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Behavioural Processes xxx (2006) xxx–xxx
BEHAVIOURAL PROCESSES
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Why do dolphins jump? Interpreting the behavioural repertoire of bottlenose dolphins (*Tursiops* sp.) in Doubtful Sound, New Zealand

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Received 27 October 2005; received in revised form 15 June 2006; accepted 19 June 2006

Abstract

Only a limited number of studies have tried to determine the purpose of surface behavioural events performed by dolphins. To date only one study has attempted to aggregate the behavioural events observed in a population in contextual groups using co-occurrence as the grouping factor. In the present study, I tried to characterise the behavioural repertoire of a bottlenose dolphin population (*Tursiops* sp.) present in Doubtful Sound, New Zealand. I first looked at the relationship between events performed by individuals depending on the behavioural state of their schools. I then assessed the likelihood for events to co-occur. Four main behavioural categories (orientation, travel, social displays and fights) emerged from this analysis. Aerial events (jumps) did not fall into one category, showing that different aerial behaviours play different roles. Moreover, it appears that dolphins used side-flopping and upside-down lobtailing to communicate motivation. Side-flops occurred when the focal schools finished a behavioural bout and started to travel, while upside-down lobtails occurred when the focal schools instigated a behavioural bout after travelling. This non-vocal communication can take place over a few meters to hundreds of meters. Having signals that are effective over very short ranges avoids unwanted signalling to prey, predators or conspecifics.

Keywords: Behaviour; Bottlenose dolphin; Non-vocal communication; Behavioural analysis

1. Introduction

Aristotle, in his History of Animals (Balme, 1991), was the first biologist to ponder on the purpose of the aerial displays performed by dolphins. Interestingly, few studies have tried to determine the context in which surface behaviours are performed in dolphin populations. The difficulties associated with the quantification of behavioural events in the wild are partly responsible for this lack of interest. Most studies have quantified behavioural budgets using behavioural states (e.g. travelling, diving, etc.) and have focused on the behavioural ecology of the studied populations (Bearzi et al., 1999; Mann, 2000; Shane, 1990; Würsig and Würsig, 1979, 1980). Others have focused on interpreting only specific behavioural events such as aerial displays (Acevedo-Gutiérrez, 1999; Herzing, 2000; Slooten, 1994; Waters and Whitehead, 1990).

The surface behaviour of dolphins can be divided into three arbitrary groups: aerial behaviours, percussive behaviours and other behaviours. Aerial behaviours are jumps, while percussive behaviours are any surface behaviour resulting in a sound being produced by slapping a body part on the water surface. Aerial and percussive behaviours are more spectacular and easier to record and they have therefore attracted most of the research attention. They seem to be more often observed during feeding bouts (Acevedo-Gutiérrez, 1999). Drawing mostly on their experience with Hawaiian spinner dolphins (*Stenella longirostris*), Norris and Dohl (1980) proposed that aerial behaviours were used socially to reaffirm social bounds before a hunt. On the other hand, Würsig and Würsig (1980) proposed that Argentinean dusky dolphins (*Lagenorhynchus obscurus*) use jumps more directly—to herd schools of prey at the surface for easier capture. These hypotheses are not mutually exclusive but they cannot apply generally (e.g. some dolphin species do not hunt co-operatively or hunt schooling fish at the surface).

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doi:10.1016/j.beproc.2006.06.006

Herzing (2000) argued that certain percussive behaviours, such as tail slapping (also called lobtailing), are performed to get the attention of other individuals in the school. She also describes aerial behaviours as displays during intra-specific contests. A recent study (Lusseau, 2006) showed that headbutting, an aerial behaviour, is indeed used during inter-alliance agonistic interactions of males. To date only one study (Slooten, 1994) has attempted to segregate the behavioural repertoire of a dolphin species into contextual groups. Often behavioural events are considered as belonging to a similar context because they look similar (jumps for example). Slooten showed that the use of these behavioural categories is potentially biased. All these authors stress the hypothesis that some of these aerial and percussive behaviours are a form of non-vocal communication between individuals advertising a motivational and/or an intentional state. Yet this purpose has not been clearly demonstrated.

