

# Patterns of Whistles Emitted by Wild Indo-Pacific Bottlenose Dolphins (*Tursiops aduncus*) During a Provisioning Program

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## Abstract

To facilitate and coordinate the complexities of fission-fusion societies, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) have developed a multilayered acoustic communication system to effectively transmit signals in the marine environment. Among the many acoustic emissions produced by dolphins, whistles are thought to play a major communicative role. Little is understood about the functions of the diverse whistle repertoire of wild bottlenose dolphins and the influence human activities can have on these sounds. This study provides a detailed investigation into the use and diversity of whistles by a group of eight wild bottlenose dolphins that participate in a provisioning program at Tangalooma, Moreton Island, Australia. Acoustic recordings and concurrent behavioural observations were made during evening feeding sessions. Behaviours were divided into three activities: (1) milling, (2) scanning/foraging (excluding human provisioning), and (3) socialising. Pod separation occasions were also examined. Whistles were classified as either stereotyped or nonstereotyped and divided into five tonal classes based on the shape of the fundamental frequency: (1) sine, (2) up-sweep, (3) down-sweep, (4) flat, and (5) concave. Whistles were then catalogued into distinct whistle types. From 943 min of recordings, 5,682 whistles were analyzed that then were catalogued into 68 distinct whistle types of which 18 were stereotyped and 50 were nonstereotyped. The repetition rate ( $\bar{x}$  = 1.12 whistles per min per dolphin [w/m/d]; SD = 0.61) and diversity of whistles varied between feeding sessions but were not related to the number of dolphins. Distinct whistle types were divided into *common* or *uncommon* categories to facilitate correspondence analysis to examine associations between whistles and behaviour activities. Results showed that around 38% of common whistles and 84% of uncommon whistles were closely associated with behaviour activities, particularly socialising and scanning/foraging. Sine whistles were the only tonal class associated with pod

separation. This study provides further evidence of the communicative functions of whistles across the repertoire of wild bottlenose dolphins.

**Key Words:** acoustics, behaviour, Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, whistle, communication

## Introduction

Vocal communication in social animals can be an essential element in the mediation of important social behaviours such as group coordination, resource defence, and reproductive success (McGregor & Peake, 2000; Tyack, 2003). For animals such as cetaceans that inhabit the marine environment where visual communication is limited, vocal transmissions are an effective method of communicating essential information to cohorts (Tyack, 2003).

Bottlenose dolphins (*Tursiops* spp.) have a highly complex communication system that involves both visual cues and acoustic emissions (Pryor, 1990; Würsig et al., 1990). Acoustic communication signals include combinations of frequency-modulated calls or whistles, broadband echolocation clicks, and burst-pulse clicks that have been described as “barks,” “squawks,” “squeaks,” “creaks,” and “brays” (Wood, 1953; Evans & Dreher, 1962; Caldwell, 1965; Morris, 1986; Caldwell et al., 1990; Markov & Ostrovskaia, 1990; Au, 1993; Herzing, 1996; Janik, 2000).

The rate of bottlenose dolphin whistle production differs between behavioural circumstances, time of year, and population (Jacobs et al., 1993; Jones & Sayigh, 2002). The diversity of whistles produced by individuals and groups of dolphins in various behavioural situations suggests that they provide a highly significant communicative function, coordinating and organizing the behaviour of the group and the interrelationships between individuals (Kaznadzei et al., 1977). Whistles appear to have communicative functions that serve to facilitate the maintenance and coordination of group

cohesion and individual identification (Caldwell et al., 1990; Tyack, 1997; Janik & Slater, 1998).

For toothed cetacea species that live in stable matrilineal groups, such as killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*), group-specific calls have been identified (Ford, 1991; Rendell & Whitehead, 2003). For bottlenose dolphins, social groupings can have a significant influence on the whistles wherein closely associated individuals can produce similar whistle types (McCowan, 1995; McCowan & Reiss, 1995, 2001; McCowan et al., 1998). The acoustic parameters of bottlenose dolphin whistles vary between geographically separated groups and populations (Wang et al., 1995). Therefore, in a natural environment, it might be possible to identify different social groups by whistle repertoires (Datta & Sturtivant, 2002).

Vocal learning plays an important role in the development of the whistle repertoire (Janik, 1999). It is suggested that each dolphin has a predominant, individually distinctive stereotyped whistle termed a *signature whistle* that could be used to advertise the identity and location of the signaler to maintain group cohesion and coordination (Caldwell, 1965; Herzog, 1996; Tyack, 1997; Janik & Slater, 1998; McCowan et al., 1998; Janik, 2000; Thomsen et al., 2001). The production of signature whistles in wild bottlenose dolphins contributes between 39 to 52% of whistle emissions (Cook et al., 2004; Watwood et al., 2005). Signature whistles are emitted more frequently when individuals are separated from other group members or are beyond visual contact (Caldwell et al., 1990; Watwood et al., 2005).

Bottlenose dolphins also produce a range of nonstereotyped whistles that can have variable acoustic parameters (Watwood et al., 2005). These whistles contribute to the remaining 50% of whistle emissions in bottlenose dolphins and can be shared between individuals (Tyack, 1986; Janik et al., 1994; Quick & Janik, 2008). Although the function and structure of these whistles is largely unknown, nonsignature whistles reportedly increase during social interactions (McCowan & Reiss, 1995; Cook et al., 2004; Watwood et al., 2005; Quick & Janik, 2008). This was evident in multiple groups of captive dolphins in which variant whistles were produced more often during social interactions and training sessions compared to during isolation (Tyack, 1986; Janik et al., 1994).

The degree of exposure to human activities and interactions can influence the acoustic emissions of bottlenose dolphins. For example, these changes can be caused by indirect interactions through an increase in ambient noise levels from human sources (Morisaka et al., 2005) or direct interactions with dolphin-swim-tour vessels (Scarpaci et al., 2000).

Provisioning of wild dolphins is another direct human-dolphin interaction that can have an influence on the behaviour, social groupings, and foraging strategies of dolphins (Wrangham, 1974; Samuels & Bejder, 1998; Mann & Kemps, 2003). Provisioning programs can cause direct detrimental impacts to the health of the dolphins through an increased dependency of dolphins on human food sources (Orams et al., 1996; Mann & Kemps, 2003). People also can be directly endangered as dolphins introduced to provisioning programs often develop increased levels of aggression that are not only directed towards other dolphins that are seen as competition but at the people who feed them as well (Orams, 2002).

Human provisioning may not only affect the behaviour of dolphins but also the patterns of acoustic emissions. For example, mothers and calves, whose proximity can be increased during provisioning programs (Mann & Kemps, 2003), may increase the rate of whistles in order to reunite after feeding times (Smolker et al., 1993). Obtaining knowledge on the use of acoustic emissions by provisioned dolphins can aid in increasing the understanding of their communication system as well as in appreciating the effects of human interactions and activities.

We investigated the use of stereotyped and nonstereotyped whistles of eight wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) that participate in a provisioning program at Tangalooma, Moreton Island, Australia, to assess the patterns in the use of whistles during different behavioural activities.

