis were done using spectrograms generated by the computer programmes *SeaPro*, *Version 1.1* (Centro Interdisciplinare di Bioacustica e Ricerche Ambientali, Università degli Studi, Pavia, Italy), *Adobe Audition®*, *Version 1.0* (Adobe Systems Incorporated, 345 Park Avenue, San Jose, CA, USA), and *SpectraPlus®*, professional edition, *Version 3.0a* (Pioneer Hill Software, Poulsbo, WA, USA, courtesy of Lee Miller, University of Southern Denmark, Odense, Denmark). The peak PRR was measured from the harmonic intervals in the spectrograms (Watkins, 1967) using *Raven*, *Version 1.1* (Cornell Lab of Ornithology, demo version). Statistical analyses were performed using *JMP* statistical computer software, *Version 4.0.2* (SAS Institute Inc., Cary, NC, USA).

Results

Play-Fight Observations

A total of 296 hours of direct observations were collected during the 2001-2002 study. Play-fights were only displayed by five of the eight juveniles/subadults (i.e., Daphne, Lotus, Dino, Ariel, and Lyra). The remaining three juveniles—Max, Fenix, and Luna—were never seen engaged in any high-intensity aggressive interactions. Behaviourally, a play-fight was characterized by one or more animals chasing each other. During these chases, the animals leaped and tumbled around each other, creating white-water in an apparent playful manner. No bites, jaw claps, direct open mouth, body slam, tail and rostrum hit, or face-to-face were seen being performed by the juveniles/subadults engaged in play-fights.

These play-fights were consistently accompanied by a characteristic sound, which was composed of a short pulse burst followed by an FM-whistle (Figure 1).

From the DAT recordings done concurrently with these direct observations, a selection of 446 pulse-burst-whistle combinations, all emitted during play-fights, was analysed. Plotting peak PRR vs. duration of the bursts, and applying 5% nonparametric bivariate density contours, two main clusters were found (Figure 2). The bottom cluster had a mean repetition rate of 59 pulses per second (pps) (SD = 26, n = 27), and a mean duration of 154 msec (SD = 61). The top one had a mean repetition rate of 502 pps (SD = 111, n = 419), and a mean duration of 149 msec (SD = 64).

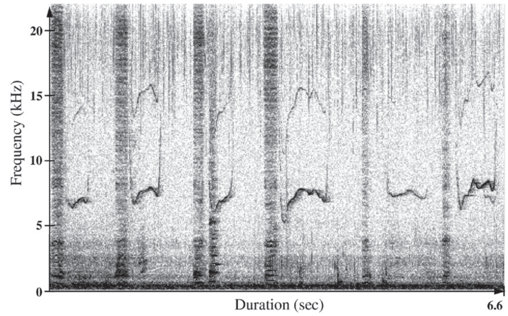

Figure 1. Spectrogram of a sequence of pulse whistles produced during play-fight by a subadult bottlenose dolphin at Kolmården Djurpark; window type: Hanning; FFT = 1,024 and 87% overlap.

The trailing whistles could be grouped into five different frequency contour categories (Figure 3 & Table 1). These did not resemble any of the signature whistles of the interacting juveniles/subadults (Figure 4). There was no preference for a specific frequency contour to be produced by a specific animal. The trailing whistles started either before or after the termination of the pulse burst (Figure 3 & Table 1). The whistle component had mean beginning and ending frequencies of 13.0 kHz (SD = 3.9 kHz) and 10.1 kHz (SD = 3.4 kHz), respectively, and a mean minimum and maximum frequency of 7.0 kHz (SD = 2.2 kHz) and 13.7 kHz (SD = 3.8 kHz), respectively. The average whistle duration was 410 msec (SD = 129 msec, n = 446) (see Table 1).

