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Interactive Behaviours of Bottlenose Dolphins (*Tursiops aduncus*) During Encounters with Vessels

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Abstract

Bottlenose dolphins (*Tursiops* spp.) are one of the most frequently encountered cetaceans in coastal regions and form the focus of a growing commercial dolphin-watching industry. Bottlenose dolphins are renowned for approaching and interacting with vessels. By obtaining information on the occurrence of interactive behaviours, further insight into the influence of vessel encounters on dolphins can be gained. This research examined the interactive behaviours (defined as bow-riding, wake-riding, and sustained approaches) displayed by Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the presence of different vessel types (motor vessel or sailing yacht) in a region with relatively low levels of commercial dolphin-based tourism activities. The patterns of acoustic emissions produced during these interactions were also recorded. Results indicated that a relatively small proportion of the population displayed interactive behaviours (22% of groups observed). Of the groups that displayed interactive behaviours, 59% contained at least one calf, and most were engaged in the behavioural state of milling (36%). The vessel type ($p < 0.05$) and vessel activity ($p < 0.05$) both significantly influenced the occurrence of interactive behaviour of the dolphins. More interactions per hour occurred with the motor vessel (0.32) compared to the yacht (0.26). The mean duration of interactions was 3 min (SD = 9.07). During interactions with vessels, dolphins emitted a diverse repertoire of whistles with a high repetition rate suggesting that either the group cohesion was affected or that there were higher levels of excitation. It is recommended that monitoring the levels and types of interactive behaviours of dolphins during vessel encounters may be useful to ensure that dolphin-watching activities do not negatively impact social cohesion and long-term survival of dolphin populations.

Key Words: bottlenose dolphin, *Tursiops aduncus*, behaviour, acoustics, tourism, dolphin-watching, vessel

Introduction

Since the establishment of the first dolphinarium in 1938 in Marineland, Florida, a considerable amount of public interest has been generated towards dolphins and, with it, a valuable tourism industry has developed (Samuels & Tyack, 2000). Due to their coastal distribution, bottlenose dolphins (*Tursiops* spp.) in particular have become the focus of an increasing vessel-based dolphin-watching tourism industry (Bejder & Samuels, 2003; International Fund for Animal Welfare [IFAW], 2004).

Recent research has found that vessel-based dolphin-watching tourism can cause short- and long-term disturbances to the populations targeted (Bejder et al., 2006; Lusseau et al., 2006). Female dolphins, particularly those with calves, are vulnerable to disturbances caused by vessels (Lusseau et al., 2006). Short-term behavioural responses of bottlenose dolphins to vessels range from no response to diving and resuming previous behaviours, approaching and interacting with vessels, reducing the level of synchronous behaviours, decreasing inter-animal distance, changing travel direction, increasing swim speed, altering respiration intervals, and completely changing activity and moving out of the area, thus showing immediate displacement or avoidance of the vessels (Acevedo, 1991; Evans et al., 1992; Matsouka et al., 1996; Nowacek et al., 2001; Hastie et al., 2003; Lusseau, 2006). The behavioural state dolphins are engaged in prior to an encounter can also have an influence on their response to a vessel (Constantine & Baker, 1997).

Acoustic emissions produced by bottlenose dolphins may also be altered in response to vessels, particularly whistles which are thought to be a vital component in the communication system of dolphins (Sayigh et al., 1990; Janik & Slater, 1998; Janik, 2000; Janik et al., 2006). Acoustic responses of dolphins to the presence of vessels include increases in whistle repetition rates and increases in whistle durations (Scarpaci et al., 2000; Van Parijs & Corkeron, 2001). Lemon et al.

(2005) suggested that no changes in acoustic emissions occur in the presence of vessels.

Behavioural and acoustical responses of bottlenose dolphins can differ between vessel types and the activity of the vessel (Acevedo, 1991; Scarpaci et al., 2000; Gregory & Rowden, 2001; Mattson et al., 2005). Short-term behavioural and acoustical responses can lead to long-term consequences. Displacement from key habitats, alterations to behavioural budgets, and reduction in reproductive success are long-term changes that have been reported in populations of bottlenose dolphins as a direct result of unsustainable vessel-based dolphin-watching tourism activities (Bejder et al., 2006; Lusseau et al., 2006). Shifts in frequency ranges of acoustic emissions produced by dolphins in areas with high levels of ambient noise, of which vessels are a major source, also have been reported (Morisaka et al., 2005).

