Journal of
Zoological and
Botanical Gardens

MDPI

Article

Vocal Cues to Assess Arousal State of Bottlenose Dolphins (*Tursiops* spp.) Involved in Public Presentations

Rachel Probert [1,2,*], Bridget S. James [1,3], Simon H. Elwen [1,3] and Tess Gridley [1,3,4]

[1] Sea Search Research and Conservation, Muizenberg, Cape Town 7945, South Africa; bsjames2685@gmail.com (B.S.J.); simon.elwen@gmail.com (S.H.E.); tessgridley@yahoo.co.uk (T.G.)
[2] School of Life Sciences, Department of Agriculture, Engineering and Science, University of KwaZulu-Natal, Durban 3629, South Africa
[3] Department of Botany and Zoology, Faculty of Science, Stellenbosch University, Cape Town 7605, South Africa
[4] Centre for Statistics in Ecology, Environment and Conservation, Department of Statistical Sciences, University of Cape Town, Cape Town 7701, South Africa
* Correspondence: rachelprbrt@gmail.com; Tel.: +27-767831809

Abstract: Emotions in animals may be expressed by arousal and understanding this often relies upon the monitoring of their behaviour. Under human care, animals' arousal states may be linked to husbandry decisions, whereby animals may display arousal responses to scheduled events such as feeding and human interaction. Here, we investigate vocal correlates of arousal associated with public presentations of bottlenose dolphins (*Tursiops* spp.) in human care by comparing vocal production rates and characteristics between high and low arousal contexts. Elevated arousal during the day compared with overnight was characterised by increased signature and non-signature whistle production. High intensity broadband crack vocalisations were produced less than whistles during the day and did not correlate with increased arousal around presentation times. Three of ten dolphins increased signature whistle production before and/or after presentation sessions, indicating elevated arousal and variation in individual responses. Many individuals elevated minimum frequency and suppressed maximum frequency of signature whistles in a way that correlated with higher arousal contexts, indicating that these may therefore be good indicators of changes in arousal state. Overall, our study demonstrates that passive acoustic monitoring can provide a useful indication of arousal linked to husbandry decisions, and that individual variation in vocal responses, likely linked to personality, is important to consider.

Keywords: arousal; bottlenose dolphins; acoustics; emotions; signature whistles; human care

Citation: Probert, R.; James, B.S.; Elwen, S.H.; Gridley, T. Vocal Cues to Assess Arousal State of Bottlenose Dolphins (*Tursiops* spp.) Involved in Public Presentations. *J. Zool. Bot. Gard.* **2023**, *4*, 711–727. https://doi.org/10.3390/jzbg4040050

Academic Editor: Laura Thompson

Received: 4 September 2023
Revised: 28 October 2023
Accepted: 1 November 2023
Published: 10 November 2023

1. Introduction

Understanding animals' internal states and minimising the effects of stressors experienced while in human care is important to ensure the positive welfare of animals [1,2], including dolphins [3]. While it is accepted that animals display emotions, these internal states are difficult to quantify in non-human animals [4]. However, emotional arousal can be interpreted through intense, short-lived behavioural responses to environmental stimuli [5,6] and can be monitored through vocal behaviour [7–9]. Monitoring behavioural responses is a common measure of internal state for animals in human care [10,11] as behavioural responses are linked to arousal [12]—the intensity of the internal state [6]—and valence—the positive or negative association [5,12]. More recently the importance of monitoring animals as individuals has become widely recognised, as individual differences in personality may influence their behavioural responses to external stimuli/events [13–16]. In facilities where animals are in human care, they have structured daily schedules where activities such as food provision or public presentations are highly predictable through signalled cues associated with the carers [17]. There is conflicting information regarding the impact of the predictability of schedules, with evidence supporting enhanced positive welfare of animals through both predictable [17–20] and unpredictable [21] schedules. More recent studies have indicated that more predictable schedules can improve levels of social behaviour [22] and increase behavioural diversity [23] of dolphins under human care. The introduction of moderate levels of randomisation in daily scheduling needs more attention [22].

Emotional arousal is known to influence vocal signals through shifts in the production rate and structural characteristics of vocalisations [7,24,25], providing both voluntary and involuntary vocal cues of changes in internal emotional states [6]. When investigated across taxa, [6] identified several common rules regarding how the vocal behaviour of mammals changed in response to arousal state. For example, many terrestrial mammal species produce calls more frequently during high arousal states with negative valence, such as aggression [26,27], and produce lower frequency sounds during aggressive interactions [6]. However, such generalities are not universal across mammal species. For example, silver foxes increase their call production rate during both positive and negative arousal [27], and various species of rhesus monkeys use higher frequency calls during negative arousal contexts, such as aggression, for example [28]. Consequently, acoustic indicators of arousal are complicated by species differences and the nuances of behavioural context. To date, the majority of research effort has focused on terrestrial mammals under negative contexts and associated vocal responses [29–31], with little focus on arousal and valence in cetaceans. The mechanisms of sound production differ in cetaceans compared with terrestrial mammals [32], thus vocal cues of arousal may also differ.

The acoustic behaviour of common bottlenose dolphins (*Tursiops truncatus*) has been widely studied in various contexts, both in the wild and while in human care [3,33–36]. Their vocal repertoire consists of a range of pulsed and tonal sounds [37], most of which have clearly defined functions [38,39]. Tonal sounds include narrow-band, frequency modulated whistles used to communicate during social interactions [34,40]. Individually distinctive 'signature whistles', which encode identity information, are the most frequently emitted whistle type used by bottlenose dolphins, among both those in the wild and those in human care [35]. Signature whistles develop in the first few months of life through vocal production learning [41] and remain stable over time [33]. These whistle types are primarily used to maintain contact with [33,39] and address [42] one another. Bottlenose dolphins have been shown to increase the production rate of signature whistles during isolation [24,43] or separation [39,44], with shifts in structural characteristics, such as frequency and duration, providing a vocal cue of the underlying arousal state of an individual [24,43,45,46]. Pulsed sounds emitted by bottlenose dolphins include echolocation used to orient and locate objects such as prey [38] and burst pulsed sounds, which are likely a graded signal with context-dependent functions used in social interactions [47,48]. A discrete category of pulsed sounds includes high intensity broadband cracks [49]. Compared with whistles and echolocation, the characteristics and function of cracks is poorly understood [50], though they are thought to be emitted in fearful [51] and aggressive [52] contexts which may be linked to high arousal states with negative valence.

As vocal cues (changes in production rate and structural characteristics) may indicate underlying arousal states [53–55], these features may be used as a non-invasive tool with which to monitor animals in human care [56–58]. uShaka Sea World dolphinarium (hereafter uShaka), established in 2004 in Durban, South Africa, houses two species and hybrids of bottlenose dolphins [59]. Vocal correlates of arousal have been previously documented for the dolphins in the facility, and results indicate that whistles are a strong indicator of arousal [25]. This study built on these prior findings to investigate shifts in vocal cues, including whistles and crack vocalisations, in response to public presentations, of which arousal valence is unknown.

2. Materials and Methods

2.1. Data Collection and Study Animals

Acoustic data were collected on the 13, 14, 15, 16 and 18 October 2010, 22 and 23 November 2016 and over 24 nights in May, July and August 2018 at uShaka. In 2010 the group consisted of 11 bottlenose dolphins and was composed of two recognised species (*Tursiops truncatus* and *Tursiops aduncus*) and hybrids thereof. Following the death of one male in 2015, the 2016 and 2018 recordings consisted of 10 individuals (Table A1). The dolphins were held in seven interconnecting pools with a total volume of 11,000 m^3 (Figure 1) and split into three social groups separated by gates through which animals in adjacent pools could maintain both visual and acoustic contact.

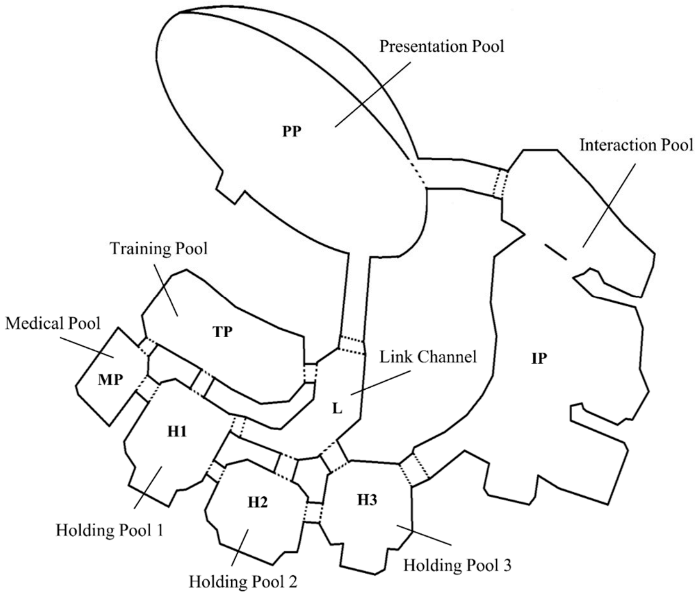

Figure 1. A schematic representation of the pools at uShaka, adapted from [60].