The provisioning program adopted at Tangalooma differs from others (e.g., Monkey Mia, Western Australia [Mann & Kemps, 2003]) as people are not permitted to remain in the water for the majority of the time dolphins are in the provisioning area. The levels of aggressive and “pushy” behaviours of dolphins during feeding sessions at Tangalooma have been decreased through the adoption of a *shallow water feeding system* (Orams et al., 1996; Mann & Kemps, 2003). This system allows dolphins to spend more time interacting with each other than with humans when they are in the provisioning area. Thus, despite the alterations to the “natural” behaviour of dolphins that can arise from wild dolphin provisioning (Bryant, 1994; Samuels & Bejder, 1998; Mann & Kemps, 2003), the program at Tangalooma provides a unique opportunity to observe detailed surface and submerged behaviours in a group of wild bottlenose dolphins.

## Materials and Methods

### *Tangalooma Wild Dolphin Provisioning Program*

In 1992, a wild dolphin provisioning (hand-feeding) program began at Tangalooma Tourist Resort

(27° 10', 153° 10'), Moreton Island, Australia (Green & Corkeron, 1991; Orams, 1994, 1995). At the time of this study, seven wild Indo-Pacific bottlenose dolphins were regularly fed as part of this program. This group included five adults (two females and three males) and two male subadults. One 6-mo-old male calf was also present but was not fed. The majority of the adult and subadult dolphins were from matrilineal groups that originated from two females that initially participated in the provisioning program. These females no longer attended the feeding or were deceased (Neil & Holmes, 2008).

Feeding sessions took place just after dusk from a shallow beach located adjacent to a pier that served as a designated provisioning area (Figure 1). The water depth of the provisioning area ranged between 0.4 to 3.0 m. Dolphins visited the provisioning area only during evening feeding sessions. For the purposes of this study, a *feeding episode* is defined as when a group of people entered the water to hand-feed the dolphins. A *feeding session* includes the period of time from when the first dolphin arrived to when the last dolphin departed the provisioning area (including all feeding episodes). The number of feeding sessions was limited to one per d, and the duration of a feeding session was typically 1 h (Neil & Holmes, 2008).

A *shallow water feeding system* was implemented wherein dolphins and people were divided into four allocated lanes and the time people spent in the water with dolphins was strictly limited (Orams, 1994, 1995). Each dolphin would return to the same allocated feeding lane for each feeding episode. All feeding episodes began and finished synchronously so that all dolphins present were fed at the same time. Between two to five people (including the trained resort staff member and tourists) per feeding lane were permitted to slowly and quietly (i.e., no splashing or excessive noise) enter the water to a depth of no more than 40 to 50 cm for the duration of a feeding episode. When the feeding episode was complete, people in all lanes exited the water at the same time. The trained staff member allocated to each lane ensured that all dolphins began and finished feeding episodes at the same time even if there were not enough tourists to evenly disperse between lanes for all episodes.

Prior to the commencement of feeding episodes, dolphins spent an average of 20 min in the feeding area (Hawkins, unpub. data). The first and last feeding episodes took place from the pier where a fish was thrown to the dolphins by trained resort staff. All other feeding episodes were made from the beach with people entering and exiting the water in respective feeding lanes. An average of

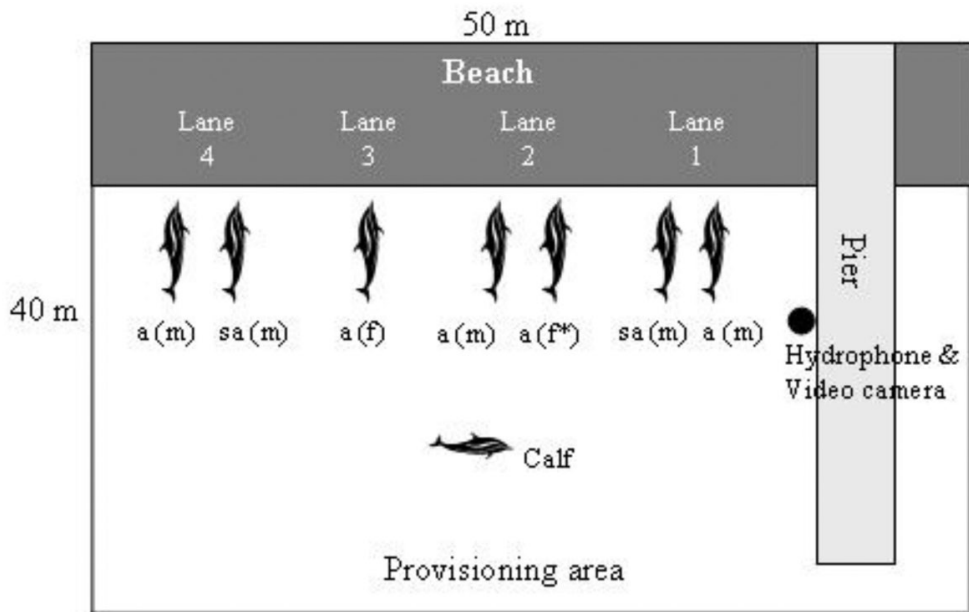
15 feeding episodes with a mean duration of 15 s (Hawkins, unpub. data) occurred during feeding sessions (i.e., 6% of the total duration of a feeding session). The time between feeding episodes was typically 3 min. During this time, no people were in the water. Following the final feed from the pier, the dolphins would immediately depart the feeding area. Therefore, for around 94% of a feeding session, no people were in the water, and dolphins used the provisioning area for a number of behaviour activities.

#### Data Collection

Behaviour and acoustic observations of the provisioned bottlenose dolphins at Tangalooma were made between 28 March and 27 April 2002 from the pier adjacent to the provisioning area. Behaviour and acoustic recordings were made synchronously for the duration of the feeding session that took place each evening between 1800 and 2000 h. Recordings began from the time a dolphin entered to when the last dolphin left the provisioning area. Three observers were positioned on the pier and allocated specific roles of acoustic recording, video recording, and noting general behaviour observations. The protected location of the provisioning area allowed for data to be collected each evening regardless of the weather conditions.

The behaviour of the provisioned dolphins was recorded using a JVC digital video camera. The camera was placed so that the entire illuminated provisioning area could be filmed. The clarity of the water in the feeding area allowed for both surface and underwater behaviour observations to be made. Each individual dolphin's behaviour was continuously scan sampled (Altmann, 1974), and observations were manually recorded on data sheets during post-field data analysis. Video recordings were used to record the occurrence and duration of each dolphin's behaviour. The times noted for each behaviour observation were used to match with concurrent acoustic emissions.

An ethogram of behaviours was prepared prior to observations to ensure consistency of behaviour recordings with some definitions referring specifically to the provisioning circumstances. Three behaviour activities were defined: (1) socialising, (2) milling, and (3) scanning/foraging (Table 1). Although not strictly a behaviour, pod separation occasions were also noted as a distinct category. *Pod separation* was defined as occasions when only one dolphin was present in the feeding area, and no other dolphin was within visual and acoustic range of the observer (> 100-m radius). Observations of behaviour during feeding sessions could only be made in the provisioning area that was illuminated by large floodlights on the



**Figure 1.** Diagrammatic representation of the illuminated Tangalooma provisioning area, the arrangement of feeding lanes, positions of dolphins (a = adult; sa = subadult; m = male; f = female; f\* = female with calf), and the placement of the video and acoustic recording equipment during feeding episodes

pier. Any behaviours that occurred outside this area could not be reliably recorded.