Dolphins may become attracted to certain vessel types such as dolphin-watching vessels and trawlers, particularly when there are potential food rewards (Chilvers & Corkeron, 2001; Samuels & Bejder, 2004). To provide customer satisfaction, some dolphin-watching tour operators reportedly feed dolphins that, in turn, may become "conditioned" to encounters (Samuels & Bejder, 1998, 2004; Green & Giese, 2004). Consequently, the behaviour of the dolphins may become predictable, a trait that is valuable to tour operators who are under pressure to satisfy customers (Green & Giese, 2004; Valentine & Birtles, 2004).

Few studies have quantified the occurrence of interactive behaviours of dolphins which may be defined as occasions where a dolphin approaches a vessel (with its orientation towards or parallel to the direction of vessel travel) and maintains a close proximity for a short (around 5 s) or long period of time (e.g., > 5 min). This study examines three types of interactive behaviours of bottlenose dolphins: (1) bow-riding, (2) wake-riding, and (3) sustained approaches (Table 1). This is similar to the "positive" responses of bottlenose dolphins to vessels as outlined by Goodwin & Cotton (2004).

Interactive behaviours of dolphins that are unrelated to food rewards may serve a number of different purposes. Bow-riding and wake-riding, for example, may aid in the maintenance or preservation of energy levels (Williams et al., 1992). The levels of interactive behaviours may also be related to the degrees of conditioning of dolphins to vessel encounters. For example, sustained approaches also may be related to chronic or risky behaviours (as defined by Samuels & Bejder, 2004) such as begging where a dolphin approaches a vessel to feed on discarded fish, bait, or hand-outs from humans. Such behaviours can be an indication of chronic or unsustainable levels of interactions between humans and dolphins (Samuels & Bejder, 2004). Chronic or unsustainable levels of dolphin-human interactions can result in an increased risk of injury or illness from, for example, physical contact with humans, vessels, and fishing gear; vandalism; or ingestion of inappropriate items (Reynolds & Wells, 2003). Thus, the occurrence of interactive behaviours may be used as an indicator for chronic or unsustainable levels of vessel-based dolphin tourism encounters.

No research has investigated in detail the level and nature of interactive behaviours of bottlenose dolphins with vessels prior to the introduction of intensive, vessel-based dolphin-watching tourism. To obtain a foundation for "natural" levels of interactive behaviours, we examined a wild population of bottlenose dolphins exposed to relatively low levels of vessel-based dolphin-watching tourism (Hawkins & Gartside, 2008a). Two different vessel types commonly used in dolphin-watching operations were (1) a motor vessel and (2) a sailing yacht. These vessels were used to investigate if interactive behaviours of dolphins were more likely to occur with a particular vessel. To determine if interactive behaviours were influenced by the movement or manoeuvring of the vessel, several types of vessel activities also were examined. Additionally, we tested if groups with or without calves were more likely to interact with a vessel or if a group was more likely to display interactive behaviours if they were engaged in a particular behavioural state. This is also the first study to report on the patterns of acoustic emissions of dolphins produced during interactive behaviours. Due to the communicative significance of whistles produced by dolphins (Caldwell et al., 1990), only whistles were investigated.

Materials and Methods

This study was conducted in the Byron Bay region, northern New South Wales (28º 27' 60" S; 28º 55' 50" N). The survey area extended along 55 km of exposed coastline to 5 nmi offshore, covering an area of approximately 226 km^2. This region has relatively low levels of vessel-based dolphin-watching operations. The average number of vessels a group of dolphins encountered (i.e., when a vessel was within 150 m) in the survey area on any given day between 0700 and 1300 h (including vessels in transit, research vessels, and kayaks) was 3/d (SD = 2.4). Further details of the levels of vessel encounters and dolphin-watching activities in the Byron Bay area are reported elsewhere (Hawkins, 2007; Hawkins & Gartside, 2008a).

Surveys were conducted seasonally (autumn, winter, spring, and summer) for 2- to 4-wk intensive periods between 2003 and 2006. Two vessels—a 6-m aluminum motor vessel with two 4-stroke 115-hp motors and a 12-m Caribbean van der Stat sailing yacht equipped with a 4-cylinder, 50-hp inboard diesel engine—were used in this study. These vessels represented two different classes of vessels commonly used for vessel-based dolphin-watching operations. Surveys were conducted from only one vessel on any particular day. The speed at which the vessels travelled during surveys varied according to the vessel type and sea conditions. Both vessel types were used in each season.

Surveys were conducted along predefined routes. The activity of the research vessel was undertaken similarly to a commercial dolphin-watching vessel operating under the *Australian National Guidelines for Whale and Dolphin Watching 2005* (Department of the Environment and Heritage, 2006). When a group of dolphins was sighted, the vessel moved to within 150 m of the nearest dolphin. The speed of the vessel was then reduced to < 5 kts and then moved within 50 m of the nearest dolphin.