Gregarious species need to make communal decisions about which activities to perform (i.e. feeding, resting, socialising, etc.) and which direction to travel. A democratic decision-making system should be widespread because it is less costly to all members of a group than a despotic system would be in most situations (Conradt and Roper, 2003). However, if information is not homogeneously distributed among members a group, some individuals are more experienced for example, a despotic system, i.e. the group following the decision made by one individual, can be advantageous (Conradt and Roper, 2003). This 'leader' would need to communicate its motivation/decision to the rest of the group effectively. In the case of dolphins, vocalisations can be detected over many kilometres (Janik, 2000). It would therefore be advantageous to be able to communicate motivation over a short-range to avoid eavesdropping by conspecifics and therefore minimise scramble competition (Dawson, 1991).

This study tries to go one step further in interpreting the contextual grouping of behavioural events. Firstly, I assessed whether behavioural events were context-dependent to understand whether they may have a communicative value. That is, I estimated whether they were more likely to occur in some context than others; contexts being coarsely defined using the behavioural state of schools. I also tested whether some events may be used as non-vocal communication by assessing whether they were more likely to occur while schools were changing their behavioural state. Following Conradt and Roper's theoretical work (2003), I expected percussive events to be more likely to be linked to communication of motivation since they would minimise inter-school competition.

I studied the behavioural repertoire of a small bottlenose dolphin population present in Doubtful Sound (Lusseau and Newman, 2004; Lusseau et al., 2003; Williams et al., 1993). First, I related the occurrence of behavioural events to the assumed behavioural state of focal schools. I tested whether certain events were likely to carry motivational or intentional information by assessing whether they were more likely to occur during transitions in behavioural state. That is, I assessed whether certain events occurred more often when a behavioural bout ended or was instigated. Finally, I also assessed the role of different behavioural events by segregating them into contextual units based on co-occurrence.

2. Materials and methods

2.1. Field techniques

I collected behavioural data in Doubtful Sound, New Zealand (45°30′S, 167°00′E) between June 2000 and May 2002. Systematic surveys of the fjord were conducted to look for dolphin schools (Lusseau et al., 2003). Once a school was detected the identity of individuals in the school was determined using photo-identification. The behavioural state of the school was then sampled every 15 min. The principal behavioural state (Appendix A) of the school was categorised via scan sampling (Altmann, 1974). The school was continuously scanned for a fixed period of 5 min, repeatedly scanning the school from 'tail' to 'head' (from individuals in the back of the schools to the ones at the head). The behaviour of each individual was therefore sampled several times within a school sample. This exercise was repeated every 10 min, hence, the 15-min interval between samples. These behavioural states were defined to be mutually exclusive and cumulatively inclusive (as a whole they described the entire behavioural budget of the dolphins) after a long-term quantitative study of the population's ethogram (Schneider, 1999). These states were similar to the ones used in other studies (Shane, 1990; Bearzi et al., 1999). Scan sampling of individuals within the school was preferred to focal school sampling because of the observer bias inherent to the latter technique (Mann, 2000). Observations ended when the weather deteriorated, the focal school was lost or the day ended, therefore, the end of a sequence of observations was not dependent on the behaviour of the focal school.