Acoustic behaviour and context data were collected in 2010 and 2016 using one to three dipping hydrophones (HTI-96-MIN; High Tech Inc., United States; flat frequency response of 2 Hz–30 kHz ± 1 dB re 1 µPa) connected to a digital Tascam recorder (model DR-680; TEAC America Inc., United States), sampling the data at 96 kHz and sample depth 24-bit stereo. Simultaneous vocal notes of activities (presentation and training sessions, and the position of various dolphins relative to the hydrophone) were documented by one to three visual observers from a pool side location and recorded into a concurrent vocal track using a headset microphone. As a control, acoustic data were collected overnight in 2018 (between 20:00 and 03:00, for the first 15 min of each hour) in the absence of training staff. These data were collected using a single Sound Trap 300 HF hydrophone (Ocean Instruments, New Zealand, frequency response: 20 Hz–150 kHz ± 3 dB, sensitivity: 183.3 dB re. 1 µPa) sampling the data at 576 kHz and sample depth 16-bit mono and recording continuously. The hydrophone was placed in the link channel, an area central to the pool network and within acoustic range of dolphins held in all pools (Figure 1) and the dolphins were left undisturbed. The hydrophone was attached to a 1 kg dive weight and suspended from a rope mid water (at 1.5 m depth; total channel depth 2.5 m) and attached to the roof with a carabiner clip to prevent movement which could produce unnecessary noise on the hydrophone.

2.2. Signature Whistle Catalogue

Whistle contours are characterised by their time–frequency modulation patterns and in bottlenose dolphins signature whistles can consist of a single contour or of repeated contours (loop). A repeated contour, or multiloop whistle, is either connected with no breaks in the entire contour or disconnected with a maximum inter-loop interval of 0.25 s between successive loops [24]. Time–frequency spectrograms of the acoustic recordings (FFT = 1024, frequency range = 0–40 kHz, time series window = 10 s, Hann window, 50% overlap) were analysed in Adobe Audition CC (v 6.0; Adobe Inc., San Jose, CA, USA). Signature whistles are often produced when animals are separated from the group [43] and temporary separation can be used to determine signature whistles of individuals [33,34]. A signature whistle catalogue was generated from temporary separation sessions recorded with simultaneous vocal notes in 2016, whereby each animal was placed in a separate pool for 10–20 min. For the separation sessions, the signature whistle was defined as the most common whistle recorded in each session and was matched to the individual by comparing the relative amplitude of signals on the three hydrophones placed at different sites. Signature whistles were then confirmed using the SIGID bout analysis approach [35] where each signature whistle type had at least three out of four whistles of the same contour shape occurring within 1–10 s of one another.

2.3. Behavioural Contexts

Shifts in vocal production rates as an indicator of arousal associated with public presentations were investigated using acoustic data collected in 2010, 2016 and 2018. Presentations took place three times a day at fixed times (see Table 1), during which time participating dolphins were moved into the link channel and then to the presentation pool to perform before an audience (Figure 1). Each presentation lasted 30 min whereby either a group (two to five dolphins at a time) or an individual was on public display for up to 10 min. During presentations the participating dolphin/s received food rewards (fish) as positive reinforcement for the successful completion of tasks as cued by the trainer.

Table 1. Details of the seven contexts under which the dolphins were recorded.

Context (Year; No. of Sessions)	Time of Day	Details	Trainers' Activities	Dolphins' Activities
Night (2018; 12 randomly selected from 24)	20:00–03:00	Lights were off, dolphinarium was quiet	Absent from facility	Minimal to no human interactions *
Daily activities (2010, 2016; 8)	09:30–16:00	All other normal daytime dolphinarium regimes excluding the morning feeding session and presentations	Interactions included training/feeding sessions with the dolphins	Involved in training sessions, feeding sessions or at rest
20–10 min pre (2010, 2016; 6)	10–20 min before presentations	The 10 min period leading up to presentation preparation	Starting preparation for the presentations (preparing boxes of fish, more staff activity around the presentation pool)	Starting to get prepared for the presentation
10–0 min pre (2010, 2016; 6)	Within 10 min before presentations	The period immediately before and within 10 min preceding presentations.	Preparing for the presentation (sound/music checks, moving dolphins around to different pools)	Moved between pools in preparation for the presentation
Presentation (2010, 2016; 11)	10:30, 12:30 and 15:00	Included one to five dolphins at a time. Music playing.	Participating in presentations and back-of-house preparing to shift dolphins around	Either participating in the presentation or back-of-house
0–10 min post (2010, 2016; 7)	Within 10 min after presentations	The period immediately after and up to 10 min following presentations. Music stops playing.	Moving dolphins around to designated pools	All dolphins were reunited, within their social groups, back-of-house and moved around to designated pools
10–20 min post (2010, 2016; 7)	10–20 min after presentations	The 10 min period after which all dolphins are reunited back of house	Either preparing for further training sessions or resting periods	All dolphins were moved into their designated pools

* Except occasional movement of the overnight security staff near their pools.

Acoustic data collection was represented by seven broad contexts reflecting dolphinarium activities (Table 1). Daytime contexts were considered higher arousal [61] than overnight, particularly during periods associated with presentations (10–0 min pre, during presentations, and 0–10 min post). Overnight was considered the lowest arousal period as human poolside presence was minimal (limited to security staff only), lights were off, and the dolphins were housed in their allocated pool configurations (see [25]).

2.4. Identification of Sound Types

The acoustic data were viewed in the spectral display of Raven Pro v 1.4 [62] to identify whistles (FFT = 1024, frequency range = 0–40 kHz) and cracks (FFT = 512–2048 depending on sampling rate, frequency range = full frequency range of recording) and were documented in a database. Whistle identification and classification was verified through independent analysis by two trained bio-acousticians (author RP and one other) following well established methods [63–65]. The signal to noise ratios (SNR) of whistles were visually assessed using the following criteria: SNR 1 = whistle is faint/barely visible, SNR 2 = whistle is clear and unambiguous, and SNR 3 = whistle is prominent [63]. Cracks were high intensity and easily distinguishable through visual and aural characteristics, and all identified cracks were included in the analysis. Bottlenose dolphins can copy whistles of others to address, draw attention from or direct information to an individual [42,63,66]. Whistle copies are not always exact replications but may incorporate features of the producer's whistle type [42,64]; however, they may also be indistinguishable from the original whistle. Without acoustic localisation, identification of whistle matching in freely interacting dolphins is problematic. We adopted the approach of [65] to limit inflation of whistle counts caused by copying by removing whistle contours of matching frequency modulation patterns if they overlap in the time domain. Additionally, we observed stereotyped whistle copying behaviour where the signature whistle of P2 was emitted at various frequencies in all three datasets. For these stereotyped whistling interactions, we could not confidently assign whistle production to P2. We assigned a series of these whistles to their own category named 'square copies' (see [25] for a full description of these whistles) and removed these sections of recording from subsequent analysis of individual production rates and characteristics. All whistles of good quality (SNR 2 and 3) were compared with the signature whistle catalogue and categorised as one of the following: a signature whistle, signature whistle copy (a copy of a signature whistle by another individual), square copy (unique stereotyped copying behaviour of the contour of P2), unclassified (masked or partial whistles that were unidentifiable and faint), or non-signature whistle (a whistle contour that does not match any of the catalogued signature whistle types).

We used broadband recordings (sampled at 576 kHz) collected in 2018 (Figure 2) to measure the structural characteristics of cracks. All 15 min acoustic files from three randomly selected recording days were used to extract 30 cracks with good SNR for measuring. A high pass filter was applied at 100 Hz to remove system noise and broadband noise reduction in Adobe Audition CC. The peak frequency (from the spectral view) and duration (from the waveform) were measured from each crack in RStudio version 4.0.3 [67] using the package "warbleR" [68] with built-in functions from packages "tuneR" [69] and "seewave" [70]. Once cracks were characterised in the full bandwidth recordings, we compared these measurements to 30 randomly selected cracks recorded with a 96 kHz sample rate (same filter processing applied) to determine if any important information was omitted from recordings at a lower sample rate. The peak frequency and duration of cracks from each sampling year were compared using Kruskal–Wallis tests as the data were not normally distributed.

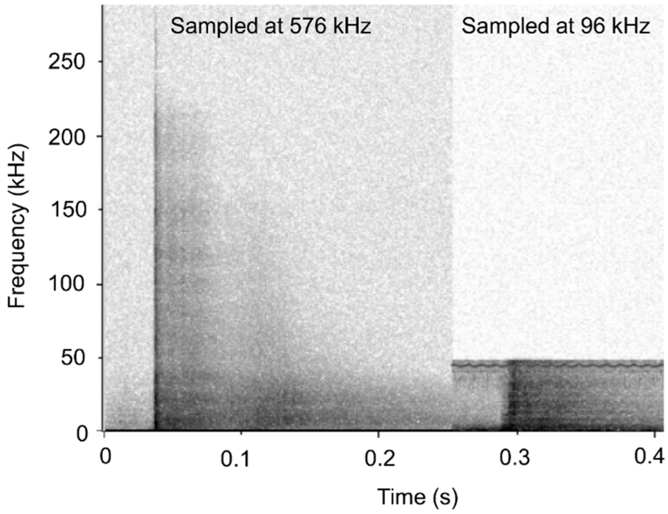

Figure 2. Spectral view of cracks recorded at full bandwidth (576 kHz) and a lower sampling rate (96 kHz).