A group was defined as an aggregation of dolphins that was moving in the same direction, either engaged in a similar behaviour or within a 100-m radius (usually with one dolphin length between individuals) (Mann, 2000). Continuous scan sampling of dolphin behaviour states (travelling, socialising, milling, and feeding) and events were made manually on data sheets (Altmann, 1974) (Table 1). An interaction with a vessel was defined as when at least one dolphin swam within 10 m of the research vessel and remained within this proximity for ≥ 5 s. The arbitrary 10-m boundary was visually estimated by extrapolating the known length of the research vessel to the nearest dolphin. This measurement was verified by at least two observers. The arbitrary duration of ≥ 5 s to define the occurrence of an interaction was developed to include those of both shorter and longer durations. As stated previously, three behaviour events identified as interactive behaviours in this study were (1) bow-riding, (2) wake-riding, and (3) sustained approaches. During a group focal follow, multiple interactive behaviours may have occurred from the same group. For the purposes of this study, a vessel encounter refers to a vessel approaching within 150 m of a group.

The group composition and GPS location were also recorded. The composition of each group was recorded as the number of adults, calves, and unknowns. Calves were defined as dolphins half the size of adults or travelling in echelon or infant position (Connor et al., 2000). A photo-identification catalogue of individual dolphins based on distinctive features, such as the shape of dorsal fins and the number of trailing edge notches, was prepared using a D100 Nikon digital camera with 70- to 300-mm zoom (Hawkins & Gartside, 2008b). The same group of dolphins (as determined from distinct dorsal fin markings of individuals) was not followed more than once per day.

The activity of the research vessel (Table 2) and distance of the vessel to the closest dolphin also were recorded each time a dolphin behaviour was noted or every 2 min during an encounter. The status of the yacht's engine was also noted (i.e., if the yacht was sailing with or without engine assistance). The engine status of the motor vessel's engine during encounters with dolphins was not consistently noted and, therefore, could not be considered in the analysis.

Table 1. Ethogram of bottlenose dolphin behavioural states and interactive behaviours with the research vessel at Byron Bay, northern New South Wales, Australia

Behaviour state	Description
Travelling	Dolphin moves in a defined direction with consistent surfacing intervals.
Socialising	Two or more dolphins making physical contact at the surface—for example, body rolls and petting; some surface activity (e.g., splashes) may be associated.
Milling	Dolphins frequently change travel direction and have slow movements consistent with resting behaviours.
Feeding/foraging	Dolphins are actively pursuing prey and feeding. Usually associated with deep diving, fast swims, or porpoising; frequent changes in travel direction and inconsistent inter-breath intervals.
Interactive behaviours	**Description**
Sustained approach	One or more dolphins approach a vessel within 10 m and remain close to the vessel for ≤ 5 s with bodies orientated towards or parallel to the vessel and swimming at a slow speed (< 3 kts).
Bow-riding	Dolphin is riding in the slip-stream or pressure wave at the bow of a travelling vessel.
Wake-riding	Dolphin rides at the stern of the vessel in the wave created by the vessel's wake.

Table 2. Ethogram of research vessel activities

Vessel activity	Definition
Travelling	Vessel moves in a defined direction often at speed and > 150 m from nearest dolphin.
Direct approach	Vessel approaches dolphins from behind (not parallel) or into the dolphins' travel path between 50 to 150 m from the closest dolphin (travel speed 3 to 5 kts).
Parallel approach	Vessel approaches dolphins from parallel and behind the travel path of dolphins between 50 to 150 m of the closest dolphin (travel speed 3 to 5 kts).
Idle/neutral	Vessel is stationary with engine off.
Parallel tracking	Vessel follows a group of dolphins during a "focal follow" and is positioned 50 m from the closest dolphin and moving parallel to the dolphins' path of travel (travel speed 2 to 5 kts).

Acoustic recordings were made opportunistically during interactive behaviours of dolphins using a single-channel hydrophone (frequency range: 7 Hz to 100 kHz; sensitivity: -179 dB ± 5 dB), HP-A1 series amp (Burns Electronics, Salamander Bay, New South Wales, Australia) and Sony TCD D100 Digital Audio Tape recorder (sample rate 44 kHz). A Burns Electronics two-channel hydrophone array (elements placed 3 m apart; frequency range: 7 Hz to 100 kHz; sensitivity: -169 dB ± 1.5 dB) connected to a CR-Max (Multiplexed Active Filter) amplifier (volume gain 0 to 40 dB; frequency response 7 Hz to 450 kHz ± 3 dB; high pass gain rumble filter 80 Hz, 6 dB/octave within input range), a DAQ (Data Acquisition) card (National Instruments, Austin, TX, USA) and Notino High Grade 3600s computer with *Sonamon* software, Version 1.0, for recording (Madry Technologies, Castle Hill, New South Wales, Australia) was also used. The hydrophone systems were not used at the same time and, therefore, data from recordings made with both systems were combined for analysis.