In addition to recording behavioural state, I recorded (for 1 h at a time) every behavioural event (see Appendix B) I observed at the surface performed by individuals from the focal school. The sampling method was therefore different from the one used for behavioural states since all occurrences of events described in the ethogram (Appendix B) were recorded. Both sampling could be carried out simultaneously because more than one observer was present onboard. The sampling period for behavioural events was limited to 1 h in order to minimise sampling bias due to observer fatigue. Sampling periods were spaced apart by at least 15 min. Events and their timing were recorded via the short-cut keys of a Psion Series 5 palmtop computer recorded by punching a shortcut code. Events were defined as a series of body movement that could be unambiguously identified as a unit. For example, the event "tail-out dive" composed the following movements: dolphin surfaces, steeply arches its body above water, raises its tail above the water, dives with its tail re-entering the water last. These behavioural events do not represent the entire behavioural repertoire of the population, but are all events that always occur at the surface. Therefore, these events could be observed every time they occurred. A code of conduct was established for the observing vessel to minimise its effects on the focal schools (Schneider, 1999). Studies showed that the behaviour of the focal schools was not affected by the presence of the observing vessel (Lusseau, 2003, in press).

2.2. Relationship between behavioural states and behavioural events

Samples of behavioural events were categorised using behavioural states. I therefore obtained two types of samples: samples representing a bout of one behavioural state (i.e. samples beginning and ending with the same behavioural state) and transitory samples (i.e. samples beginning with one state and ending with another). I was interested in determining whether certain events were performed more often when a socialising, diving, or resting bout ended or started. To avoid confusion, I therefore kept transitory samples that started or ended with a travelling or a milling state. Samples were thus classified into nine possible states: travelling, resting, milling, socialising, diving, travelling to another state, a state to travelling, milling to another state and a state to milling.

I first assessed the relationship between the occurrence of each event with the length of the sampling period and the number of individuals present in the school. The dataset (counts) was fourth root transformed to approach a normal distribution (Quinn and Keough, 2002). I then carried out a multiple linear regression analysis using a generalised linear model on all the events together because of the dependence of the events on one another (Quinn and Keough, 2002). If a relationship between an event and sampling period or school size was detected, the event was standardised by dividing its counts by the independent variable to which it was related.

I then performed a multivariate analysis of variance on the standardised dataset to determine whether certain events were observed more often during one or several of the nine behavioural states. The standardised counts were fourth root transformed to approach normality. I determined the state in which each event was more likely to occur using a Bonferroni post hoc test on each univariate ANOVA. I also carried out a discriminant function analysis to determine which behavioural events were the most important to discriminate behavioural states. I used a backward stepwise method (Quinn and Keough, 2002) using SPSS (Chicago, IL, USA) to isolate events more likely to segregate behavioural states. This technique can appear circular because some of these events were used to define the behavioural state of the school (Appendix A). However, this helped to assess the context in which non-trivial events were more likely to occur. In order to assess the potential biased from including behavioural events used in the definition of behavioural states, I also carried out a second analysis in which events used to define states were removed.

2.3. Contextual grouping of behavioural events

Using the same dataset I carried out a hybrid multidimensional scaling analysis, using Kruskal loss function to relate distances to dissimilarities (Belbin, 1991). Because of the nonlinearity of the data I used a power regression between distances and dissimilarities (Legendre and Legendre, 1998). This technique uses different transformations for different dissimilarity scales; for events that are close to one another within the Euclidean space and events that are further away from one another. Dissimilarities were calculated from the standardised dataset using the Bray-Curtis dissimilarity index. This dissimilarity index was chosen because of its reliability with count-based data (Quinn and Keough, 2002).

Finally, I tested the relevance of the grouping I observed in the re-scaled data by carrying out a discriminant function analysis on the observed groups using the scores of each event in the re-scaled dimensions.

3. Results

During the study period I spent 137 days (879.2 h) looking for dolphins. I followed focal schools for 716.5 h (over 133 days) and recorded the occurrence of behavioural events for 172 h (over 74 days). The observation period was divided in 641 samples based on behavioural state. I discarded 19 samples that could not be categorised as one of the nine behavioural states. The analysis is therefore based on 622 samples. The average length of a sample was 16.8 min (S.E. = 0.43, range: 2.1–81.7 min).