2.5. Influence of Context on Group and Individual Vocal Production Rates

The production rate of whistles (signature whistles, non-signature whistles and square copies) and cracks were assessed through the recordings by counting the number of each vocalisation within each category separately for each context. The vocal production rate was calculated by dividing the total count of each call per context session and dividing it by the duration of the session (in minutes). There were significantly more 'Night' sessions than any other context and, as a result, half of these were randomly selected and used for subsequent analyses. A preliminary analysis was carried out using Welch *t*-tests to compare the production rates of each call type between the two sampling years (2010 and 2016) to determine whether data from these two years can be combined. Once determined, call production rates were compared across the seven contexts for each call separately using Kruskal–Wallis tests (data not normally distributed). Multiple *post hoc* tests were run using the package "conover.test" [71] following a significant result, adjusting the alpha value using the Benjamini–Hochberg method.

As crack vocalisations were produced more commonly than whistles overnight, the production rate was compared between four configurations in which the social groups were housed for the night [25], sometimes limiting visual contact between certain groups (see Figure 1). Configurations were as follows: (1) all social groups back-of-house with one group having access to the IP, and none having access to the PP; (2) female group housed in the PP while the mixed and male groups were back-of-house, with one group having access to the IP; (3) male group housed in the PP while the mixed and female groups were back-of-house, with one group having access to the IP; and (4) mixed group housed in the PP while the male and female groups were back-of-house, with one group having access to the IP. The IP and PP are linked and only separated by a gate through which the dolphins have visual contact with one another. The production rate of cracks was compared using Kruskal–Wallis tests (data not normally distributed).

Changes in individual vocal production rates across contexts were investigated using individually unique signature whistles. For each dolphin, signature whistle production rates were zero-inflated, therefore three count models accounting for excess zeros were run for each (zero-inflated Poisson, zero-inflated negative binomial, and hurdle negative binomial models). Each of these model types are composed of a binomial model (presence/absence of signature whistles), and within each session where signature whistles are present, an abundance model (either negative binomial or zero-truncated) determines the distribution of signature whistles. Session duration (in minutes) was set as the offset variable, and all contexts were compared with the "Presentation" context. The best model fit for each signature whistle type was selected using the Bayesian information criterion (BIC).

2.6. Shifts in Individual Signature Whistle Characteristics between Low and High Arousal Contexts

We investigated changes in time–frequency characteristics of individual signature whistles across contexts. Whistle duration and minimum and maximum frequency were measured in Raven Pro using the selection function, and the number of loops per whistle were manually counted. As many dolphins either produced few or no signature whistles during some of the contexts, changes in production rate and structural characteristics were compared between the low arousal (overnight) context and one high arousal (during presentations) context. Individual signature whistles were only included in the analysis if a minimum of ten whistles were produced for each context to allow for any inter-contour variation. Sample sizes were evened out for both contexts for each signature whistle by random selection. Each time-frequency characteristic was compared between contexts using Wilcoxon signed-rank tests (data not normally distributed).

3. Results

A total of ~61 h of data were collected across recording contexts totalling 49 recording sessions (see Table 1 for details). Within these recording periods, 6772 vocalisations were identified, including 3815 whistles and 2957 cracks. Of the whistles, 2512 (65.8%) were signature whistles, 998 (26.2%) were non-signature whistles, 28 (0.7%) were whistle copies and 277 (7.3%) were square copies. Ten signature whistles were documented for the group of 11 dolphins. The whistle of male M4 was not identified in the 2010 recordings and as he subsequently died this animal was not included in the 2016 isolations or subsequent analyses, therefore the signature whistle remains unconfirmed. Eight of the ten signature whistles were confidently assigned to individuals (P1, P2, F1–5 and M3). The two remaining stereotyped whistles (M1 and M2) could not be confidently differentiated between individuals Ingelosi and Khwezi (Table A1; Figure 3) and it is possible that these individuals have a shared repertoire.

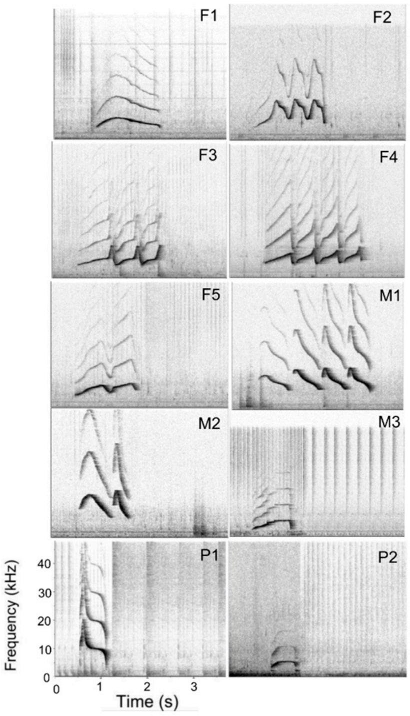

Figure 3. Signature whistle catalogue for ten of the dolphins housed at uShaka. F1–5 are whistles from the female group, M1–3 are whistles from the male group, and P1 (male) and P2 (female) are whistles from the mixed group (see Table A1).

To measure and compare the structural characteristics of cracks, 60 cracks were measured (30 sampled at 96 kHz from daytime recordings and 30 from full bandwidth recordings collected overnight). Mean peak frequency as measured from the spectral view was 1.46 ± 1.02 kHz from full bandwidth recordings and 1.10 ± 0.82 kHz from lower sampling rate recordings (Kruskal–Wallis; $n = 60$; $p > 0.05$) with a similar coefficient of variation (CV) within each subset of data (CV for full bandwidth = 0.70 and lower bandwidth = 0.75). Cracks in full bandwidth recordings were measured with a mean waveform duration of 0.02 ± 0.00 s, similar to cracks recorded at a lower sample rate (0.02 ± 0.00 s) (Kruskal–Wallis; $n = 60$; $p > 0.05$). These measurements indicate that cracks recorded at the 96 kHz sample rate are not missing important structural information. Furthermore, similar structural characteristics between recording periods (daytime or overnight recordings) indicate that context has no effect on the structure of cracks, therefore only the production rate of cracks was further investigated for arousal responses.

3.1. Influence of Context on Group and Individual Vocal Production Rates

Acoustic data collected in 2010 and 2016 were merged as one dataset as Welch *t*-tests presented no significant differences in call rates between the sampling years ($p > 0.05$ for each call type). The production rates of signature and non-signature whistles were significantly higher during daytime contexts compared with overnight (Figure 4, significance levels represented). The production rate of square copies did not shift significantly between recording contexts ($p > 0.05$). Cracks were produced least overnight, particularly when compared with the 0–20 min following presentations (Figure 4, significance levels represented). When comparing the overnight production rate of cracks between the four pool configurations, there were no significant differences ($p > 0.05$), with production rates being 0.51 ± 0.29, 0.72 ± 0.57, 0.36 ± 0.07, and 0.71 ± 0.37 cracks per minute for pool configurations 1–4, respectfully.

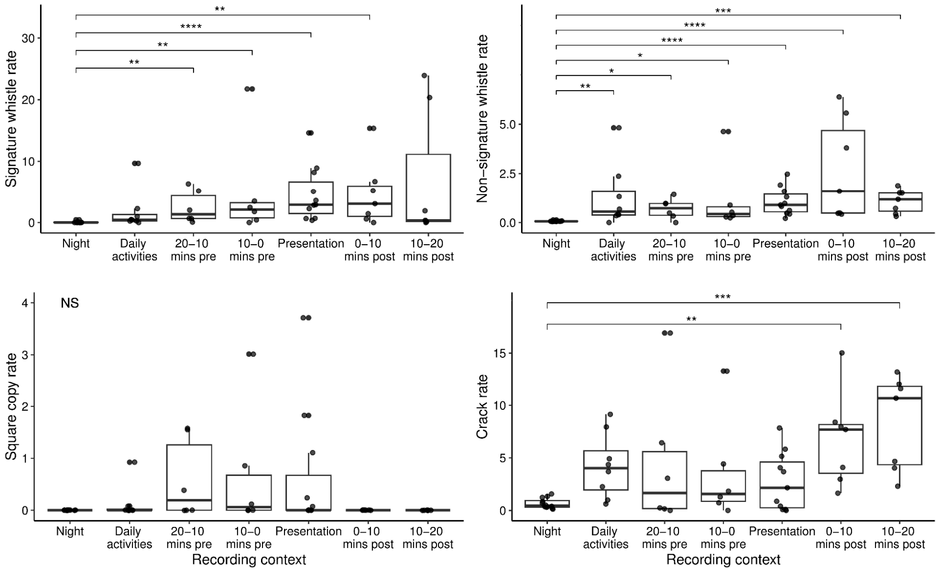

Figure 4. Vocal production rates (per minute) of four call types for all dolphins at the facility under each recording context. Adjusted significance levels are indicated: **** $p < 0.0001$, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS not significant.