Sonographic analysis of acoustic recordings was conducted using sonograms in *CoolEdit 2000* (Syntrillium Software, Scottsdale, AZ, USA). Based on the patterns of fundamental frequencies displayed in the sonograms, whistle emissions were divided into five tonal classes: (1) sine, (2) rise (also called upsweep), (3) downsweep, (4) flat, and (5) concave (Tyack, 1986; Azevedo & Sluys, 2004; Hawkins & Gartside, this issue). All whistles were individually classified and given an identification number. Each distinct whistle type was then catalogued and defined by the tonal shape and acoustic parameters (i.e., duration, start frequency, end frequency, low frequency, and high frequency) (Azevedo et al., 2007; Hawkins & Gartside, this issue). Figure 1 shows examples of sonograms of five distinct whistle types from each tonal class. Whistles that could not be individually distinguished due to high background noise were noted as PR (poor resolution) whistles. All data were entered and stored on a specially designed *Access 2000* (Microsoft Corporation, Redmond, WA, USA) database on a laptop computer.

The occurrence and durations of interactive behaviours were tallied for each group with respect to group composition (presence/absence of calves). Chi-square and single factor ANOVA tests were used to examine if there was a difference in the occurrence of behaviour states before, during, and after interactive behaviours. Correlation tests were conducted to assess the strength of association between the duration of interactions and the size of groups. *t*-tests and single factor ANOVA were used to examine the differences in the durations of interactive behaviours between the motor vessel, the yacht with its engine on, and the yacht under sail with no engine assistance. Chi-square tests were used to examine the differences in the occurrence of interactive behaviours between different vessel types by the behaviour state of dolphins. Kruskal-Wallis tests and Post Hoc Tukey tests with Tamhane variance were used to determine if there was a difference in the occurrence of interactive behaviours between vessel activities. Due to the low number of samples, the vessel activity referred to as "direct approach" was not included in this analysis. The repetition rate of whistles (number of whistles/min/dolphin) for each interactive behaviour occurrence was calculated by summing the total number of whistles recorded (including PR whistles) for each group and dividing this value by the duration (min) for which recordings of dolphin acoustics were made and the number of individuals within the group. Correlation tests were used to investigate if there was a relationship between the number of whistles and the repetition rate of whistles with the size of interactive groups. All statistical tests were performed at the $\alpha = 0.05$ level of significance.

Results

Between 2003 and 2006, 314 h of vessel-based surveys were conducted with 163 h on the motor vessel and 151 h on the yacht. During surveys, 201 groups were encountered consisting of 2,485 dolphins. Of the 201 groups observed, only 44 showed interactive behaviours with survey