All data transformations were successful in approaching normal distributions. Occurrence of 15 of the 35 events was related to the length of the sampling period and the number of individuals present in the focal school (Table 1; $p < 0.01$, 2 and 638 degrees of freedom for all regression analyses). A smaller portion (22%) of them was not related to any of these parameters (Table 1).

3.1. Relationship between behavioural states and behavioural events

The three multivariate statistics rejected the null hypothesis that there was no difference in behavioural state group centroids (Table 2). All but six events (‘fb’, ‘wlt’, ‘rub’, ‘startled’, ‘mirror’ and ‘we’) varied significantly depending on behavioural states ($F_{8,613} > 1.98$, $p < 0.05$). Pairwise contrasts among the behavioural states indicated that most states were different from one another (Table 3) and that only 15 events were necessary to discriminate among group centroids (discriminant function analysis, Wilk’s $\lambda_{120,4276} = 0.235$, $p < 0.0001$; Table 3). A similar analysis carried out on a censored dataset which removed events used to defined behavioural states, that is ‘cd’, ‘ta’, ‘tsd’, ‘tod’, reached similar conclusions (Wilk’s $\lambda_{224,4537} = 0.220$,

Table 1
Relationship between behavioural events and both the length of the sampling period (period) and the number of individuals in the focal school (school size)

Events depend on	Events
Period and school size	as, bb, bi, ch, eo, fb, fob, lt, pn, sh, sn, tod, toj, tsd, wlt
Period	cd, hb, hj, to, bf, ta
School size	hf, twj, tws, vj
No dependence	hbm, sf, sp, tf, ts, ult, rub, startled, mirror, we

Each row represents a group of events significantly related to the variables heading the row ($p < 0.01$, 2 and 638 degrees of freedom for all regression analyses). Counts were fourth root transformed for the analyses.

Table 2
Multivariate statistics testing for differences between the nine different behavioural states depending on the frequency of occurrence of the 35 behavioural events

	Statistic	d.f.	F	p-Value
Wilk's λ	0.171	288, 4539	4.00	<0.001
Pillai trace	1.423	288, 4680	3.52	<0.001
Hotelling–Lawley trace	2.312	288, 4610	4.63	<0.001

Standardised behavioural events were fourth root transformed before the MANOVA.

Table 4
Bonferroni post hoc test comparing the likelihood of occurrence of the 15 events kept in the discriminant analysis (*) and the other events

	TR	REST	MI	DIVE	SO	x-TR	TR-x	x-MI	MI-x
AS*				+	+				
BB*			+	+					
CD*			+	+				+	
EO*		+	+					+	+
HJ*					+				
PN*			+		+				
SF*						+			
SH*			+						+
SN*		+	+					+	+
TOD*			+	+	+				
TS*					+				
TWJ*					+				
ULT*							+		
VJ*					+				
BF*					+				
BI					+				
FB									
FOB									
HB					+				
HBM					+				
HF			+		+		+		
LT			+						
SP			+		+			+	+
TF			+		+			+	+
TO					+			+	+
TOJ				+	+				
TSD				+					
TWS					+				
WLT									
RUB									
Startled									
Mirror									
TA			+					+	+
WE									

p-values were adjusted for multiple comparisons. A '+' represents a state in which the event is more likely to occur. See Appendix B for a definition of each behavioural event.

$p < 0.0001$) showing that the difference between states was not solely caused by artificial segregation of events by the observers. The transitory states involving milling (x-MI, MI-x; Table 3) could not be differentiated from each other, nor could the milling state be distinguished from these transitory states. The seven other states, however, could be differentiated from one another. Finally, the transitory state ending with milling (x-MI) could not be differentiated from resting state (Table 3). Despite the significant differences between group centroids the discriminant functions could only classify 40% of all samples correctly (based on jack-knifed classification matrix). The variation of behavioural states over the discriminant functions was still large.