Investigating individual signature whistles, the occurrence of signature whistles (presence/absence model) did not differ significantly across contexts (M1: zero-inflated negative binomial model, $p > 0.05$; P1–2, F1–5, M2–3: hurdle negative binomial models, $p > 0.05$). However, the production rate of signature whistles shifted significantly around presentation times for three of the ten dolphins (F5, M1 and M3). All three dolphins increased signature whistle production pre-presentation compared with during presentations, one of which (F5) also increased signature whistle production post presentation (Figure 5, significance levels represented).

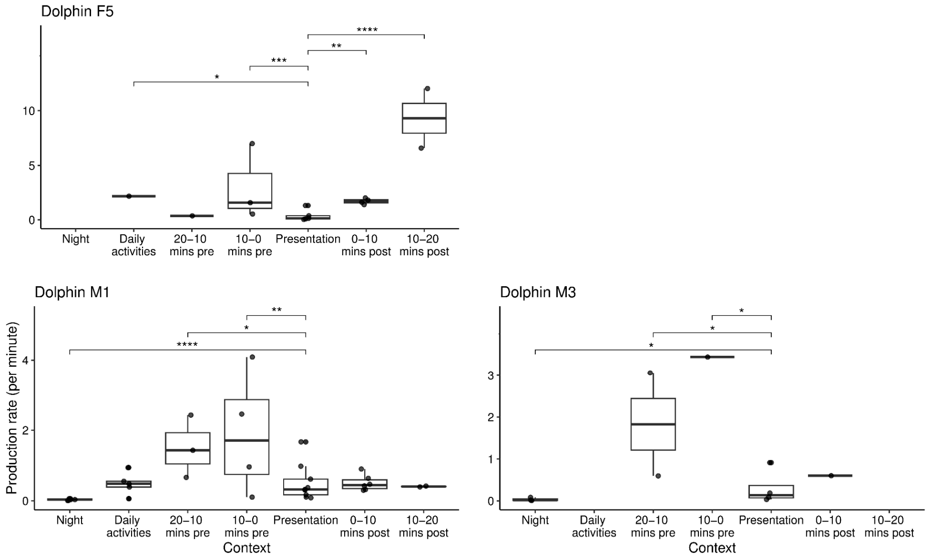

Figure 5. Zero-truncated/negative binomial whistle production rates for three dolphins with significant model outputs. Significance levels are indicated: **** $p < 0.0001$, *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

3.2. Shifts in Individual Signature Whistle Characteristics between Low and High Arousal Contexts

Only five dolphins had sufficient data to investigate changes in time–frequency characteristics of individual signature whistles (three males—M1, M2, M3; two females—F2, P2). Of these, the majority (3) shifted the frequency of their whistles upwards but reduced the bandwidth (i.e., higher minimum and lower maximum frequency) in the context of increased arousal (Figure 6, significance levels represented). Shifts in signature whistle duration and number of loops varied among individuals between the two contexts (Figure 6, significance levels represented).

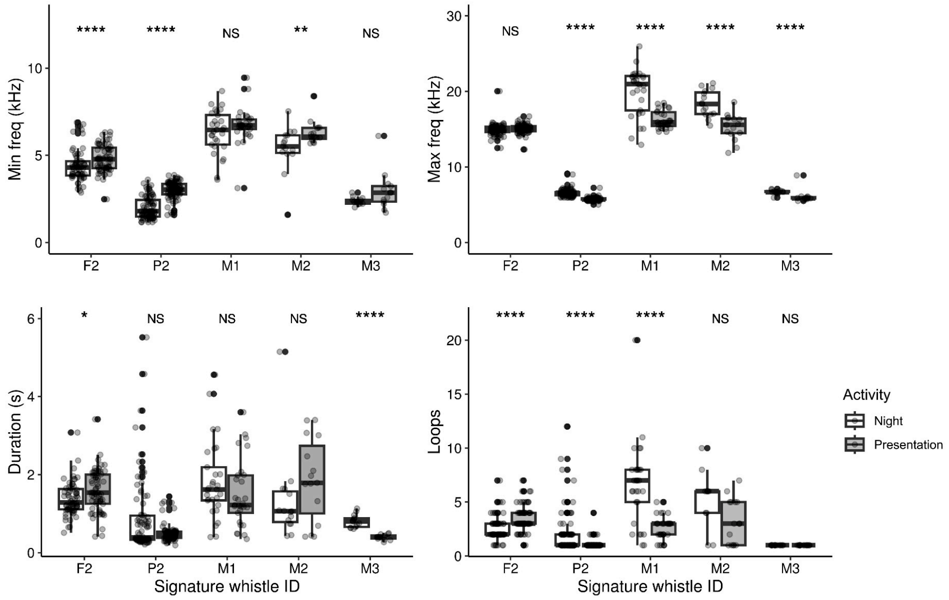

Figure 6. Signature whistle characteristics between low (night) and high (presentations) arousal contexts for individuals ($n = 5$) with sufficient data. Significance is indicated above: **** $p < 0.0001$, ** $p < 0.01$, * $p < 0.5$, NS not significant.

4. Discussion

This study demonstrates acoustic cues of arousal through shifts in whistle characteristics. The production rate of signature whistles and non-signature whistles differed between overnight and daytime contexts, with higher production rates during the day. Three dolphins expressed arousal around daily presentation times through shifts in signature whistle production rates. When comparing signature whistle characteristics between high and low arousal contexts, results indicate that changes in minimum and maximum frequency (lowering the bandwidth) are good indicators of arousal. This study contributes to the understanding of the vocal behaviour of bottlenose dolphins housed at uShaka and provides further motivation for individual-based acoustic monitoring of bottlenose dolphins in human care.

The dolphins produced more signature whistles throughout the day compared with the overnight period, likely resulting from high levels of activity at the facility throughout the day. There was no evidence of elevated arousal through acoustic cues associated with daily public presentations for the group of dolphins as a whole. This contrasts with the group arousal responses (increased signature whistle production) associated with staff presence and the morning feeding schedule previously reported for the dolphins at this facility [25]. Positive reinforcement (food reward) is an integral part of presentations, and, as arousal responses associated with food provision and presentations have been previously reported for bottlenose dolphins in human care [25,36,61], arousal responses were expected around presentation times. However, more recent evidence suggests that the motivation of dolphins may not be driven and reinforced by food but rather the interactions with the trainers [72]. As the vocal behaviour of all dolphins were pooled, this indicates high levels of vocal activity at the facility throughout the day regardless of the type of stimulation and does not consider individual responses to stimuli.

Individual signature whistle production shifted around presentation times for three dolphins, indicating considerable variability in behaviour across individuals. The increase in signature whistle production before presentations may reflect dolphins cueing in on the general increase in activity at the dolphinarium from trainers and the sounds of the gathering crowds and music prior to the start of public presentations. This likely indicates anticipatory-related arousal to a predictable event for these three dolphins. In a previous study, bottlenose dolphins increased vigilance and surface behaviours, indicating anticipation preceding public presentations; however, increased general activity was rarely observed [61]. The amount of anticipatory behaviour from a dolphin before a predicted event can determine the level of participation in the event in various contexts [73]. Motivation can therefore be measured by anticipatory behaviour [73,74]. Public presentations are anticipated through cues, and such predictability may improve levels of social behaviour [22] as well as promote behavioural diversity [23], which can lead to improved overall welfare. In the wild, signature whistles function as contact calls. The shift in production rate of signature whistles from one dolphin supports this function in human care as this individual increased signature whistle production after presentation sessions, when the participating dolphins were reunited back-of-house. During presentations the dolphins are under trainer control and engage in set behaviours, but once returned to back-of-house, individuals may need to relocate each other within the facility pool network and thus increase signature whistle production to regain acoustic contact during this time. However, this behaviour would be expected for more than one individual. Bottlenose dolphins exhibit inter-individual variation in acoustic cues and behaviour throughout the day [72,75] which may be the result of personality traits [76]. Previous studies on dolphins in human care have provided evidence for consistent personality traits [16], which are also supported anecdotally by the trainers at uShaka. Identifying these personality differences enables caretakers to understand individual behaviour and responses [77]. Individuals may not behave the same way day-to-day [78], as individual responses may be dependent not only on the meaning of the signal, but the internal state and situation assessment of the individual at the time of the event [79]. This emphasises the importance of monitoring individual states rather than taking a unified approach [80–82].