Adult Aggressive Encounters

A high-intensity adult aggressive interaction was commonly initiated by one of the animals aiming its rostrum at the other from a distance, either remaining stationary or moving very slowly towards the other. This situation escalated when the targeted animal responded by turning towards the aggressor, resulting in a face-to-face orientation, or a mutual approach, face-to-face. During the face-to-face phase, the most frequently displayed behaviours were open mouth and head and pectoral fin jerks, concurrent with fast emissions of short pulse bursts with high PRR, apparently emitted by both animals. Loud jaw claps also occurred frequently during this phase of the interaction—in some cases, emitted in fast succession (c.f. Defran & Pryor, 1980; Dudzinski, 1996; Overstrom, 1983). Adults were never seen engaged in play-fight behaviour.

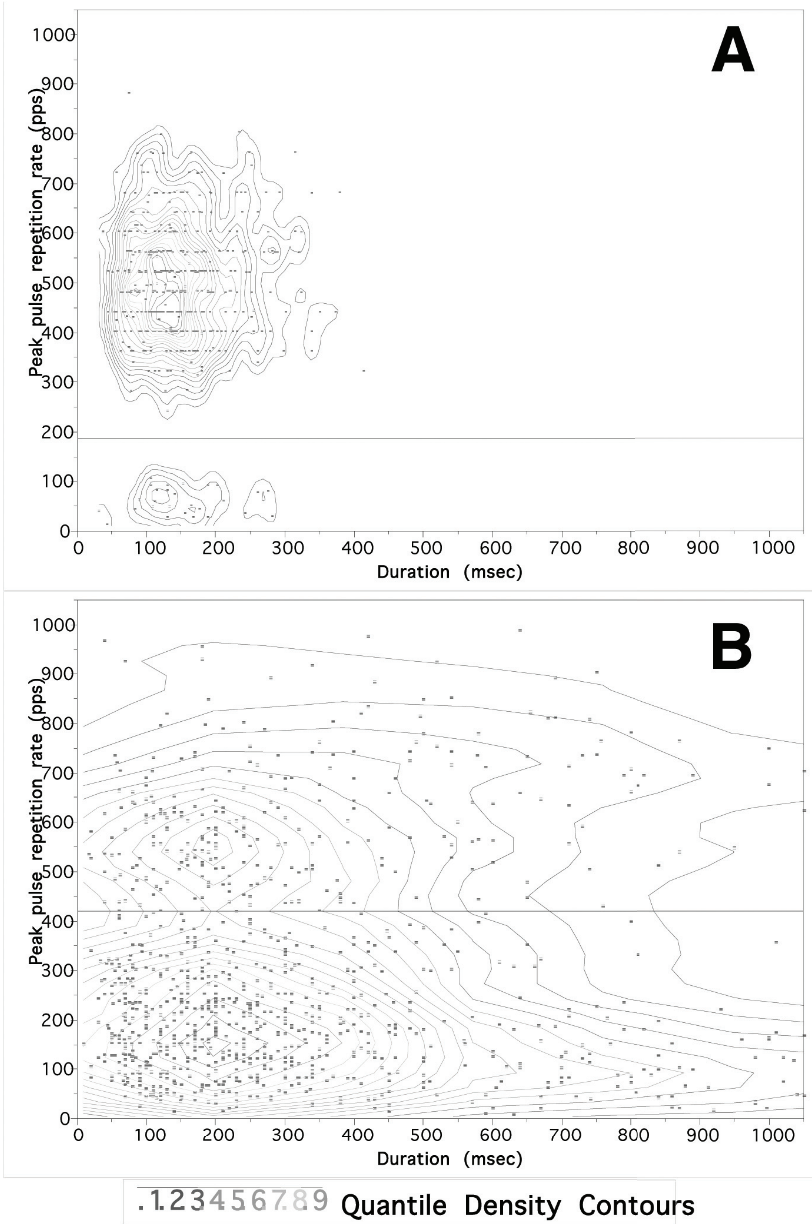

Figure 2. A nonparametric bivariate density plot of the peak pulse repetition rate (pps) by pulse duration (msec) for the pulse sounds recorded during play-fights (A) and for the pulse bursts produced during aggressive interactions (B); the Kernel SD for the peak repetition rate (in pps) and the pulse duration (in msec) were 38.63 and 22.56 in (A) and 36.48 and 79.12 in (B), respectively.