Bonferroni post hoc tests showed that two behavioural events (upside-down lobtails and side-flops) occur strikingly more during transitory states involving travelling (x-TR, TR-x; Table 4). Side-flops were observed predominantly during x-TR transitions and to a lesser extend (10 samples) during travelling bouts. Upside-down lobtails were observed predominantly during TR-x transitions and to a lesser extend during MI-x transitions.

I further compared travelling bouts in which side-flops occurred to other travelling bouts using a MANOVA. During these travelling bouts pouncing, horizontal jumps, chasing and throat flops were more likely to be observed (Wilk's $\lambda_{31,130} = 0.418$, $p < 0.001$; all four univariate ANOVAs $F_{1,160} > 6.0$, $p < 0.01$) than during other travelling bouts during which no side-flopping was observed. Looking at the sequence of the samples, chasing, pouncing, and horizontal jumps typically occurred before side-flops while throat flops typically occurred after. Side-flops and upside-down lobtails are not a diagnostic characteristic of all x-TR and TR-x transitions, as there were several bouts (73 and 67 samples, respectively) in which they did not occur. There was no significant difference between the samples in which these events occur and others (MANOVAs, $p > 0.1$).

Table 3
Pairwise contrasts among all behavioural states

	TR ($n = 162$)	REST ($n = 35$)	MI ($n = 23$)	DIVE ($n = 98$)	SO ($n = 98$)	x-TR ($n = 95$)	TR-x ($n = 78$)	x-MI ($n = 13$)	MI-x ($n = 20$)
TR	0								
REST	2.47	0							
MI	2.70	2.16	0						
DIVE	9.04	9.26	4.09	0					
SO	34.22	19.31	9.53	25.45	0				
x-TR	6.02	6.05	4.23	8.17	29.79	0			
TR-x	5.06	3.67	2.00	6.26	24.88	6.70	0		
x-MI	2.52	1.55	1.15	3.24	7.32	3.03	1.73	0	
MI-x	3.94	3.69	1.22	4.84	5.02	5.80	2.47	1.92	0

Values are F statistic for each comparison ($F_{p=0.02}$ is $F_{15,599} = 1.98$). The p-value was lowered to a more conservative value (0.02) because of the relaxed behaviour of multiple tests on type I errors (Quinn and Keough, 2002). The 15 behavioural events kept in the discriminant analysis were: 'as', 'bb', 'cd', 'eo', 'hj', 'pn', 'sf', 'sh', 'sn', 'tod', 'ts', 'twj', 'ult', 'vj' and 'bf'. The number of samples for each behavioural state is given in the heading row (n). 'x' can be either 'REST' or 'DIVE' or 'SO'. Comparisons that are not significant are in bold. See Appendix A for a definition of each behavioural state.

The post hoc tests also showed that certain events (pouncing, tail slaps, twisted jumps, vertical jumps, back flops and horizontal jumps) occur predominantly during socialising bouts (Table 4). Twisted jumps and vertical jumps were typically observed before agonistic interactions and seemed to relate to displays. Horizontal jumps were observed when individuals chased one another and/or occurred when animals were porpoising at high speed. Snaggling, eye-out, sharking, and change of direction occurred more during milling bouts. Snaggling was also present during resting bouts. It is interesting to note that in 51% of eye-outs ($n = 110$), the eye of the individual was closed, indicating that this behaviour is not used to gain visual cues. Unsurprisingly, behaviours that allow the individuals to increase the steepness of dives (tail-out dive, tail-stock dive and tail-out jumps) were more often observed during diving bouts.

3.2. *Contextual grouping of behavioural events*

The multidimensional scaling analysis (MDS) was able to reduce the relationship among the 35 behavioural events into three dimensions without critically distorting the original structure of the dissimilarity matrix (Kruskal stress = 8.98%, the proportion of variance explained is 80.6%; Fig. 1). Four groups became apparent from the MDS (Fig. 1). Two of these groups contain events that can be defined as social interactions. One group has events linked with forceful physical contact (biting, pouncing, headbutting, chasing, horizontal jumps and headbutt miss). The other social group is composed of events more often observed during socialising bouts (Table 4). They do not involve direct physical contact (except for tail slapping; Table 4), yet are linked to inter-individual displays. For example, twisted jumps and twisted surface are commonly observed between two individuals before they headbutt and may be related to pre-fight displays (personal observation).