An increase in signature whistle production has previously been identified during brief capture-release, an event expected to evoke elevated arousal linked to stress [24], contexts associated with trainer presence and food provision [25], and contexts with unknown valence of arousal responses, for example "swim-with-dolphin" tour operations [83]. This has also been documented in other populations (Table A2). Similarly, an increase in call production is indicative of the level of emotional arousal, but not valence of arousal, in terrestrial mammals [26,27,84]. Shifts in structural characteristics of calls have also indicated arousal levels in terrestrial mammals [6,26]. Contrary to levels of arousal, valence indicators may be more species specific [85], and universal indicators of valence in structural characteristics of signature whistles have not yet been identified. We compared time-frequency characteristics of individual signature whistles, and the results indicate that minimum and maximum frequency, and thus frequency range, are good indicators of heightened arousal in the context of presentations [25]. Considering other relevant published studies on the vocal behaviour of bottlenose dolphins (Table A2), the structural characteristics of whistles do not conform to any consistent rules when considering valence indicators. Although public presentations were not perceived as stressful for bottlenose dolphins in a previous study [61] we could not definitively determine whether the dolphins were experiencing positive or negative arousal during periods associated with public presentations, even though positive reinforcement is an integral part of these events. This needs further investigation in which time–frequency characteristics of signature whistles can be measured under different contexts, for example when dolphins experience stressful situations such as pool scrubbing [36,86] or social stress [1].

Individual identity is not encoded in square copies (as far as we know), and these were produced sporadically throughout the day and overnight and were not associated with arousal levels. The function and producers of square copies remain unknown and may not be correlated with scheduled arousal-eliciting activities, but rather used in other social contexts and perhaps between certain individuals only. Furthermore, non-signature whistle production was highest during the day compared with overnight. It was reported by [87] that non-signature whistles were produced more when swimming alone, and less when physically interacting with conspecifics. Our results contrast these findings as daytime activities at uShaka are composed mostly of interactions and enrichment. More focus on the production context of non-signature whistles and square copies is needed.

Cracks were first documented by [51], where it was found that most of the energy of the call lies within 0.1 to 8 kHz; however, their equipment limited recordings to 10 kHz so analysis of the full spectrum of the call was not carried out. We document the first spectral measurements of cracks recorded at this facility. Within the full frequency spectrum, we measured the peak frequency, which lies between 0.09 and 3.81 kHz and has a duration of 100–200 ms. Previously, cracks were described as alarm calls that are produced during fearful contexts [49], and during aggressive behaviour between males, and mother–calf pairs [48]. Cracks can be produced both with concurrent "jaw claps", which are loud noises produced by a snapping shut of the jaws and are associated with aggression [88], or without [49]. Cracks were produced more commonly than whistles overnight, although the production rate was very low. The production of cracks could not be linked to individuals and results provided no evidence that cracks are associated with high arousal presentations. Similar production rates of cracks when the dolphins were housed in four different pool configurations indicates that these calls are likely produced within social groups, and not between social groups. Production of cracks without jaw claps was commonly observed at uShaka when individuals were swimming around the pools not interacting (personal observation), indicating that there may be another function of cracks as this observed behaviour was not associated with either aggressive or fearful contexts. This context of crack production when stimulation is minimal may be indicative of boredom (personal observation) and may thus be a welfare concern that needs to be considered [89]. However, the function of this call type remains unclear and requires further investigation.

Behaviour is a good measure of welfare in animals in human care and may be useful in identifying physical health issues before medical diagnoses [90,91]. Measures of behaviour have previously been used to monitor the welfare of bottlenose dolphins. Concurrent behavioural data and vocal cues could be assessed for more conclusive results [6]; however, stereotyped behaviour should never be the sole indicator of poor or improved welfare [92]. Vocalisation rate has been used to detect welfare in animals in human care, such as slaughter-related stress in cattle [93], cold- and hunger-related stress in piglets [94], presence of disease in chickens [95], and presence of environmental stressors in beluga whales [56]. Using vocal responses is a promising method for the welfare monitoring of bottlenose dolphins in human care [96] and requires more attention in such facilities. Welfare monitoring is essential for animals in human care, and understanding the responses of the group as well as each individual is important for the detection of the shifts in welfare state that are likely indicated by shifts in behaviour. Daily public presentations at uShaka play a role in the enrichment of the group as they are an integral part of the dolphins' lives. Future studies on dolphin welfare should integrate monitoring of vocal behaviour and measurements of physiological parameters that are known to fluctuate under stress in order to provide a comparative study on the reliability of the use of vocal behaviour as a welfare tool. These should include other events, such as routine medical checks, cleaning of pools, and construction and maintenance, that may occasionally occur. As the level of arousal correlates to the animal's participation in a subsequent event [73], it is important to consider which individual or group of individuals the event, such as routine medical exams or public presentations, is aimed at. Moving forward, a factor that needs to be addressed when assessing vocal behaviour is the unique behaviour displayed by dolphins in human care compared with wild populations. These animals spend a considerable amount of time with their heads out of the water, including during feeding time, training sessions, presentations, resting sessions where they have enrichment "toys" in the pools, and curious spy-hopping behaviour. This may affect the vocal behaviour, as well as how it is captured on the underwater hydrophones. Furthermore, the lack of individual identity information present for cracks, square copies and non-signature whistles limited this part of the study to overall group arousal responses only. Effort should be taken to identify call producers in future as arousal information, and thus individual welfare indicators, may be encoded in the production characteristics of calls other than signature whistles. Paired with [25], this study provides a useful index of baseline vocal behaviour across various states of arousal linked to the scheduled daily activities of the dolphins at uShaka.

Author Contributions: Conceptualization, R.P. and T.G.; methodology, R.P.; validation, B.S.J., S.H.E. and T.G.; formal analysis, R.P.; investigation, R.P.; data curation, R.P.; writing—original draft preparation, R.P.; writing—review and editing, R.P., B.S.J., S.H.E. and T.G.; visualization, R.P.; supervision, T.G. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the South African National Research Foundation, NRF-DAAD doctoral grant (grant number: MND200416513925) awarded to author R.P. (2021–2023).

Institutional Review Board Statement: The housing of the dolphins at this facility is permitted by a South African Department of Forestry, Fisheries and the Environmental (DFFE) permit (permit number confidential). No ethics clearance or permit was required for the acoustic monitoring of these animals as passive, non-invasive methodology was used and there was no direct contact with the animals.

Data Availability Statement: All data sheets are publicly available on the BioStudies online repository, accession number S-BSST1170.

Acknowledgments: We would like to thank the National Research Foundation for funding the write-up phase of this study (grant awarded to Rachel Probert) and volunteer Catherine Keanly for assisting in acoustic data processing. We would also like to thank Larry Oellermann and Gabrielle Harris at uShaka for allowing us to spend time at the dolphinarium to collect data, and student

Corrine Buhrmann, trainer Kelly de Klerk, and the rest of the dolphinarium staff for assisting with acoustic data collection.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Genetic, social grouping and individual data for the dolphins at uShaka, adapted from [25,59]. Tt = *Tursiops truncatus*, Ta = *Tursiops aduncus*.

Social Group	Name	Species	Sex	In Human Care Since	Date of Birth	Age in 2018	Signature Whistle ID
Female group	Affrika	Tt	F	Born in facility	12/05/1995	23	F1
	Zulu	Ta-Tt Hybrid	F	Born in facility	09/12/1998	19	F2
	Khanya	Ta-Tt F2	F	Born in facility	17/07/1993	25	F3
	Tombi	Ta-Tt Hybrid	F	Born in facility	23/05/1993	25	F4
	Khethiwe [b]	Ta-Tt Hybrid	F	Born in facility	25/11/2008	9	F5
Male group	Ingelosi	Ta-Tt Hybrid	M	Born in facility	22/05/2004	14	M1/M2
	Khwezi	Ta-Tt Hybrid	M	Born in facility	07/09/1995	24	M1/M2
	Kelpie	Tt	M	Born in facility	22/01/1984	34	M3
	Jula	Ta-Tt Hybrid	M	Born in facility	28/07/1990	Deceased 2015	M4
Mixed group	Gambit	Tt	M	08/12/1976	≤08/12/1971 [a]	46	P1
	Frodo	Ta	F	26/06/1979	≤26/06/1974 [a]	44	P2

[a] Estimated date of birth from age at capture. [b] Moved from the mixed group to the female social group in 2012

Table A2. Review of relevant literature considering indicators of valence from bottlenose dolphin (*Tursiops* spp.) whistles.