Acoustic recordings were made using a Burns Electronics single Aquear hydrophone (80 Hz to 18 kHz,  $-165 \pm 3$  dB sensitivity) and AP-1A series preamplifier (12 to 24 v; 12 dB octave filter) with a portable Sony TCD D100 Digital Audio Tape (DAT) recorder (48 kHz sample rate). When more than one dolphin was in acoustic range of the hydrophone, the vocalizing dolphin could not be identified. The hydrophone was suspended in midwater (50 to 100 cm depending on the tidal conditions). Acoustic recordings were analyzed on sonograms using *CoolEdit 2000* (Syntrillium Software, 512 band resolution; Blackmann window function; FFT 24,000). Although it could not be tested here, it was assumed, due to the limited propagation and the ability to detect

whistles over large distances in shallow water, that only whistles emitted by dolphins within a 100-m radius of the provisioning area could be detected.

Sound spectrograms were used to visually categorize whistles based on the tonal shape of the fundamental frequency as follows: sine (ascending-descending) (1), up-sweep (ascending) (2), down-sweep (descending) (3), flat (constant) (4), and concave (descending-ascending) (5) (Tyack, 1986; Azevedo & Van Sluys, 2005). Each distinct whistle was then defined by several acoustic parameters of the fundamental tone, including duration (s), high frequency (Hz), low frequency (Hz), and the number of harmonics (Azevedo et al., 2007). The median frequency of the whistle frequency range was also calculated in Hz. Whistles were further categorized as either stereotyped (ST) or nonstereotyped (NST). Those

**Table 1.** Ethogram of behaviour activities

Behaviour state	Definition
Milling	Dolphins are not moving in a consistent direction and frequently change heading with slow travel speeds (generally < 2kts). Dolphins may float or remain stationary for short periods of time (> 3 s) either just below or at the water's surface (provisioned dolphins may rest on the bottom in shallow water adjacent to the beach).
Scanning/foraging	When the dolphin is submerged and moves its head from side-to-side while swimming with no defined travel direction around the feeding area.
Socialising	Two or more dolphins have physical contact such as body rolls and petting. Splashes at the surface, chasing, and tail slapping are considered social behaviours.

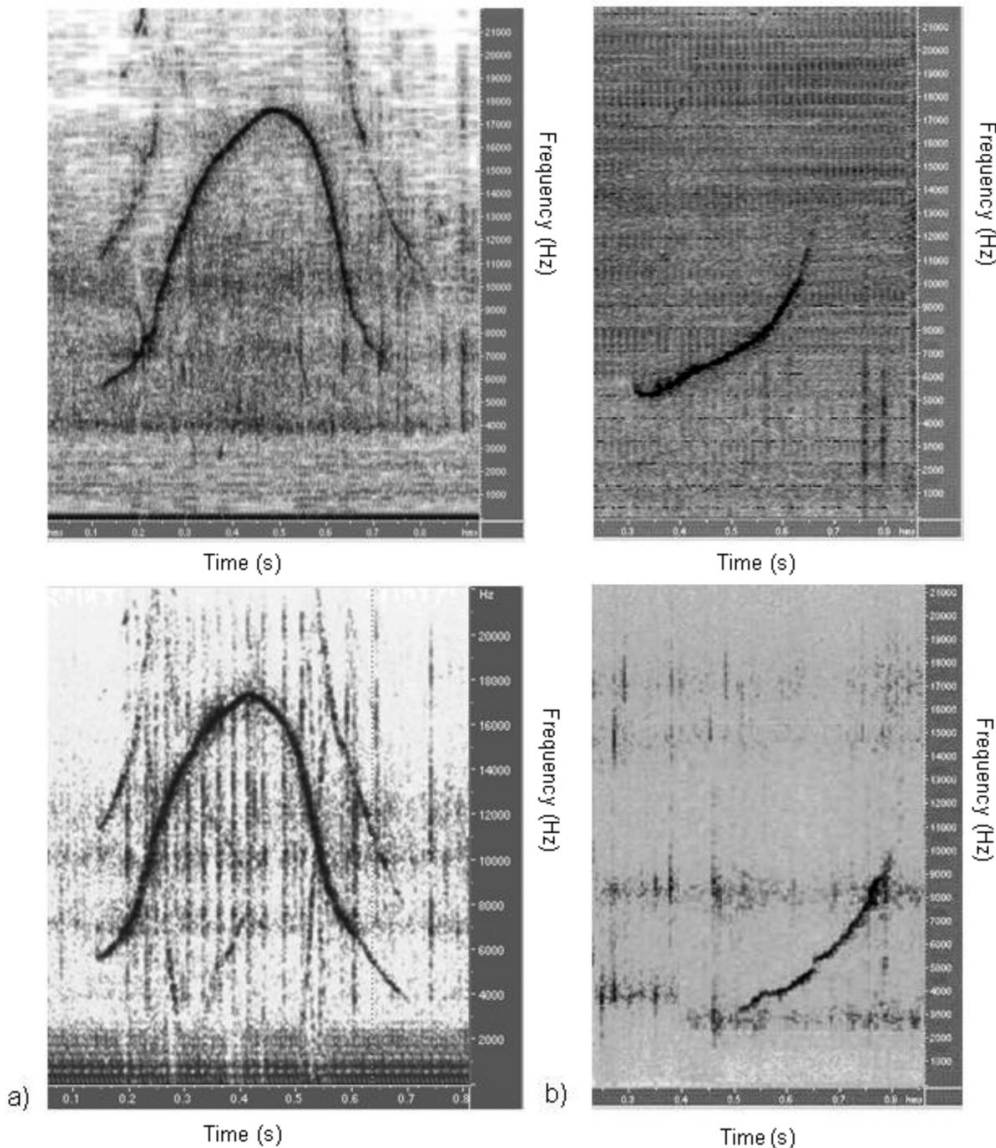
that were stereotyped had a distinct and repetitive contour (dos Santos et al., 2005). These whistles had little variation in the acoustic parameters. Whistles that had some variability in the acoustic parameters (but stability in contour) were termed nonstereotyped whistles (Figure 2).

*Data Analysis*

The repetition rate of whistles (# whistles/minute/dolphin) per feeding session were calculated by summing the total number of whistles recorded and dividing this by the total recording time and

the number of dolphins present. The diversity of whistles (i.e., number of unique whistle types recorded) was also calculated for each feeding session. Correlation and regression analysis were used to test the relationship between whistle emissions (diversity and repetition rate) and the presence of individual dolphins (number of dolphins present per feeding session).

The 24-h time of each acoustic emission was noted along with the record time and the corresponding behaviour observations in an *Excel 2000* spreadsheet (Microsoft Corp., Redmond, WA, USA).



**Figure 2.** Representative sonograms of (a) a stereotyped sine whistle (1A) and (b) a nonstereotyped rise whistle (2F)

If more than one behaviour was observed between individual dolphins at the same time, the corresponding whistle was scored for both behaviours. Acoustic emissions made during feeding episodes (i.e., when people were in the water and hand-feeding the dolphins) were excluded from this analysis.

Single factor ANOVA was used to test the differences between the occurrences of whistle classes and behaviour activities. Correspondence analysis using *SPSS 11.0.1* (SPSS Inc., Chicago, IL, USA) were employed to conduct detailed investigations into the associations between distinct whistle types and behaviour activities. Correspondence analysis is an exploratory method that was used to find multidimensional representations of the associations between behaviour activities and whistles in a two-way contingency table (Gifi, 1996). To facilitate this statistical analysis, whenever possible, only recordings and observations taken when the majority of dolphins were engaged in a single behavioural activity were used. In addition, whistles were classified as either *common* (whistles emitted at least 100 times over the study period), or *uncommon* (whistles emitted between 10 and 60 times over the study period). Whistles emitted between 1 to 9 times ( $N = 26$  NST whistle types) and 61 to 99 times ( $N = 4$  whistle types;  $ST = 2$ ;  $NST = 2$ ) were eliminated from the correspondence analysis to reduce bias and provide a more accurate representation of differences in the use of common and uncommon whistles. These whistles contributed 2,290 whistles to the total number of whistles recorded. Whistles emitted between 1 to 9 times were eliminated due to too few samples and the possibility of some misidentification of whistle types. To allow for clear contrasts to be assessed between the use of uncommon and common whistles during behaviour activities, those whistles emitted between 61 to 99 times were also eliminated.