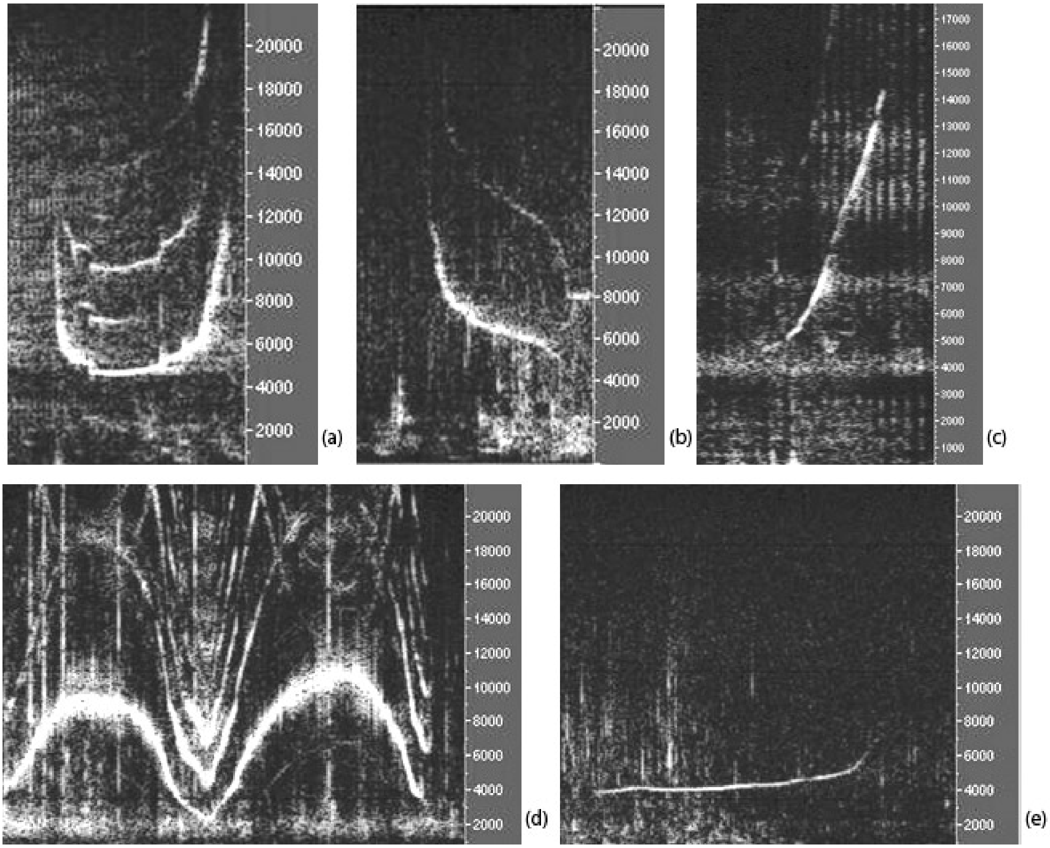

Figure 1. Examples of sonograms of five distinct whistle types from each tonal class with frequency (Hz) on the y axis and time on the x axis: (a) concave, (b) downsweep, (c) rise, (d) sine, and (e) flat.

vessels (bow-riding, wake-riding, and sustained approaches). The majority (157 groups) showed no interactive behaviours with the survey vessels.

Composition of Interactive Groups

The mean size of interacting groups was 13 individuals (Range = 1 to 150 individuals; SD = 12.0; N = 44). The number of individual dolphins that interacted with the vessels at any one time varied between one and ten individuals ($\bar{x}$ = 3.1; SD = 2.3; N = 80). Fifty-nine percent of dolphins displaying interactive behaviours were from groups containing mothers and calves (N = 26), 9% were groups comprised of only adults (N = 4), and the remaining 34% were groups where the presence or absence of calves could not be confirmed (N = 14). The mean size of interactive mother-calf groups was 22 individuals (SD = 15.0). Comparatively, the mean non-calf group size was 3 (SD = 1.73). There were too few cases to determine if there was a significant difference in the occurrence of interactive behaviours between mother-calf and non-calf groups.

Behaviour State of Interactive Groups

The majority of interactive behaviours occurred in groups that were milling (36%; n = 56), travelling (29%; n = 46), and socialising (24%; n = 37), but rarely in groups that were feeding (11%; n = 17). The behaviour state of the dolphins changed at the onset of an interaction. The travelling state declined and the milling state increased (Figure 2). In this case, "before" refers to group behaviours prior to an interactive behaviour with the vessel; "during" refers to the behaviour state of interactive and non-interactive dolphins when an interactive behaviour was occurring; and "after" refers to behaviour states of groups that occurred following an interaction with the vessel. Travelling changed from the most common group behaviour state prior to an interaction at 40% to 70% during interactions. Milling changed from around 30% before an interaction to become the most frequent behaviour state during (42%) and after (37%) the interaction. Social behaviours increased during interactions with the vessel from 18 to 29%. Differences in the occurrence of behaviour states before, during, and after interactions were not significant ($p = 0.622$; $F_{2,6} = 0.51$).

Occurrence of Dolphin Interactive Behaviours with Vessel Types

Interactive behaviours of dolphins were recorded during approximately 1% (4 h) of the total research vessel survey time. Forty-four groups interacted with the research vessels (22% of the total groups observed) resulting in a total of 82 interactive occasions (motor vessel: $n = 52$; yacht: $n = 34$).

Dolphins had a higher rate of interactions per hour (0.32 interactions/h) with the motor vessel compared to with the yacht (0.26 interactions/h). The number of repeated interactions (i.e., the number of times individuals from a group approached and interacted with the vessel during a focal follow) per group varied from one to nine ($\bar{x} = 2.4$; SD = 1.9).

Chi-square tests showed significant heterogeneity between the occurrence of interactive behaviours and the vessel type ($\chi^2 = 0.0001$; df = 2; $p < 0.05$). For the motor vessel, sustained approach (51%; $n = 51$) was the most common, followed by bow-riding (45%; $n = 46$) and wake-riding (4%; $n = 4$) (Figure 3). For interactive behaviours involving the yacht, bow-riding (54%; $n = 77$) occurred most often, followed by wake-riding (23%; $n = 32$) and sustained approaches (23%; $n = 33$). Both bow-riding and wake-riding occurred more frequently with the yacht when the motor was off, and sustained approaches occurred more frequently when the yacht's motor was on. These differences were not significant, however ($\chi^2 = 0.08$; df = 2; $p > 0.05$).