In the 25 high-intensity adult aggressive interactions selected from the 1996 recordings, 1,085 pulse bursts were analyzed for duration and peak PRR (see Blomqvist, 2004). Plotting PRR vs. burst duration and applying 5% nonparametric bivariate density contours to this plot again revealed two main clusters (Figure 3.2). Selecting all values above the 55% density contour, with a border between the two clusters set at 422 pps (Figure 3), a mean repetition rate of 542 pps (SD = 44, n = 67), and a mean duration of 194 msec (SD = 43) were found in the top cluster. In the bottom

Table 1. Summary statistics of the acoustic parameters for each bottlenose dolphin's play-fight trailing whistle contour

Whistle contour	1	2	3	4	5
n	73	2	13	229	129
	X±SD	X±SD	X±SD	X±SD	X±SD
Duration (msec)	388.0±126.0	399.0±10.0	493.0±146.0	429.0±131.0	380.0±118.0
Start frequency (kHz)	13.9±3.9	13.8±6.1	13.3±4.4	12.7±3.8	13.0±4.1
End frequency (kHz)	9.2±2.9	12.8±2.3	11.1±4.1	10.1±3.4	10.4±3.4
Minimum frequency (kHz)	6.9±1.6	8.6±2.4	8.5±4.2	6.9±2.2	7.0±2.2
Maximum frequency (kHz)	13.9±3.1	13.9±3.1	13.9±3.1	13.9±3.1	13.9±3.1
Whistle start within pulse burst	53.8±45.9	-	34.8±0	55.2±48.5	52.0±53.5
n	33	-	7	40	24
Whistle start after pulse burst	85.8±64.4	98.7±49.3	126.3±100.6	94.9±77.4	107.2±57.6
n	40	2	6	189	105