## Results

One thousand and three minutes of acoustic and behaviour recordings were analyzed ( $\bar{x} = 45$  min per feeding session;  $SD = 14$  min) from 22 feeding sessions. During one feeding session, a group of nonprovisioned dolphins (four individuals) entered the feeding area and remained until the feeding session was complete. These data were excluded from the following analysis. From the 21 feeding sessions analyzed, 5,682 whistles were counted. From these, 68 distinct whistle types were identified and catalogued.

*Behaviour and Attendance of Provisioned Dolphins* Milling (56%;  $n = 528$  min) and scanning/foraging (29%;  $n = 273$  min) were the most common

behaviour types observed during feeding sessions, followed by socialising (15%;  $n = 142$  min). Pod separation occasions were recorded on 12 separate occasions.

The mean number of dolphins that attended feeding sessions was six ( $SD = 1.5$ ). The mother and calf were the only dolphins that attended every feeding session.

### *Whistle Production Rates and Diversity*

The number of whistles (Range: 71 to 922;  $\bar{x} = 277.9$ ;  $SD = 193.9$ ) and the diversity of whistle types (Range: 11 to 60;  $\bar{x} = 20.4$ ;  $SD = 4.7$ ) varied considerably between feeding sessions. Correlation tests indicated that there was no strong association between the number of dolphins present in the provisioning area and the number of whistles emitted ( $R^2 = 0.183$ ) (Figure 3). There was also no strong relationship between the number of different whistle types and the number of dolphins in the provisioning area ( $R^2 = 0.168$ ). The dip in the graph on feeding session 14 corresponds to 16 April 2002 when the mother and calf were the only two dolphins that attended the feeding session. Comparatively, there were no unusual circumstances that occurred during the 11th feeding session, which corresponds with a notable drop in whistle rate and diversity.

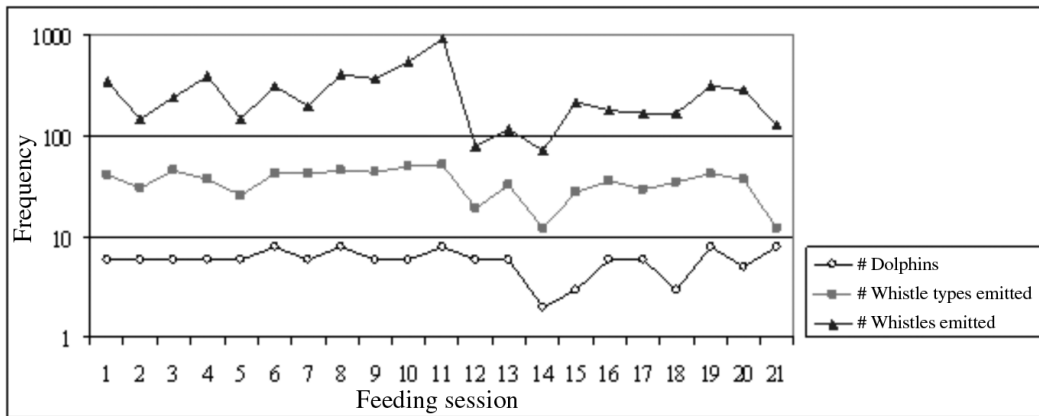
The repetition rate of whistles varied greatly from 0.27 whistles/minute/dolphin (w/m/d) to 2.52 w/m/d ( $\bar{x} = 1.12$  w/m/d;  $SD = 0.61$ ). The highest mean repetition rate was recorded when eight dolphins were in the feeding area ( $\bar{x} = 1.39$  w/m/d;  $SD = 0.80$ ). However, there was also no strong association between the number of dolphins present at the feeding sessions and the whistle repetition rate ( $R^2 = 0.0003$ ).

### *Occurrence of Whistle Tonal Classes*

Of the 68 distinct whistles identified, 18 were stereotyped and 50 were nonstereotyped. Overall, nonstereotyped whistles were emitted more ( $N = 3,162$ ) than stereotyped whistles ( $N = 2,520$ ). The mean values of acoustic parameters for each stereotyped and nonstereotyped whistle tonal class are presented in Table 2.

The occurrence of distinct whistle types varied greatly from 1 to 530 ( $\bar{x} = 74$ ;  $SD = 112.8$ ). Over all feeding sessions, 41% of distinct whistle types were emitted  $\leq 25$  times and 45% over 50 times (Figure 4). A stereotyped sine whistle labeled 1A (shown in Figure 2) was the most frequently emitted whistle type over all feeding sessions.

Sine was the most diverse tonal class with 30 distinct whistles identified ( $ST = 10$ ;  $NST = 20$ ), followed by up-sweep ( $N = 11$  whistle types;  $ST = 1$ ;  $NST = 10$ ), concave ( $N = 10$ ;  $ST = 1$ ;  $NST = 9$ ), flat ( $N = 9$ ;  $ST = 3$ ;  $NST = 6$ ), and down-sweep ( $N = 8$ ;  $ST = 2$ ;  $NST = 6$ ).



**Figure 3.** Line graph comparing the number of dolphins in the provisioning area, the number of whistle types emitted, and the total number of whistles emitted with consecutive data collection events

The most frequently emitted whistles were also sine (50%;  $N = 2,817$ ) and up-sweep (26%;  $N = 1,473$ ) whistles, followed by down-sweep (11%;  $N = 642$ ), flat (8%;  $N = 470$ ), and concave (5%;  $N = 280$ ). Sine whistles were the most frequently emitted stereotyped whistles ( $N = 2,153$ ), while up-sweep whistles were the most frequently emitted nonstereotyped whistles ( $N = 1,279$ ).

#### *Associations Between Whistles and Behaviours*

The diversity of whistles significantly differed between behaviour activities ( $F_{24,1.98}$ ;  $p < 0.001$ ). The highest number and diversity of whistles was emitted during milling behaviours (diversity = 66; total number of whistles emitted = 2,177) and the least during pod separation occasions (diversity = 29; total number of whistles emitted = 358). Figure 5 shows the occurrence of whistle classes between behaviours.

Thirteen whistle types were classed as common (ST = 7; NST = 6), and a further 25 were classed as uncommon (ST = 3; NST = 22). These whistles accounted for 56% of distinct whistle types and 60% of all whistles emitted.

The frequency of occurrence of the five tonal shape categories was calculated for common and uncommon whistles (Figure 6). Sine and up-sweep were the most frequently emitted whistle types for both common (sine:  $N = 2,107$ ; up-sweep:  $N = 1,153$ ) and uncommon (sine:  $N = 386$ ; up-sweep:  $N = 184$ ) categories. Down-sweep and flat whistles were less frequently emitted for the common (down-sweep:  $N = 641$ ; flat:  $N = 297$ ) and uncommon (down-sweep:  $N = 64$ ; flat:  $N = 161$ ) categories. While concave whistles were only evident in the uncommon whistle ( $N = 94$ ).