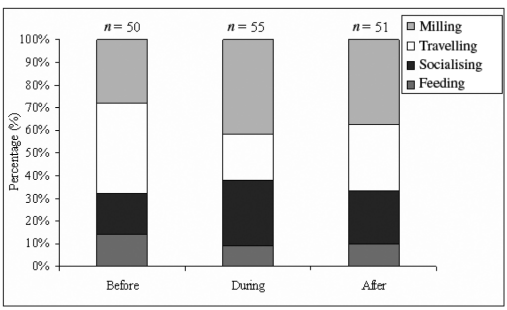

Figure 2. Occurrence of bottlenose dolphin behaviour states before, during, and after interactions (bow-riding, wake-riding, and sustained approaches) with vessels at Byron Bay, northern New South Wales, Australia, between 2003 and 2006. **Note:** before = the group behaviour prior to the occurrence of interactive behaviour; during = the behaviour state of the group when interactive behaviours are occurring; and after = the behaviour state of the group following interactive behaviours (i.e., when interactive behaviours have ceased).

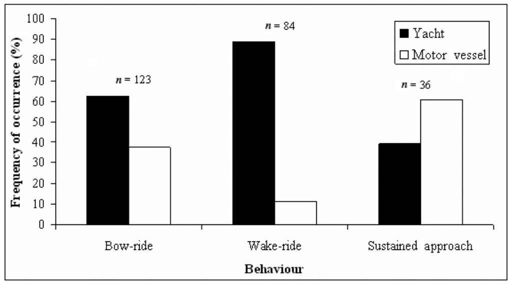

Figure 3. Frequency of occurrence (%) of interactive behaviours of bottlenose dolphins between the yacht and motor vessels at Byron Bay, northern New South Wales, Australia, between 2003 and 2006

Duration of Dolphin Interactive Behaviours

The duration of a single interaction varied from brief encounters of < 1 min to > 24 min, with 68% of all interactions being < 2 min and 14% between 5 and 7 min (Figure 4). The mean duration of interactions was 3 min (SD = 9.07; $n = 82$). Correlation tests showed that the relationship between the duration of interactions and group size was weak (r calculated = 0.002; r critical = 0.205; df = 80).

Dolphin interactions with the motor vessel were generally of shorter duration ($\bar{x} = 3$ min; SD = 4.08) compared to those with the yacht ($\bar{x} = 4$ min; SD = 4.63), but this difference was not significant as indicated by t-test analysis ($t = 2.13$; df = 16; $p = 0.65$). However, when the durations of vessel interactions with the motor vessel ($n = 68$), the yacht with motor off ($n = 23$), and the yacht with the motor on ($n = 11$) were examined, a significant difference (single factor ANOVA) between the vessels and the duration of interactions was evident ($p = 0.02$; $F_{2,99} = 4.01$). Sixty-eight percent of yacht interactions ($n = 23$) occurred when the engine was off with sail only, and 32% ($n = 11$) occurred when the engine was on. The mean duration of interactions was longer when the yacht was under sail with the engine off (5 min; $n = 25$) than when the engine was on (1 min; $n = 11$).

Influence of Vessel Activity on the Occurrence of Interactive Behaviours

There was a significant difference in the occurrence of dolphin interactive behaviours between the activities of the motor vessel (Kruskal-Wallis = 17.687; df = 3; $p = 0.001$) and the yacht (Kruskal-Wallis = 36.367; df = 3; $p = 0.0001$). Interactive behaviour events occurred significantly more often when the motor vessel was parallel approaching or passively travelling than when idling (parallel approach – idle $p < 0.05$; parallel tracking – idle $p < 0.05$). Dolphins interacted more often when the motor vessel was parallel tracking (52%; $n =$

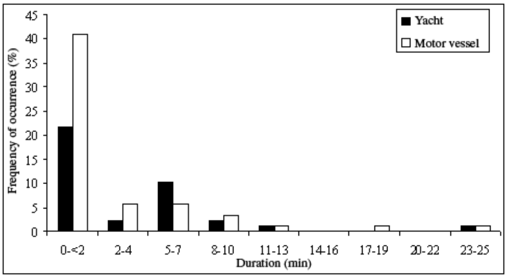

Figure 4. Duration of interactive behaviours of bottlenose dolphins with the motor vessel and yacht at Byron Bay, northern New South Wales, Australia, between 2003 and 2006

27) and parallel approaching (31%; $n = 16$) than when it was idling (12%; $n = 7$) or travelling (5%; $n = 2$) (Figure 5).