Valence	Context	Setting	Whistle Production	Frequency Parameters	Duration	Loops	Reference
Unsure	Tour boat presence	Wild	NA	Increase Min F Increase Max F	No shifts	NA	[46]
Unsure	Tour boat presence	Wild	Increase	No shifts	No shifts	NA	[97]
Unsure	Birth	Human care	Increase	NA	NA	NA	[98]
Unsure	Public presentations	Human care	Increase	Decrease Max F	Increase	Varied between individuals	This study
Likely positive	Human in-water interactions	Human care	Increase	NA	NA	NA	[99]
Positive	Feeding, staff presence	Human care	Increase	Decrease Max F	Decrease	Decrease	[25]
Positive	‘Swim with dolphin’ tours	Wild	Increase	NA	NA	NA	[83]
Positive	Social, feeding	Wild	Increase	NA	NA	NA	[100]
Positive	Social, dispersed	Wild	Increase	NA	NA	NA	[101]
Positive	Social, feeding	Wild	Increase	NA	NA	NA	[102]
Positive	Social	Wild	Increase	NA	NA	NA	[34]
Positive	Feeding, social	Wild	NA	Increase Max F (feeding) Decrease Max F (social)	No shifts	NA	[103]
Positive	Feeding, social	Wild	NA	Increase Max F (feeding) Decrease Max F (social)	Increase (feeding) Decrease (social)	NA	[104]
Positive	Social, foraging	Wild	Increase	NA	NA	NA	[105]

Table A2. *Cont.*

Valence	Context	Setting	Whistle Production	Frequency Parameters	Duration	Loops	Reference
Positive + negative	Sexual + aggressive combined	Wild	Increase	Decrease Min F Decrease F range	No shifts	NA	[85]
Negative	Capture-release	Wild	Increase	Increase Max F	Increase	Increase	[24]
Negative	Lowering water levels in tanks	Human care	Decrease	NA	NA	NA	[43]

References

1. Waples, K.A.; Gales, N.J. Evaluating and minimising social stress in the care of captive bottlenose dolphins (*Tursiops aduncus*). *Zoo Biol.* **2002**, *21*, 5–26. [CrossRef]
2. Mason, G.J. Species differences in responses to captivity: Stress, welfare and the comparative method. *Trends Ecol. Evol.* **2010**, *25*, 713–721. [CrossRef] [PubMed]
3. Clegg, I.L.K.; Borger-Turner, J.L.; Eskelinen, H.C. C-Well: The development of a welfare assessment index for captive bottlenose dolphins (*Tursiops truncatus*). *Anim. Welf.* **2015**, *24*, 267–282. [CrossRef]
4. de Waal, F.B.M. What is an animal emotion? *Ann. N. Y. Acad. Sci.* **2011**, *1224*, 191–206. [CrossRef] [PubMed]
5. Mendl, M.; Burman, O.H.; Paul, E.S. An integrative and functional framework for the study of animal emotion and mood. *Proc. R. Soc. B Biol. Sci.* **2010**, *277*, 2895–2904. [CrossRef] [PubMed]
6. Briefer, E.F. Vocal expression of emotions in mammals: Mechanisms of production and evidence. *J. Zool.* **2012**, *288*, 1–20. [CrossRef]
7. Briefer, E.F.; Tettamanti, F.; McElligott, A. Emotions in goats: Mapping physiological, behavioural and vocal 2 profiles. *Anim. Behav.* **2015**, *99*, 131–143. [CrossRef]
8. Baciadonna, L.; Briefer, E.F.; Favaro, L.; McElligott, A. Goats distinguish between positive and negative emotion-linked vocalisations. *Front. Zool.* **2019**, *16*, 25. [CrossRef]
9. Maigrot, A.L. Vocal Expression of Emotions in Przewalski's Horses and Wild Boars: Encoding and Decoding. Doctoral Dissertation, University of Bern, Bern, Switzerland, 2018.
10. Carder, G.; Semple, S. Visitor effects on anxiety in two captive groups of western lowland gorillas. *Appl. Anim. Behav. Sci.* **2008**, *115*, 211–220. [CrossRef]
11. Yon, L.; Williams, E.; Harvey, N.D.; Asher, L. Development of a behavioural welfare assessment tool for routine use with captive elephants. *PLoS ONE* **2019**, *14*, e0210783. [CrossRef]
12. Linhart, P.; Ratcliffe, V.F.; Reby, D.; Špinka, M. Expression of emotional arousal in two different piglet call types. *PLoS ONE* **2015**, *10*, e0135414. [CrossRef]
13. Luo, L.; Reimert, I.; de Haas, E.N.; Kemp, B.; Bolhuis, J.E. Effects of early and later life environmental enrichment and personality on attention bias in pigs (Sus scrofa domesticus). *Anim. Cogn.* **2019**, *22*, 959–972. [CrossRef] [PubMed]
14. Melotti, L.; Oostindjer, M.; Bolhuis, J.E.; Held, S.; Mendl, M. Coping personality type and environmental enrichment affect aggression at weaning in pigs. *Appl. Anim. Behav. Sci.* **2011**, *133*, 144–153. [CrossRef]
15. Kuczaj, S.A., II; Highfill, L.; Byerly, H. The importance of considering context in the assessment of personality characteristics: Evidence from ratings of dolphin personality. *Int. J. Comp. Psychol.* **2012**, *25*, 309–329. [CrossRef]
16. Highfill, L.E.; Kuczaj, S.A. Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquat. Mamm.* **2007**, *33*, 380. [CrossRef]
17. Waitt, C.; Buchanan-Smith, H.M. What time is feeding? How delays and anticipation of feeding schedules affect stump-tailed macaque behavior. *Appl. Anim. Behav. Sci.* **2001**, *75*, 75–85. [CrossRef]
18. Bassett, L.; Buchanan-Smith, H.M. Effects of predictability on the welfare of captive animals. *Appl. Anim. Behav. Sci.* **2007**, *102*, 223–245. [CrossRef]
19. Ulyan, M.J.; Burrows, A.E.; Buzzell, C.A.; Raghanti, M.A.; Marcinkiewicz, J.; Phillips, K.A. The effects of predictable and unpredictable feeding schedules on the behavior and physiology of captive brown capuchins (*Cebus apella*). *Appl. Anim. Behav. Sci.* **2006**, *101*, 154–160. [CrossRef]
20. Gottlieb, D.H.; Coleman, K.; McCowan, B. The effects of predictability in daily husbandry routines on captive rhesus macaques (*Macaca mulatta*). *Appl. Anim. Behav. Sci.* **2013**, *143*, 117–127. [CrossRef]
21. de Oliveira, L.B.S.; da Silva Vasconcellos, A. May unpredictable events affect monkey welfare under human care? *Behav. Process.* **2022**, *200*, 104665. [CrossRef]
22. Miller, L.J.; Lauderdale, L.K.; Mellen, J.D.; Walsh, M.T.; Granger, D.A. Assessment of animal management and habitat characteristics associated with social behavior in bottlenose dolphins across zoological facilities. *PLoS ONE* **2021**, *16*, e0253732. [CrossRef]
23. Miller, L.J.; Lauderdale, L.K.; Mellen, J.D.; Walsh, M.T.; Granger, D.A. Relationships between animal management and habitat characteristics with two potential indicators of welfare for bottlenose dolphins under professional care. *PLoS ONE* **2021**, *16*, e0252861. [CrossRef] [PubMed]