Whistle 1A was the most frequently emitted whistle during pod separation ( $N = 50$ ), milling ( $N = 250$ ), and scanning/foraging ( $N = 104$ ) activities

were observed. During socialising, a nonstereotyped concave whistle labeled 5E occurred most frequently ( $N = 45$ ).

Results from correspondence analysis suggested that some whistles were associated with different behaviour activities. The assumption that common and uncommon whistles were related to behaviour activities was justified for both tests (common whistles:  $\chi^2 = 380.74$ ,  $df = 36$ ,  $p = 0.0001$ ; uncommon whistles:  $\chi^2 = 184.24$ ,  $df = 72$ ,  $p = 0.0001$ ). For common whistles, the first two dimensions accounted for 91% (74% in Dimension 1) of the variance in the behaviour and whistle matrix. For the common whistle and behaviour analysis, inertia values indicated that the differences between pod separation and foraging contributed most to the variance of the data (pod separation inertia = 0.072; socialising = 0.013). For the uncommon whistle analysis, the differences in inertia between pod separation and milling contributed the most to the variance of the data (pod separation inertia = 0.173; milling inertia = 0.030).

The strengths of associations (based on dimension scores and correlation values) between whistles and behaviour activities are presented in symmetrical normalization biplots (Figures 7 & 8). The strength of associations between whistles and behaviours are represented by the closeness in proximity of variable points.

The majority of associations between common whistles and behaviour activities were relatively weak (around 62%) (Figure 7). Those that showed close associations (around 38%) were related to foraging and social behaviour activities. Common whistles associated with foraging and socialising were all up-sweep (ST = 1; NST = 2) and down-sweep (ST = 1; NST = 1) tonal classes.

Comparatively, the majority of uncommon whistles (around 84%) showed relatively strong

**Table 2.** Summarized acoustic parameters for each tonal class, including the Minimum (Min), Maximum (Max), Mean, and Standard Error (SE) values. **Note:** D = Duration; SF = Start Frequency; EF = End Frequency; LF = Low Frequency; HF = High Frequency; MeF = Median Frequency; and HAR = Harmonics

			Acoustic parameter						
			D	SF	EF	LF	HF	MeF	HAR
Stereotyped	Sine	N	2,153	2,153	2,153	2,153	2,153	2,153	2,153
		Min	0.25	2,500	4,000	3,730	7,390	5,560	0
		Max	0.67	8,700	10,200	5,600	18,107	11,374	7
		Mean	0.54	4,912	5,862	4,572	12,648	8,610	2.5
		SE	0.04	666.7	794.2	168.3	1,063.9	531.5	0.8
	Up-sweep	N	194	194	194	194	194	194	194
		Min	0.12	3,500	9,500	3,500	9,500	5,250	1
		Max	0.39	8,500	15,000	8,500	15,000	11,250	4
		Mean	0.20	5,666	11,666	5,666	11,666	8,670	1.8
		SE	0.03	457.8	663.8	4,573.8	663.8	450.5	0.2
	Down-sweep	N	110	110	110	110	110	110	110
		Min	0.50	4,450	3,000	4,450	15,800	10,125	0
		Max	0.54	18,000	15,800	4,700	18,050	11,375	5
		Mean	0.52	11,225	9,400	4,575	16,925	10,750	2.5
		SE	0.02	6,775.0	6,400.0	125.0	1,125.0	625.0	0.4
	Flat	N	47	47	47	47	47	47	47
		Min	0.19	4,900	4,900	4,750	10,250	7,650	0
		Max	0.53	7,000	22,000	5,250	10,750	7,825	4
		Mean	0.36	5,633	10,633	4,966	10,516	7,741	1.8
		SE	0.10	683.9	5,683.4	148.1	145.3	50.7	0.2
Concave	N	16	16	16	16	16	16	16	
	Min	0.14	4,150	11,390	3,500	15,000	3,750	0	
	Max	0.44	13,100	14,500	8,500	4,000	10,500	4	
	Mean	0.21	9,347	12,796	5,615	9,654	7,635	1.3	
	SE	0.03	2,618.0	909.9	599.6	953.0	708.0	0.4	
Total	N	2,520	2,520	2,520	2,520	2,520	2,520	2,520	
	Min	0.19	2,500	3,000	3,730	7,390	5,560	0	
	Max	0.67	18,000	22,000	5,600	18,107	11,375	7	
	Mean	0.49	5,910	7,973	4,627	12,645	8,636	2.1	
	SE	0.04	940.7	1,366.8	113.1	760.3	376.4	0.5	
Nonstereotyped	Sine	N	664	664	664	664	664	664	664
		Min	0.25	3,000	3,000	3,500	6,100	4,800	0
		Max	0.91	13,950	12,200	8,000	17,320	10,570	5
		Mean	0.57	5,167	5,817	4,613	11,885	8,163	2.2
		SE	0.05	731.6	739.0	246.3	703.2	378.6	0.4
	Up-sweep	N	1,279	1,279	1,279	1,279	1,279	1,279	1,279
		Min	0.10	3,800	8,200	4,450	9,100	7,300	0
		Max	0.58	9,000	19,000	6,800	15,930	19,380	5
		Mean	0.28	5,000	12,867	5,482	12,317	9,976	1.7
		SE	0.05	818.1	1,677.6	261.5	795.7	1,235.9	0.8
	Down-sweep	N	532	532	532	532	532	532	532
		Min	0.10	12,200	4,000	4,360	8,770	4,298	1
		Max	0.51	18,000	10,200	10,000	18,000	14,000	3
		Mean	0.23	14,666	6,066	6,830	11,890	8,898	2.3
		SE	0.07	1,729.5	2,066.7	835.0	1,570.7	1,427.9	0.7



Flat	N	423	423	423	423	423	423	423
	Min	0.1	3,000	5,500	5,450	6,650	6,650	1
	Max	0.33	9,000	10,100	9,000	13,500	11,250	4
	Mean	0.17	6,475	7,775	6,675	9,400	8,037	2.5
	SE	0.04	1,508.5	987.7	539.8	976.3	667.5	0.8
Concave	N	264	264	264	264	264	264	264
	Min	0.26	3,500	6,500	3,250	9,230	6,850	1
	Max	0.82	14,200	10,000	5,250	21,000	13,000	3
	Mean	0.45	9,380	7,900	4,417	12,668	8,542	1.6
	SE	0.07	1,824.9	678.2	256.9	1,590.7	825.1	0.4
Total	N	3,162	3,162	3,162	3,162	3,162	3,162	3,162
	Min	0.1	3,000	3,000	3,250	6,100	4,298	0
	Max	0.91	18,000	19,000	10,000	21,000	19,380	5
	Mean	0.40	6,848	7,732	5,283	11,770	8,635	2.1
	SE	0.03	713.8	672.3	211.5	463.5	359.0	0.3

associations with particular behaviour activities (Figure 8). Of the 17 uncommon whistles that were strongly associated with foraging and socialising, 16 were nonstereotyped. These whistles represented sine ( $n = 7$ ), up-sweep ( $n = 5$ ), flat ( $n = 3$ ), and concave ( $n = 2$ ) tonal classes. Common ( $n = 3$ ) and uncommon whistles ( $n = 4$ ) associated with milling were also nonstereotyped whistles from all five tonal classes.

Both common and uncommon whistles that showed closer associations with occasions of pod separation were all sine whistle types. Common whistles associated with pod separation were all stereotyped ( $N = 3$ ), whereas uncommon whistles were all nonstereotyped ( $N = 3$ ).