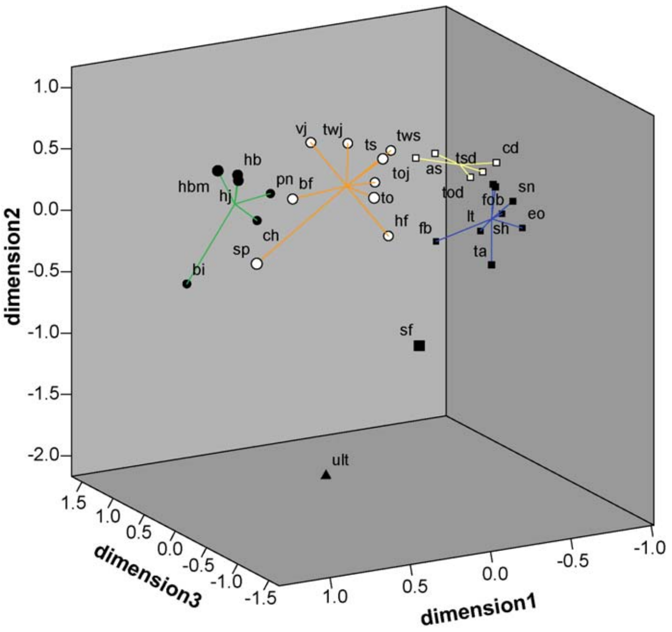

Fig. 1. Scatterplot of each event on the three dimensions of the multidimensional scaling. The three dimensions explain 80.6% of the dataset variance (stress = 8.98%). Groups are represented by different shapes: filled squares for orientation behaviours, open squares for general swimming behaviours, open circles for social displays, and filled circles for agonistic behaviours. ULT (filled triangle) and SF (filled diamond) do not belong to any group. To ease visualisation each event has been linked to the centroid of its group with a spike.

On the other hand, two other groups, not related to social interactions, emerge from the MDS. One is composed of general swimming behaviours (active surfacing, tail-out dive, tail-stock dive and tail-out jump). The other group seems to be related to the orientation of the group because of the occurrence of turnaround and change of direction in this group (snaggle, lobtail, turnaround, change of direction, eye-out, bubble-blow, fart blow, forced blow and sharking). Interestingly, all in-air vocalisations are in this cluster. Finally, side-flops and upside-down lobtails do not seem to be related to any other events. A discriminant function analysis based on the scores of events on each dimension of the MDS was able to discriminate the four groups and two singletons ($F_{15,61} = 19.81$, $p < 0.0001$) and classify 100% of the events correctly.

4. Discussion

The relationship between behavioural states and events yielded some obvious results because some of the events were used to define the states. For example, I was more likely to observe changes in direction and turnarounds during milling bouts and tail-stock dives and tail-out dives during diving bouts. However, these relationships allowed for interpreting non-trivial events such as lobtailing and snaggling, which were related to turnarounds and occurred more often during milling bouts. It also showed that behavioural states recorded in the field represented true groups along the behavioural continuum of this population (the group centroids were significantly different from one another). However, it also showed that states are indeed clusters along a continuum. Even if states were distinctive, samples could not be classified into a state or another reliably.

Specific aerial behaviours seemed to have different functions and therefore aerial behaviours could not be lumped into one contextual group. Active surfacing (as) and tail-out jumps (toj) seemed to be different swimming variants which depended on the speed or the depth the animals wanted to reach. Other aerial, non-percussive, behaviours seem to serve a social function as they were more often observed during socialising bouts.