24. Esch, H.C.; Sayigh, L.S.; Blum, J.E.; Wells, R.S. Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). *J. Mammal.* **2009**, *90*, 638–650. [CrossRef]
25. Probert, R.; Bastian, A.; Elwen, S.H.; James, B.S.; Gridley, T. Vocal correlates of arousal in bottlenose dolphins (*Tursiops* spp.) in human care. *PLoS ONE* **2021**, *16*, e0250913. [CrossRef]
26. Rendall, D. Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. *J. Acoust. Soc. Am.* **2003**, *113*, 3390–3402. [CrossRef] [PubMed]
27. Trut, L.; Kharlamova, A.; Gogoleva, S.; Volodina, E.; Volodin, I. Sign and strength of emotional arousal: Vocal correlates of positive and negative attitudes to humans in silver foxes (*Vulpes vulpes*). *Behaviour* **2010**, *147*, 1713–1736. [CrossRef]
28. Gouzoules, H.; Gouzoules, S. Agonistic screams differ among four species of macaques: The significance of motivation-structural rules. *Anim. Behav.* **2000**, *59*, 501–512. [CrossRef]
29. Robbins, R.; McCreery, E.K. African wild dog pup vocalizations with special reference to Morton's model. *Behaviour* **2003**, *140*, 333–351. [CrossRef]
30. Feighny, J.A.; Williamson, K.E.; Clarke, J.A. North American elk bugle vocalizations: Male and female bugle call structure and context. *J. Mammal.* **2006**, *87*, 1072–1077. [CrossRef]
31. Taylor, A.M.; Reby, D.; McComb, K. Context-related variation in the vocal growling behaviour of the domestic dog (*Canis familiaris*). *Ethology* **2009**, *115*, 905–915. [CrossRef]
32. Cranford, T.W. In search of impulse sound sources in odontocetes. In *Hearing by Whales and Dolphins*; Fay, R.R., Popper, A.N., Eds.; Springer: New York, NY, USA, 2000; pp. 109–155.
33. Sayigh, L.S.; Tyack, P.L.; Wells, R.S.; Scott, M.D. Signature whistles of free-ranging bottlenose dolphins *Tursiops truncatus*: Stability and mother-offspring comparisons. *Behav. Ecol. Sociobiol.* **1990**, *26*, 247–260. [CrossRef]
34. Cook, M.L.H.; Sayigh, L.S.; Blum, J.E.; Wells, R.S. Signature–whistle production in undisturbed free–ranging bottlenose dolphins (*Tursiops truncatus*). *Proc. R. Soc. B Biol. Sci.* **2004**, *271*, 1043–1049. [CrossRef] [PubMed]
35. Janik, V.M.; King, S.L.; Sayigh, L.S.; Wells, R.S. Identifying signature whistles from recordings of groups of unrestrained bottlenose dolphins (*Tursiops truncatus*). *Mar. Mammal Sci.* **2013**, *29*, 109–122. [CrossRef]
36. Therrien, S.C.; Thomas, J.A.; Therrien, R.E.; Stacey, R. Time of Day and Social Change Affect Underwater Sound Production by Bottlenose Dolphins (*Tursiops truncatus*) at the Brookfield Zoo. *Aquat. Mamm.* **2012**, *38*, 65–75. [CrossRef]
37. Herzing, D.L. Clicks, whistles and pulses: Passive and active signal use in dolphin communication. *Acta. Astronaut.* **2014**, *105*, 534–537. [CrossRef]
38. Au, W.W. (Ed.) Characteristics of dolphin sonar signals. In *The Sonar of Dolphins*; Springer: New York, NY, USA, 1993; pp. 115–139.
39. Janik, V.M.; Slater, P.J. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim. Behav.* **1998**, *56*, 829–838. [CrossRef] [PubMed]
40. Jones, G.J.; Sayigh, L.S. Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Mar. Mammal Sci.* **2002**, *18*, 374–393. [CrossRef]
41. Janik, V.M.; Sayigh, L.S. Communication in bottlenose dolphins: 50 years of signature whistle research. *J. Comp. Physiol. A* **2013**, *199*, 479–489. [CrossRef]
42. King, S.L.; Sayigh, L.S.; Wells, R.S.; Fellner, W.; Janik, V.M. Vocal copying of individually distinctive signature whistles in bottlenose dolphins. *Proc. R. Soc. Lond.* **2013**, *280*, 20130053. [CrossRef]
43. Caldwell, M.C.; Caldwell, D.K.; Tyack, P.L. Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In *The Bottlenose Dolphin*; Leatherwood, S., Reeves, R.R., Eds.; Academic Press: Cambridge, MA, USA, 1990; pp. 199–234. [CrossRef]
44. Quick, N.J.; Janik, V.M. Bottlenose dolphins exchange signature whistles when meeting at sea. *Proc. R. Soc. B Biol. Sci.* **2012**, *279*, 2539–2545. [CrossRef]
45. Janik, V.M.; Todt, D.; Dehnhardt, G. Signature whistle variations in a bottlenosed dolphin, *Tursiops truncatus*. *Behav. Ecol. Sociobiol.* **1994**, *35*, 243–248. [CrossRef]
46. Heiler, J.; Elwen, S.; Kriesell, H.; Gridley, T. Changes in bottlenose dolphin whistle parameters related to vessel presence, surface behaviour and group composition. *Anim. Behav.* **2016**, *117*, 167–177. [CrossRef]
47. Blomqvist, C.; Amundin, M. High-frequency burst-pulse sounds in agonistic/aggressive interactions in bottlenose dolphins, *Tursiops truncatus*. In *Echolocation in Bats and Dolphins*; Thomas, J., Moss, C., Vater, M., Eds.; The University of Chicago Press: Chicago, IL, USA, 2004; pp. 425–431.
48. Gridley, T.; Nastasi, A.; Kriesell, H.; Elwen, S. The acoustic repertoire of wild common bottlenose dolphins (*Tursiops truncatus*) in Walvis Bay, Namibia. *Bioacoustics* **2015**, *24*, 153–174. [CrossRef]
49. Caldwell, M.C.; Caldwell, D.K. Dolphin community life. *Quarterly* **1967**, *5*, 12–15.
50. Jones, B.; Zapetis, M.; Samuelson, M.M.; Ridgway, S. Sounds produced by bottlenose dolphins (*Tursiops*): A review of the defining characteristics and acoustic criteria of the dolphin vocal repertoire. *Bioacoustics* **2020**, *29*, 399–440. [CrossRef]
51. Caldwell, M.C.; Haugen, R.M.; Caldwell, D.K. High-energy sounds associated with fright in the dolphin. *Science* **1962**, *138*, 907–908. [CrossRef]
52. Sayigh, L.; Dziki, A.; Janik, V.; Kim, E.; McHugh, K.; Tyack, P.L.; Wells, R.; Jensen, F.H. Non-whistle sounds used in bottlenose dolphin aggressive interactions recorded on digital acoustic tags. *Acoust. Soc. Am.* **2017**, *141*, 3947. [CrossRef]
53. Boissy, A.; Manteuffel, G.; Jensen, M.B.; Moe, R.O.; Spruijt, B.; Keeling, L.J.; Winckler, C.; Firkman, B.; Dimitrov, I.; Langbein, J.; et al. Assessment of positive emotions in animals to improve their welfare. *Physiol. Behav.* **2007**, *92*, 375–397. [CrossRef]

54. Brudzynski, S.M. Vocalizations as indicators of emotional states in rats and cats. In *Evolution of Emotional Communication: From Sounds in Nonhuman Mammals to Speech and Music in Man*; Altenmüller, E., Schmidt, S., Zimmermann, E., Eds.; Oxford University Press: Oxford UK, 2013; pp. 75–91.
55. Soltis, J.; Leong, K.; Savage, A. African elephant vocal communication II: Rumble variation reflects the individual identity and emotional state of callers. *Anim. Behav.* **2005**, *70*, 589–599. [CrossRef]
56. Castellote, M.; Fossa, F. Measuring acoustic activity as a method to evaluate welfare in captive beluga whales (*Delphinapterus leucas*). *Aquat. Mamm.* **2006**, *32*, 325–333. [CrossRef]
57. Leliveld, L.M.; Düpjan, S.; Tuchscherer, A.; Puppe, B. Vocal correlates of emotional reactivity within and across contexts in domestic pigs (*Sus scrofa*). *Physiol. Behav.* **2017**, *181*, 117–126. [CrossRef]
58. Watts, J.M.; Stookey, J.M. Vocal behaviour in cattle: The animal's commentary on its biological processes and welfare. *Appl. Anim. Behav. Sci.* **2000**, *67*, 15–33. [CrossRef]
59. Gridley, T.; Elwen, S.H.; Harris, G.; Moore, D.M.; Hoelzel, A.R.; Lampen, F. Hybridization in bottlenose dolphins—A case study of *Tursiops aduncus*× *T. truncatus* hybrids and successful backcross hybridization events. *PLoS ONE* **2018**, *13*, e0201722. [CrossRef]
60. Joseph, C.A. An Assessment of Behaviour, Stress and Gastric Ulceration in Bottlenose Dolphins, *Tursiops* sp., at uShaka Sea World. Masters' Thesis, University of KwaZulu-Natal, Durban, South Africa, 2020.
61. Jensen, A.-L.M.; Delfour, F.; Carter, T. Anticipatory behaviour in captive bottlenose dolphins (*Tursiops truncatus*): A preliminary study. *Zoo Biol.* **2013**, *32*, 436–444. [CrossRef] [PubMed]
62. Center for Conservation Bioacoustics. *Raven Pro: Interactive Sound Analysis Software*, Version 1.6.1; The Cornell Lab of Ornithology: Ithica, NY, USA, 2019. Available online: http://ravensoundsoftware.com/(accessed on 28 October 2023).
63. Gridley, T.; Berggren, P.; Cockcroft, V.G.; Janik, V.M. Whistle vocalizations of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) inhabiting the south-west Indian Ocean. *J. Acoust. Soc. Am.* **2012**, *132*, 4032–4040. [CrossRef]
64. King, S.L.; Harley, H.E.; Janik, V.M. The role of signature whistle matching in bottlenose dolphins, *Tursiops truncatus*. *Anim. Behav.* **2014**, *96*, 79–86. [CrossRef]
65. Kriesell, H.J.; Elwen, S.H.; Nastasi, A.; Gridley, T. Identification and characteristics of signature whistles in wild bottlenose dolphins (*Tursiops truncatus*) from Namibia. *PLoS ONE* **2014**, *9*, e106317. [CrossRef]
66. Janik, V.M. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science* **2000**, *289*, 1355–1357. [CrossRef] [PubMed]
67. R Core Team. *R: A Language Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020. Available online: https://www.R-project.org/ (accessed on 28 October 2023).
68. Araya-Salas, M.; Smith-Vidaurre, G. warbleR: An r package to streamline analysis of animal acoustic signals. *Methods Ecol. Evol.* **2017**, *8*, 184–191. [CrossRef]
69. Ligges, U.; Krey, S.; Mersmann, O.; Schnackenberg, S. tuneR: Analysis of Music and Speech. 2018. Available online: https://CRAN.R-project.org/package=tuneR (accessed on 28 October 2023).
70. Sueur, J.; Aubin, T.; Simonis, C. Seewave: A free modular tool for sound analysis and synthesis. *Bioacoustics* **2008**, *18*, 213–226. [CrossRef]
71. Dinno, A. Conover.test: Conover-Iman Test of Multiple Comparisons Using Rank Sums. R Package Version 1.1.5. 2017. Available online: https://CRAN.R-project.org/package=conover.test (accessed on 28 October 2023).
72. Platto, S.; Serres, A. A quantitative assessment of trainers-dolphins' interactions in the absence of food reward. *Animals* **2023**, *13*, 1651. [CrossRef]
73. Clegg, I.L.; Rödel, H.G.; Boivin, X.; Delfour, F. Looking forward to interacting with their caretakers: Dolphins' anticipatory behaviour indicates motivation to participate in specific events. *Appl. Anim. Behav. Sci.* **2018**, *202*, 85–93. [CrossRef]
74. Spruijt, B.M.; Van den Bos, R.; Pijlman, F. A concept of welfare based on how the brain evaluates its own activity: Anticipatory behaviour as an indicator for this activity. *Appl. Anim. Behav. Sci.* **2001**, *72*, 145–171. [CrossRef]
75. Galhardo, L.; Appleby, M.C.; Waran, N.K.; Dos Santos, M.E. Spontaneous activities of captive performing bottlenose dolphins (*Tursiops truncatus*). *Anim. Welf.* **1996**, *5*, 373–389. [CrossRef]
76. Díaz López, B.D. When personality matters: Personality and social structure in wild bottlenose dolphins, *Tursiops truncatus*. *Anim. Behav.* **2020**, *163*, 73–84. [CrossRef]
77. Vazire, S.; Gosling, S.D. Personality and temperament. In *Encyclopedia of Animal Behavior*; Bekoff, M., Ed.; Greenwood Press: Westport, UK, 2004; pp. 818–822.
78. Hertel, A.G.; Niemelä, P.T.; Dingemanse, N.J.; Mueller, T. A guide for studying among-individual behavioral variation from movement data in the wild. *Mov. Ecol.* **2020**, *8*, 30. [CrossRef]
79. Fischer, J.; Hammerschmidt, K.; Todt, D. Factors affecting acoustic variation in Barbary-macaque (*Macaca sylvanus*) disturbance calls. *Ethology* **1995**, *101*, 51–66. [CrossRef]
80. Anzai, H.; Hirata, M. Individual monitoring of behavior to enhance productivity and welfare of animals in small-scale intensive cattle grazing systems. *Front. Sustain. Food Syst.* **2021**, *5*, 694413. [CrossRef]
81. Stoinski, T.S.; Jaicks, H.F.; Drayton, L.A. Visitor effects on the behavior of captive western lowland gorillas: The importance of individual differences in examining welfare. *Zoo Biol.* **2012**, *31*, 586–599. [CrossRef]
82. Whitham, J.C.; Wielebnowski, N. Animal-based welfare monitoring: Using keeper ratings as an assessment tool. *Zoo Biol. Publ. Affil. Am. Zoo Aquar. Assoc.* **2009**, *28*, 545–560. [CrossRef]