#### Whistles Emitted During Pod Separation

The mother-calf pair and a subadult male were recorded in the feeding area alone on three and two occasions, respectively. These dolphins had a preference for whistle type 1A during pod separation (Figure 2). Fifty-two percent ( $n = 37$ ) of the mother-calf pair's emissions and 86% ( $n = 34$ ) of the male subadult's were 1A whistles. The mother-calf pair also emitted an additional 12 distinct whistle types ( $N = 36$ ) during pod separation, although none of these were emitted as frequently as 1A. The male subadult emitted six other whistle types ( $N = 6$ ) during pod separation; however, like the mother-calf pair, these whistles were not emitted as frequently as 1A. It is worth noting that the

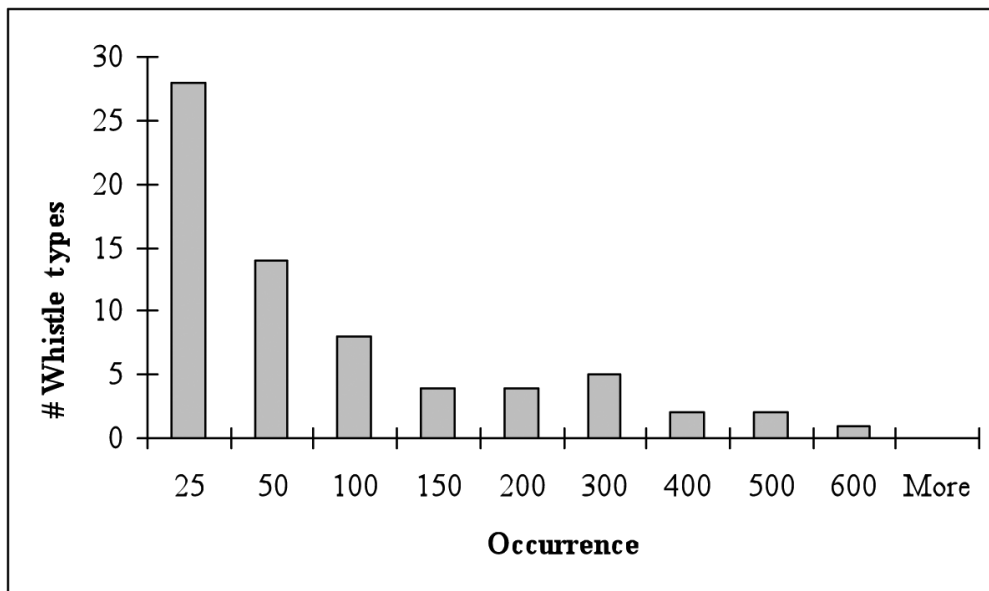
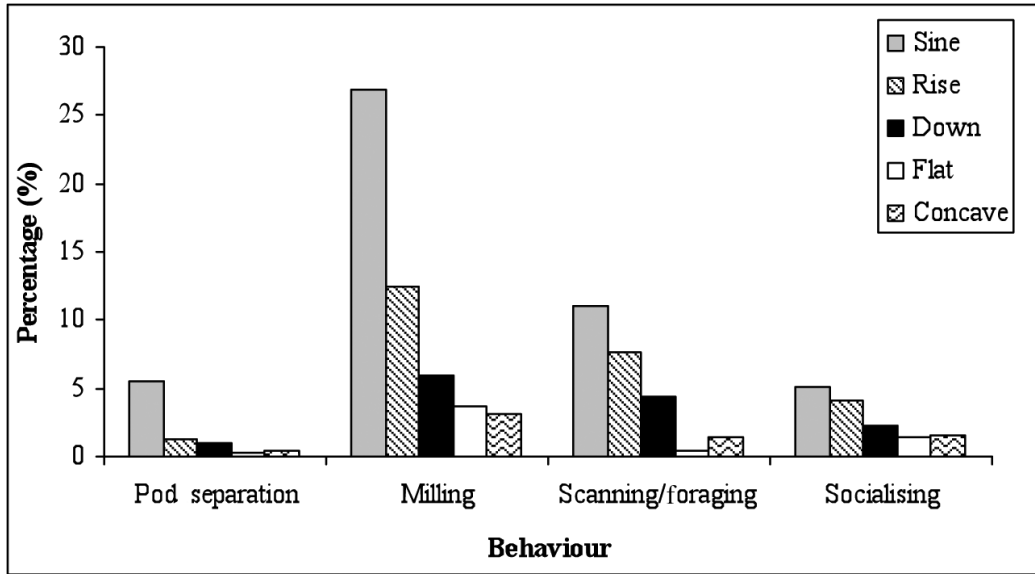
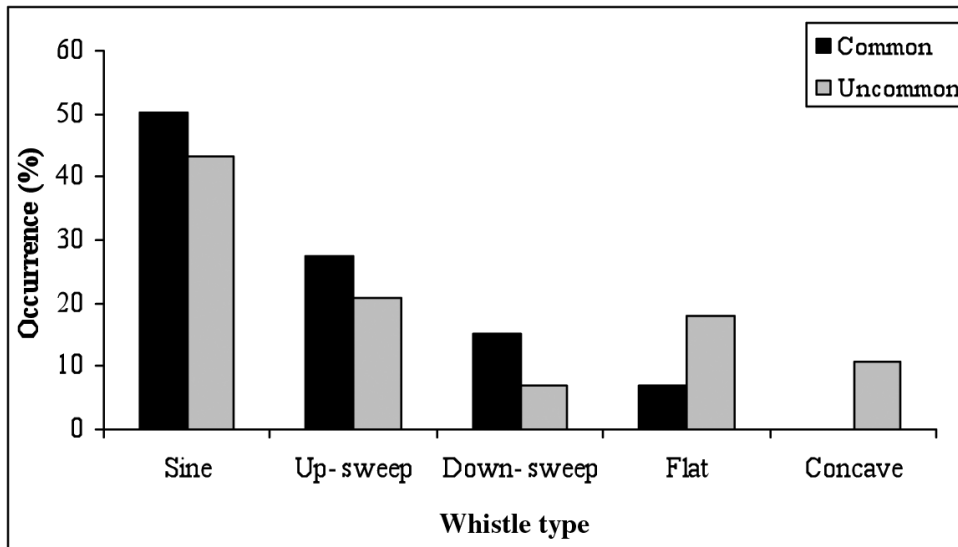


Figure 4. Binned histogram showing the occurrence of distinct whistles



**Figure 5.** Frequency of occurrence of whistle classes emitted during the four behaviour activities. **Note:** Foraging does not include feeding episodes (N = 5,682).