The most frequent occurrence of interactive behaviours of dolphins occurred when the yacht was travelling under sail with or without the motor on. There were significant differences in dolphin interactive behaviours between the yacht's travelling and parallel approaching behaviours ($p < 0.001$), travelling and parallel tracking approaches ($p < 0.001$), and travelling and idling ($p < 0.001$). Dolphins interacted more often when the yacht was travelling (45%; $n = 68$) than when parallel tracking (27%; $n = 41$), idling (16%; $n = 24$), or parallel approaching (12%; $n = 18$) (Figure 5).

Acoustic Emissions of Dolphins During Interactive Behaviours

Eight acoustic recordings (total duration: 82 min) from eight different groups were made during 13 interactions with the research vessels. Two recordings were made from the motor vessel and six were made from the yacht. Research vessels were either travelling (54%; $n = 7$), idling (23%; $n = 3$), or approaching (23%; $n = 3$) when acoustic recordings were made. The majority of recordings were made during bow-riding and sustained approach

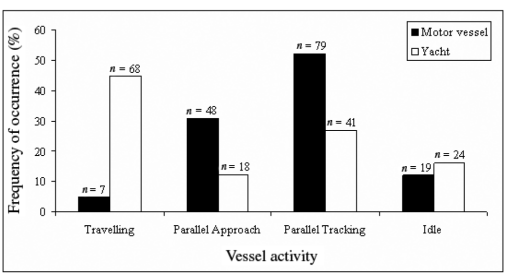

Figure 5. Frequency of occurrence of interactive behaviours of bottlenose dolphins in Byron Bay, northern New South Wales, during each of the four vessel activities of each vessel type between 2003 and 2006

behaviours of dolphins, with one recording made when dolphins were wake-riding. Due to the low number of recordings made, all acoustic data recorded from both vessels were combined for analysis. The majority of acoustic recordings were made when the research vessels' engines were off, except for two recordings that were made when the motor vessel was approaching a group.

All groups recorded contained at least one calf. Six hundred and ninety-nine whistles were recorded, of which 47 distinct whistle types were identified, and 212 were noted as PR whistles. Rise (45%; $n = 215$) and sine (44%; $n = 213$) whistles were the most common tonal shapes recorded, followed by flat (9%; $n = 44$) and downsweep (1%; $n = 6$). No concave whistles were recorded during interactive behaviours. The number of whistle types emitted by single interactive groups varied from two to 39 ($\bar{x} = 15.8$; SD = 14.3). The repetition rate of whistles varied from 0.2 whistles/min/dolphin to 25.8 whistles/min/dolphin during interactive behaviours ($\bar{x} = 12.1$; SD = 8.9). There was no relationship found between the number of whistles or the repetition rate of whistles and the number of dolphins (r calculated = 0.338; r critical = 0.754; df = 5). Only one of the 47 distinct whistle types identified in this study, a flat whistle type labelled "2b," was recorded on more than one occasion from different groups.

Discussion

Bottlenose dolphins are known for interacting with vessels; however, this is the first study to report detailed observations on the nature of these interactive behaviours in a wild population exposed to relatively low levels of vessel-based dolphin-watching operations (Hawkins & Gartside, 2008a). Around one quarter (22%) of the groups of dolphins encountered in Byron Bay displayed interactive behaviours, and of these, around 60% contained calves. It is possible that some of the interactions that occurred in this study may have been influenced by the unusual activity of the research vessels. The motor vessel and the yacht were the only two vessels that consistently approached and followed the dolphins in the Byron Bay area for any length of time. Comparatively, in Panama City Beach, Florida, conditioned dolphins were observed to interact with humans for 77% of the hours surveyed, and they frequently displayed chronic or risky behaviours (Samuels & Bejder, 2004). Alterations in the levels of interactive behaviours over time, particularly occurrences of sustained approaches, may provide information on the levels of habituation or conditioning of dolphins to vessels and human activities.

When interactive behaviours occurred, bottlenose dolphins at Byron Bay reduced travelling behaviours and increased milling behaviours during interactions. In contrast, on approach of a vessel, bottlenose dolphins in New Zealand were more likely to change their behaviour to bow-riding when feeding or socialising (Constantine & Baker, 1997). These contrasting results may be due to differences in the levels of vessel encounters and the nature of the encounter (e.g., swim-with-dolphin tours compared to non-swim-with-dolphin tours) between the two locations. Environmental factors such as the time of day and tidal conditions when dolphin-vessel encounters occurred may also have an influence on these population differences.