83. Scarpaci, C.; Bigger, S.W.; Corkeron, P.J.; Nugegoda, D. Bottlenose dolphins (*Tursiops truncatus*) increase whistling in the presence of 'swim-with-dolphin' tour operations. *J. Cetacean Res. Manag.* **2000**, *2*, 183–185. [CrossRef]
84. Pongrácz, P.; Molnár, C.; Miklósi, A.; Csányi, V. Human listeners are able to classify dog (*Canis familiaris*) barks recorded in different situations. *J. Comp. Psychol.* **2005**, *119*, 136. [CrossRef]
85. McGovern, B. Flexible Information within the Communication Signals of Wild, Provisioned Indo-Pacific Bottlenose Dolphins. Doctoral Dissertation, University of Queensland, St Lucia, QLD, Australia, 2022.
86. Serres, A.; Xu, C.; Hao, Y.; Wang, D. The click production of captive yangtze finless porpoises (*Neophocaena asiaeorientalis asiaorientalis*) is influenced by social and environmental factors. *Animals* **2021**, *11*, 511. [CrossRef]
87. Lopez-Marulanda, J.; Rödel, H.G.; Colpaert, N.; Vanderheul, S.; Adam, O.; Delfour, F. Contexts of emission of non-signature whistles in bottlenose dolphins (*Tursiops truncatus*) under human care. *Behav. Process.* **2020**, *181*, 104255. [CrossRef] [PubMed]
88. Overstrom, N.A. Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (*Tursiops truncatus*). *Zoo Biol.* **1983**, *2*, 93–103. [CrossRef]
89. Meagher, R.K. Is boredom an animal welfare concern? *Anim. Welf.* **2019**, *28*, 21–32. [CrossRef]
90. Dawkins, M.S. Behaviour as a tool in the assessment of animal welfare. *Zoology* **2003**, *106*, 383–387. [CrossRef]
91. Buchanan-Smith, H.M.; Griciute, J.; Daoudi, S.; Leonardi, R.; Whiten, A. Interspecific interactions and welfare implications in mixed species communities of capuchin (*Sapajus apella*) and squirrel monkeys (*Saimiri sciureus*) over 3 years. *Appl. Anim. Behav. Sci.* **2013**, *147*, 324–333. [CrossRef]
92. Mason, G.; Clubb, R.; Latham, N.; Vickery, S. Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Appl. Anim. Behav. Sci.* **2007**, *102*, 163–188. [CrossRef]
93. Grandin, T. The feasibility of using vocalization scoring as an indicator of poor welfare during cattle slaughter. *Appl. Anim. Behav. Sci.* **1998**, *56*, 121–128. [CrossRef]
94. Cordeiro, A.F.; Nääs, I.D.; Oliveira, S.R.; Violaro, F.; Almeida, A.C.; Neves, D.P. Understanding vocalization might help to assess stressful conditions in piglets. *Animals* **2013**, *3*, 923–934. [CrossRef]
95. Sadeghi, M.; Banakar, A.; Khazaee, M.; Soleimani, M.R. An intelligent procedure for the detection and classification of chickens infected by clostridium perfringens based on their vocalization. *Braz. J. Poult. Sci.* **2015**, *17*, 537–544. [CrossRef]
96. Jones, B.L.; Oswald, M.; Tufano, S.; Baird, M.; Mulsow, J.; Ridgway, S.H. A system for monitoring acoustics to supplement an animal welfare plan for bottlenose dolphins. *J. Zool. Bot. Gard.* **2021**, *2*, 222–233. [CrossRef]
97. Buckstaff, K.C. Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Mar. Mammal Sci.* **2004**, *20*, 709–725. [CrossRef]
98. King, S.; Guarino, E.; Donegan, K.; Hecksher, J.; Jaakkola, K. Further insights into postpartum signature whistle use in bottlenose dolphins (*Tursiops truncatus*). *Mar. Mammal Sci.* **2016**, *32*, 1458–1469. [CrossRef]
99. Frohoff, T.G. Behavior of Captive Bottlenose Dolphins (*Tursiops truncatus*) and Humans during Controlled in-Water Interactions. Doctoral Dissertation, Texas A & M University, College Station, TX, USA, 1993.
100. Luís, A.R.; Couchinho, M.N.; Dos Santos, M.E. Signature whistles in wild bottlenose dolphins: Long-term stability and emission rates. *Acta Etholog.* **2016**, *19*, 113–122. [CrossRef]
101. Quick, N.J.; Janik, V.M. Whistle rates of wild bottlenose dolphins (*Tursiops truncatus*): Influences of group size and behavior. *J. Comp. Psychol.* **2008**, *122*, 305. [CrossRef]
102. Dos Santos, M.E.D.; Louro, S.; Couchinho, M.N.; Brito, C.M. Whistles of bottlenose dolphins (*Tursiops truncatus*) in the Sado Estuary, Portugal: Characteristics, production rates, and long-term contour stability. *Aquat. Mamm.* **2005**, *31*, 453–462. [CrossRef]
103. La Manna, G.; Rako-Gòspic, N.; Manghi, M.; Ceccherelli, G. Influence of environmental, social and behavioural variables on the whistling of the common bottlenose dolphin (*Tursiops truncatus*). *Behav. Ecol. Sociobiol.* **2019**, *73*, 121. [CrossRef]
104. Díaz López, B. Whistle characteristics in free-ranging bottlenose dolphins (*Tursiops truncatus*) in the Mediterranean Sea: Influence of behaviour. *Mamm. Biol.* **2011**, *76*, 180–189. [CrossRef]
105. Lemon, M.; Cato, D.H.; Lynch, T.P.; Harcourt, R.G. Variation in sound production in relation to behavior of bottlenose dolphins (*Tursiops aduncus*). *J. Acoust. Soc. Am.* **2006**, *120*, 3014. [CrossRef]