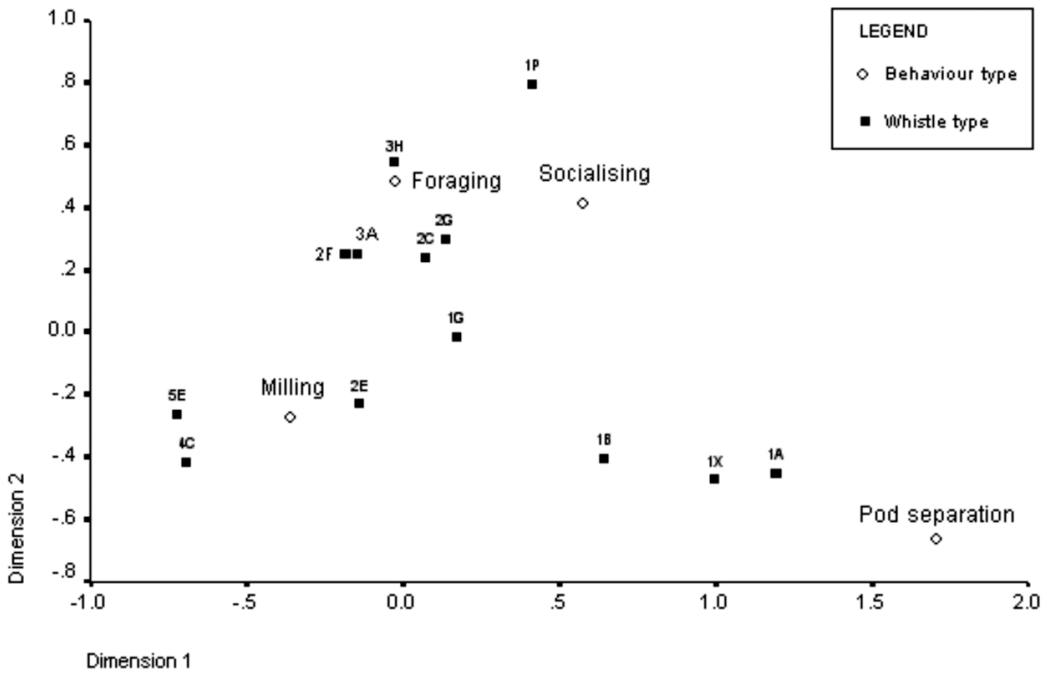


**Figure 6.** Frequency of occurrence of the five tonal shape categories of common and uncommon whistles of provisioned bottlenose dolphins (common, N = 4,198 whistles; uncommon, N = 889 whistles)

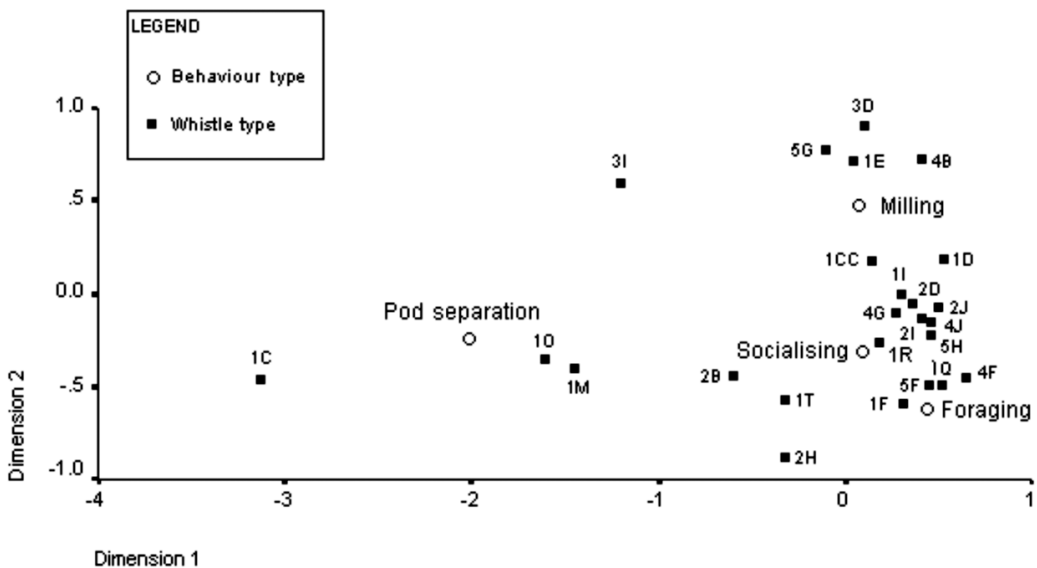
preferred whistle (1A) of the mother-calf pair and male subadult was associated with occasions of pod separation as shown in Figure 7.

An adult male and another adult female were also recorded alone in the provisioning area, but each on only one occasion. The female had a preference for a stereotyped sine whistle 1G (33% of

the 6 whistles emitted), and the male had a preference for stereotyped whistle 1K (24% of the 87 whistles emitted). The female also emitted four (N = 4) and the male 19 (N = 66) additional distinct whistle types that included 1A. These whistles occurred less often than their apparent preferred whistle types.



**Figure 7.** Correspondence analysis symmetrical normalisation biplot of common whistles (those emitted  $\geq 100$  times) and behaviour activities; tonal categories of whistles are represented numerically on the plot (i.e., sine = 1, up-sweep = 2, down-sweep = 3, flat = 4, and concave = 5) in front of the alphabetical label of each individual whistle type (i.e., A, B, C, etc.). **Note:** The proximity of points indicates the strength of association. The Foraging behaviour type refers to scanning/foraging behaviours only, not provisioned feeding episodes.



**Figure 8.** Correspondence analysis symmetrical normalisation biplot of uncommon whistles (those emitted 10 to 60 times) and behaviour activities; tonal categories of whistles are represented numerically on the plot (i.e., sine = 1, up-sweep = 2, down-sweep = 3, flat = 4, and concave = 5) in front of the alphabetical label of each individual whistle type (i.e., A, B, C, etc.). **Note:** The Foraging behaviour type refers to scanning/foraging behaviours only, not provisioned feeding episodes.

## Discussion

The diversity of the whistle repertoire (68 distinct whistle types) recorded from the eight provisioned dolphins at Tangalooma, Moreton Island, demonstrates the complex nature of the acoustic communication system characteristic of many social Delphinid species. Such a large diversity of whistles also has been demonstrated for bottlenose dolphins at Sarasota Bay, Florida, where 199 whistles were identified from 13 individuals (Watwood et al., 2005). Herzing (1996) identified 146 whistles from 33 spotted dolphins (*Stenella frontalis*), a similar species to the bottlenose dolphin, in the Bahamas. The development of such diverse whistle repertoires in social Delphinid species facilitates the functional aspects of their complex social systems such as the maintenance of group cohesion and advertising individual identity (May-Collado et al., 2007).

The repetition rate of whistles in wild bottlenose dolphin varies between behaviour activities (Jones & Sayigh, 2002). When feeding, the repetition rate of wild nonprovisioned dolphins can vary greatly between locations from 0.45 w/m/d in the Sado Estuary in Portugal (dos Santos et al., 2005) to 2.7 w/m/d in Costa Rica (Acevedo-Gutierrez & Stienessen, 2004). For most populations of nonprovisioned dolphins, more whistles were generally produced during socialising than during milling, travelling, or feeding behaviours (Jones & Sayigh, 2002; dos Santos et al., 2005; Quick & Janik, 2008). The higher repetition rates of whistles recorded from the Tangalooma dolphins (2.5 w/m/d) were comparable to those of feeding dolphins in Costa Rica; however, the average rate of whistles produced by the provisioned dolphins (1.12 w/m/d) was more comparable to the higher whistle rates recorded from socialising bottlenose dolphins in nonprovisioned populations (Sado Estuary, Portugal: 0.75 w/m/d; Scotland: 0.53 w/m/d; and Sarasota Bay, Florida: 0.7 to 1.1 w/m/d) (Jones & Sayigh, 2002; dos Santos et al., 2005; Quick & Janik, 2008). Therefore, the conditions and the situation presented by the provisioning program at Tangalooma may have increased the arousal levels of the dolphins involved and consequently stimulated an increase in vocal production. The presence of people in and near the provisioning area may also be an external source of stimuli contributing to the comparatively high levels of whistle production.