Williams et al. (1992) suggested that the purpose of bow-riding or wake-riding in the pressure wave or slip stream of a vessel may be to reduce the energetic costs of swimming for dolphins. During interactive behaviours of dolphins in the present study, groups marginally increased milling and social behaviours and decreased travelling behaviours. Therefore, it is unlikely that interactive behaviours such as bow-riding and wake-riding were used for the sole purpose of energy conservation. Interactive behaviours of dolphins may also have an element of "play" and curiosity.

There were differences in the occurrence of interactive behaviours of dolphins between the motor vessel and the sailing yacht. Dolphins in Byron Bay typically had a higher rate of interactive behaviours per hour with the motor vessel than with the yacht. In Teignmouth Bay, UK, Goodwin & Cotton (2004) also observed a higher number of interactive behaviours of bottlenose dolphins with moving planing vessels compared to non-motor or displacement vessels.

The overall interaction with both research vessels was quite short: around 3 min. The duration of interactions was longer with the yacht under sail (with no engine assistance) than with the engine on or with the motor vessel (with engine on or off). The sound properties of propeller cavitation, which is the primary source of vessel noise (Richardson et al., 1995), may be influencing the duration of interactive behaviours with vessels with their motor on and may be related to the tolerance levels of dolphins to exposure to such noise.

Dolphins were more likely to sustain approaches with the motor vessel and the yacht when the engine was on. However, bow-riding and wake-riding occurred more frequently with the yacht under sail with its motor off. The hydrodynamic properties of a yacht under sail (with no engine assistance) are different to those of engine-assisted vessels (Marchaj, 1985). When a yacht is sailing with engine assistance, the movement of the propeller creates a high amount of turbulent water movement. Comparatively, a yacht under sail (with no engine assistance) creates a less turbulent displacement wave, making consistent pressure waves that emanate from the bow and stern of the vessel (Marchaj, 1985; Carr, 1998). These conditions may be more favourable for dolphins to bow-ride or wake-ride with the possible advantage of reducing the energetic costs of movement (Williams et al., 1992).

The occurrences of interactive behaviours of dolphins are not only influenced by the type of vessel, but also by its activity. In the Bay of Islands, New Zealand, bottlenose dolphins were more likely to interact with dolphin-swim-tour vessels if they were idle (Constantine & Baker, 1997). In the present study, dolphins were more likely to interact with the motor vessel when it was parallel tracking or parallel approaching and when the yacht was travelling or parallel tracking. Dolphins were therefore more likely to interact with vessels that were displaying predictable, non-invasive movements, with consistent travel direction and speed.

This study is the first to report the patterns of whistles of bottlenose dolphins displaying interactive behaviours. The mean repetition rate of whistles from interactive groups (12 whistles/min/dolphin) was 12 × that of socialising groups (1.3 whistles/min/dolphin) in the same population (Hawkins, 2007). The high repetition rate of whistles may reflect the heightened levels of arousal experienced during interactive behaviours (Caldwell et al., 1990). It may also be an indication that the cohesion of groups was disrupted during occurrences of interactive behaviours because of the separation of individuals and the increase in noise produced by the vessel. Increases in whistle production served to maintain contact between individuals. Whistles produced during interactive behaviours were also highly diverse, with only one flat whistle type (labelled "2b") recorded on numerous occasions from different groups. The repetition rate and diversity of whistles varied between the groups observed and were likely to be dependent on the number and identity of individuals present. It is unlikely this whistle was produced by the same individual on all occasions recorded (as confirmed from photo-identification analysis).

The diversity of whistles produced by bottlenose dolphins is likely to be related to the number of individuals in groups and the advertisement of individual identity through the emissions of possible *signature whistles* (Caldwell et al., 1990; Janik et al., 2006). The large number of rise and sine whistles recorded during interactive behaviours in the present study suggests that these whistle types are particularly important in maintaining group cohesion. The high level of whistle production from interactive groups found in this study, therefore, reflects the apparent functions of whistles reported in previous research—that is, to convey to the other members of the group the location and identity of the dolphins involved (Caldwell et al., 1990; Janik, 2000; Janik et al., 2006).

Results of this study have demonstrated that only a small portion of dolphins in a population exposed to relatively low levels of vessel-based dolphin-watching interact with vessels. The type of vessel, the vessel's activity, and its engine status are factors that influence the occurrence of dolphin interactions. During interactive behaviour displays, the group cohesion may be disrupted, and levels of heightened excitation arise causing changes in the production of acoustic emissions.

Several factors may affect the levels of occurrence of interactive behaviours in populations, including the dolphins' history with vessels and the levels of vessel encounters, in addition to environmental and ecological conditions. Information on the levels and types of interactive behaviours of dolphins during vessel encounters may assist in the assessment of potential long-term impacts of dolphin-watching activities on individuals and populations of dolphins.

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