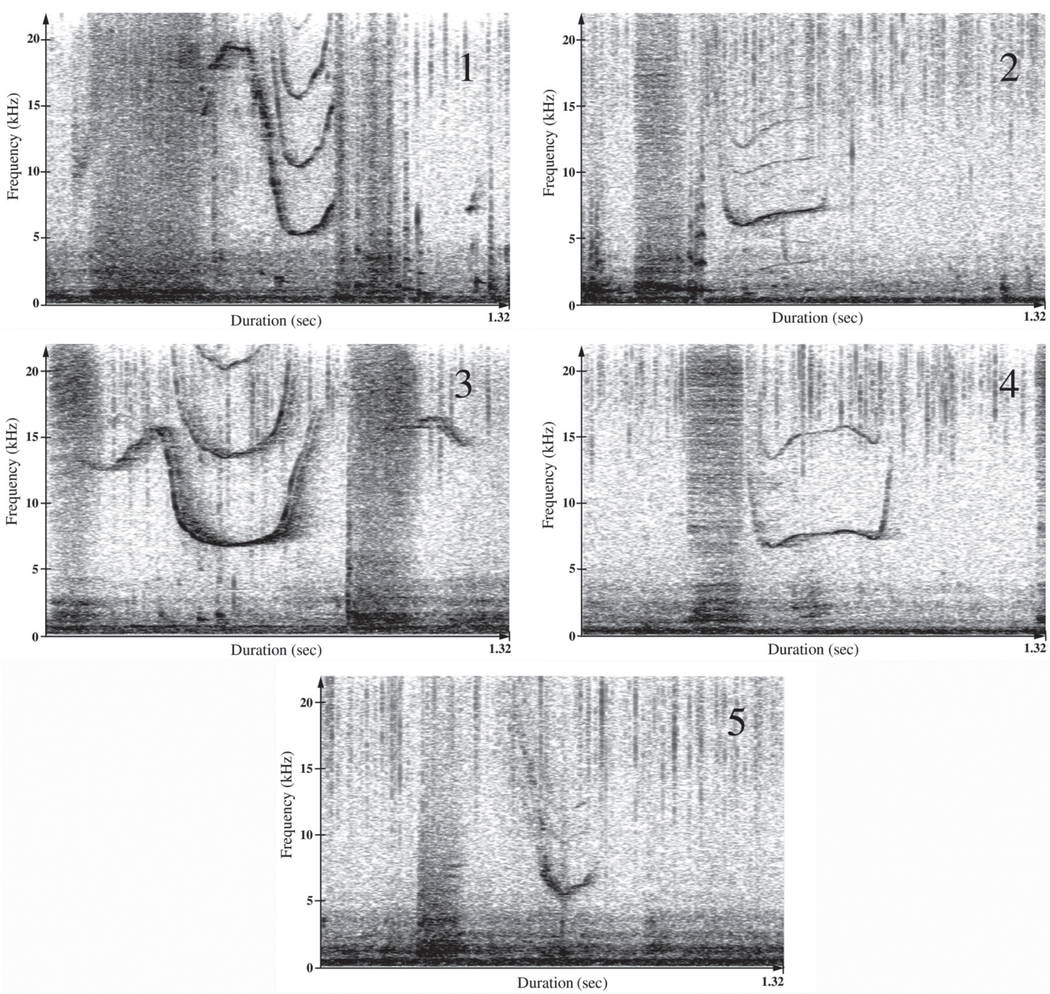

Figure 3. Spectrogram of the five different trailing whistle frequency contours of the pulse whistles produced during play-fight by subadult bottlenose dolphins; window type: Hanning; FFT = 1,024 and 87% overlap.