Previous studies have reported that the whistle repetition rate increases with group size (Jones & Sayigh, 2002). Quick & Janik (2008) recently reported that the whistle repetition rate of bottlenose dolphins increases until the group size reaches around 10 individuals. At that point, when the whistle production per individual decreased to

apparently counteract the effects of masking. The repetition rate of the provisioned dolphins varied greatly and was not significantly related to the number of dolphins present in the feeding area (although the highest repetition rate of whistles was recorded when all eight dolphins were present). It is therefore likely that the activity levels or behaviour of the provisioned dolphins were more influential than the number of individuals present.

Similar to groups of nonprovisioned bottlenose dolphins, the rate, diversity, and type of whistles produced by the provisioned dolphins were associated with different behaviours (Evans & Dreher, 1962; Herzing, 1996; dos Santos et al., 2005). Our results showed that the highest diversity and number of whistles were emitted during milling behaviours. Comparatively, wild nonprovisioned dolphins increased the diversity of whistles during behaviours in which heightened levels of arousal may be experienced—for example, feeding and socialising (dos Santos et al., 2005). This variation may be due to the unusual situation of the provisioning program during which the dolphins were likely to have relatively higher levels of arousal compared to during nonprovisioning times. In addition, some provisioned dolphins spent more time milling, while other dolphins were engaged in social or scanning/foraging behaviours. Therefore, it is possible the number of whistles relating to milling behaviours identified in this study are overestimated. The rate and diversity of whistles emitted by the provisioned dolphins may also be influenced by other factors that were not assessed here—for example, reunions between individuals at the start of feeding sessions, completion of feeding episodes, and the time of day.

Foote et al. (2008) distinguished between *dominant* call types of killer whales that were likely to function as pod identification calls and less common whistles that were related to social behaviours. In the present study, the common whistle types were loosely associated with behaviour activities and were therefore more likely to be used in a number of different activities. Comparatively, uncommon whistles, the majority of which were nonstereotyped, were more closely associated with specific behaviour activities, particularly socialising and foraging. Similarly, nonsignature whistles were produced during socialising and feeding behaviours in Sarasota Bay, Florida (Cook et al., 2004). In captive dolphins, the number of nonsignature or variant whistles also increased during social interactions with other pool mates and training sessions compared to when they were isolated (Tyack, 1986; Janik et al., 1994).

The production of different tonal classes of whistles can be related to the behaviour activities of several Delphinid species, including

bottlenose dolphins (*Tursiops truncatus*), spotted dolphins, pilot whales (*Globicephala melas*), and killer whales (Weilgart & Whitehead, 1990; Herzing, 1996; Cook et al., 2004; Riesch et al., 2008). Similarly, the present study also showed that some tonal classes and distinct whistle types were strongly associated with particular behaviour activities. For example, up-sweep and down-sweep common whistles were closely associated with scanning/foraging and socialising behaviours. In both captive and wild bottlenose dolphins, up-sweep whistles have been emitted more often during social situations (McCowan & Reiss, 1995; Janik & Slater, 1998; Hawkins & Gartside, in prep). It appears, therefore, that not only nonstereotyped whistles are related to social behaviours in captive, nonprovisioned, and provisioned dolphins, but also up-sweep whistles.

Comparisons with other studies that report the use of whistles during different behaviour activities were made difficult due to the differences in classification systems. Although the aforementioned studies have provided specification on the use of up-sweep whistles, no other breakdown of the use of different tonal classes of whistles produced by bottlenose dolphins have been provided. Most other studies on bottlenose dolphins classify signature whistles into a separate and collective category that does not specify the pattern of tonal inflection or class (e.g., Janik & Slater, 1998; Cook et al., 2004). In this study, we did not classify presumed signature whistles separately in order to obtain a detailed perspective on how and when stereotyped and nonstereotyped whistles of each tonal class were emitted. Additional difficulties in the comparison between populations of whistles produced by bottlenose dolphins were due to the different behavioural circumstances that were created by the anthropogenically altered feeding environments and invasive research techniques (i.e., captive, provisioned, and temporarily restrained dolphins).

Around 52% of whistles produced by bottlenose dolphins in Sarasota Bay, Florida, were classified as *signature* or *probable signature* whistles (Cook et al., 2004). Comparatively, stereotyped whistles accounted for 43% of the total number of whistles emitted from the Tangalooma dolphins. Of these, 38% were common stereotyped whistles, and these may be considered signature whistles.

In a number of terrestrial mammals (e.g., ungulates and primates), the diversity and number of calls is reduced during isolated or stressful situations and an isolation call becomes predominant (Tyack, 2003). This pattern is also evident in bottlenose dolphins in circumstances of isolation or stress when the diversity of whistles is dramatically reduced and the *signature* whistle may be continuously repeated (Caldwell et al., 1990;

Tyack, 2003). When the provisioned dolphins at Tangalooma were separated from other group members, the diversity of whistle types emitted was reduced, and a preference for a particular stereotyped sine whistle was evident for each individual. Janik et al. (2006) suggested that dolphins can identify between cohorts by the pattern of frequency modulation (contours) of whistles. Therefore, stereotyped sine whistles appear to be used as group contact calls for the provisioned dolphins, wherein the whistle tonal class may be shared across the social group. Variations in the tonal inflection of whistles are likely to be used as a signature whistle and advertise caller identity.

The subadult male and a mother-calf pair showed a preference for the same whistle when separated from other provisioned pod members. There are three possible explanations for this occurrence. First, the whistle sharing between the mother-calf pair and the subadult may be evidence of vocal mimicry or whistle matching (Janik, 2000), wherein the isolated dolphins were initiating a reunion with other provisioned dolphins. Second, as reported by Tyack (1986), this may be mimicry of a group member's favoured whistle type or signature whistle. Third, it may be evidence of a predominant whistle type that is possibly shared between members of a closely bonded social group (McCowan & Reiss, 1995, 2001).

Interactions between nonprovisioned and provisioned dolphins occurred during daylight hours outside feeding session time (Hawkins, unpub. data). It is unknown if nonprovisioned dolphins had an influence on the acoustic emissions of the provisioned dolphins during feeding sessions. When a group of nonprovisioned dolphins entered the provisioning area during a feeding session, the whistle diversity increased from 20 to 30 distinct whistle types, but the repetition rate decreased from 0.63 w/m/d to 0.45 w/m/d. Only six distinct whistle types were recorded during this interaction, four of which were recorded prior to and increased after the arrival of the nonprovisioned dolphins. Four up-sweep and down-sweep whistles that had been recorded during other feeding sessions also increased considerably after the arrival of the nonprovisioned dolphins. It would be interesting to investigate how often nonprovisioned dolphins are potentially within acoustic range of the provisioned dolphins, using passive acoustic techniques to determine the degree to which they affect whistle emissions during feeding sessions.

This study is the first to report on the patterns of whistles emitted by dolphins during a provisioning program. To assess the influence of provisioning programs on both the behaviour and acoustics of the dolphins involved, further investigations are required to conduct comparisons of these elements

both during the feeding session and nonfeeding session times. In addition, further comparative assessments between wild dolphins involved in other provisioning programs with different management systems will provide further insights into the implications of such interactions.

Few studies have categorically assessed and reported the patterns of whistle usage across the repertoire of wild bottlenose dolphins. This study demonstrates the complexity and intricate nature of whistle usage of Indo-Pacific bottlenose dolphins. Our results provide further evidence that both common and uncommon stereotyped and nonstereotyped whistles have specific communicative functions.

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