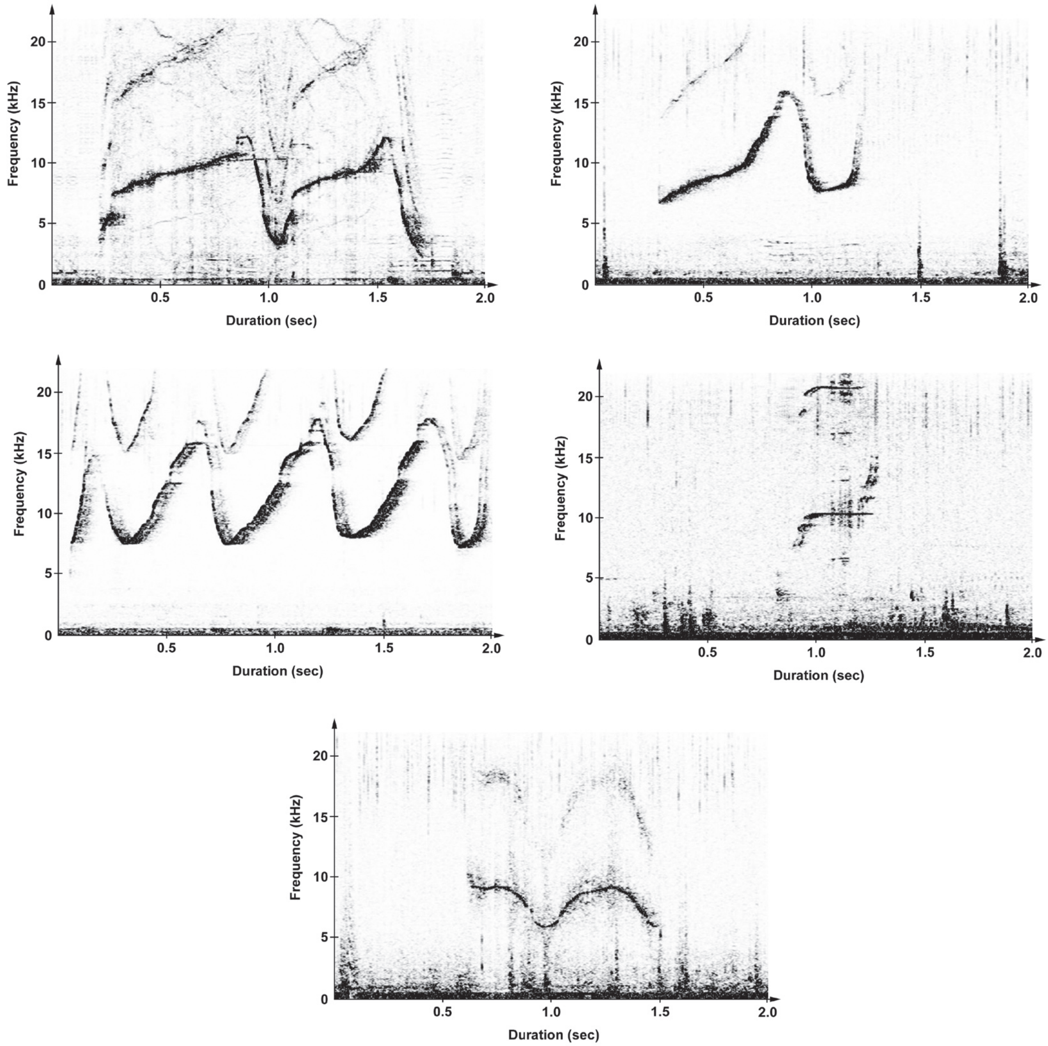

Figure 4. Spectrogram of the different signature whistle frequency contours of the juvenile/subadult dolphins engaged in play-fight; window type: Hanning; FFT = 512.

cluster, the average repetition rate was 177 pps (SD = 88, n = 573) and the mean duration was 213 msec (SD = 118).

Comparing the Two Data Sets

Each play-fight pulse burst PRR vs. burst duration cluster was compared to the corresponding aggressive adult pulse burst clusters. Taking both PRR and duration into consideration, no significant difference was found between the top clusters (MANOVA: F = 2.17, p = 0.1405) and the bottom clusters (MANOVA: F = 3.20, p = 0.0738).

Discussion

Juvenile and subadult dolphins engaged in behaviours interpreted as play-fight while emitting a characteristic sound, which was a combination of a short pulse burst and a trailing FM-whistle. Although the pulse burst component was aurally similar to the pulse bursts recorded in aggressive interactions between adults (Blomqvist, 2004), the latter never had a trailing whistle. Comparing each PRR/duration cluster separately, there were no significant differences between the play-fight pulse burst and the aggressive pulse burst. Hence, the trailing whistle in the play-fight may be important to distinguish the play-fighting from real aggression. Whistles are produced significantly more often during affiliative activities (Caldwell & Caldwell, 1977; Herzing, 1996; Sayigh, 1992; Tyack, 1997), whereas pulse bursts mainly occur during conflicts (Blomqvist & Amundin, 2004; Brownlee & Norris, 1994; Östman, 1991; Overstrom, 1983). Combining the more aggressive pulse burst with a whistle would be a way to "take the edge" off the potential threat conveyed by the pulse burst. This could also be accomplished by the absence/presence of different visual behaviour and/or body contact; however, this aspect was not considered in the present study. We propose that this sound is analogous to the play-fight "laugh" in chimpanzees (*Pan troglodytes*) (Goodall, 1986) and the "chuckle" in gorillas (*Gorilla gorilla gorilla*) (Estes, 1991; Hoff et al., 1981; Maple & Hoff, 1982), having the same function to ensure that the play-fight does not escalate into a real fight.

The apes' laughing and chuckling is merely an exaggerated panting, having a rather low intensity that is only audible to the playmates and conspecifics at close distance. As diving animals, dolphins cannot use such an exaggerated panting as a play signal; therefore, a different type of sound is expected. A play-fight sound should be omnidirectional, so it can be heard in all body orientations, in murky waters, and in the dark by the playmates, as well as by conspecifics in the vicinity. The observed pulse-burst-whistle combination fulfills this criterion. Although the precise source level could not be calculated with the present setup, the pulse burst whistle was quieter to the human ear than the adult dolphin's aggressive pulse bursts.

So far, this signal is only observed in the Kolmården dolphin colony. To confirm that it is characteristic for the species, further studies need to be done on other groups of dolphins in human care and preferably also in the wild. In such studies, sex differences and behaviour sequences during play-fight should be considered.

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