4.1. *Interpreting surface behaviours*

The multidimensional scaling analysis was able to discriminate between two types of social interactions. Agonistic interactions in which individuals chased, pounced, bit, and/or headbutted each other were segregated from other behaviours most often observed during socialising bouts. I expected these events to be linked because they were the only ones in the repertoire that relate to direct agonistic interactions. The other group of social behaviours was less expected. In Slooten's (1994) sequence analysis, spy-hopping was classified as a sexual behaviour. In many species spy-hopping has been assumed to be orientation behaviour, whales and dolphins using in-air visual cues to orient their movement (Pryor, 1986; Shane, 1990). The present analysis agrees with Slooten's study, as spy-hopping is related to these non-agonistic behaviours and not to orientation behaviours (Fig. 1). The behaviours observed in this social contextual unit seem to be performed in the vicinity of another dolphin (personal observation) and most likely are directed at another dolphin.

Non-social events were also discriminated in two clusters. The first seems to be related to increase in swimming speed (active surfacing and tail-out jumps) or increase in diving angle (tail-out and tail-stock dives). These four behaviours are more often observed during diving bouts. The other non-social behavioural unit seems to be linked to orientation because of the close link with turnaround. Interestingly, there was no behaviour that could have permitted dolphins to use in-air visual cues to orient. However, dolphins tended to spend more time at the surface (stationary or swimming at the surface) during these behaviours. Dolphins may acquire information while at the water surface during these events. For example, in snaggling, the dolphin's melon contracts and the lower jaw is placed stationary at the water surface. This behaviour gives the impression that the animal may be processing acoustic cues at the surface. This behaviour may be counter-intuitive because sound is strongly attenuated at the water surface. More research effort is necessary to fully understand the role of snaggling, especially in the light of recent findings on acoustic communication at the water surface in hippopotamids, a sister phylum to cetaceans (Barklow, 2004). Snaggling is also typically followed by eye-out, yet since the eye of the animals is often closed during eye-outs, visual cues are not sought. Eye-out is therefore more likely related to a lifting of the head that happens to reveal the eye above the water. Bubble-blows, raspberries (fart blows) and chuffs (forced blows) have been described as aggressive displays before (Herzing, 2000). In this study, these behaviours were not related to a social context but to orientation. It is possible that discordance arises during decision-making in orientation and that this discordance is expressed by annoyance/aggressive behaviours such as these vocalisations. These vocalisations can be heard underwater (personal observation) and could therefore be another level of social display. Social displays could range from expression of annoyance, to non-agonistic displays, to agonistic interactions. Yet it is also possible that these vocalisations serve an orientation purpose and may carry information on individual's motivations. The discrepancies between this study and others may be related to species–specific differences or indeed differences in sampling methodology. For example, some signals may function differently underwater as opposed to at the surface, and therefore studies in which dolphins are followed underwater may reach different conclusions from the ones I present (Herzing, 2000).

It is important to note the lack of behaviours associated with feeding. Feeding (dolphins seen with fish in their mouth or chasing fish) is rarely observed in Doubtful Sound. The fjord is deep (200 m on average, 431 m maximum depth) and co-ordinated movements similar to foraging activities described in other studies (Shane, 1990) are only observed during diving bouts. The percussive behaviours apparently used to herd fish schools elsewhere (Shane, 1990; Weinrich et al., 1992; Würsig and Würsig, 1980) would be useless in Doubtful Sound because of the depth at which fish occur. Yet these very behaviours are still observed in Doubtful Sound. This demonstrates the plasticity of bottlenose dolphin behaviours and their potential multi-purpose. The main purpose of percussive behaviours is to produce sound. That sound can be used to drive fish or to carry information. It is therefore important to assess the context in which behavioural events are performed to understand the purpose of a behavioural event.

4.2. The role of non-vocal communication

Percussive behaviours seem to carry motivational or intentional information. Lobtailing was more often observed during milling bouts. This could be related to Herzing's hypothesis (2000) that lobtails are used to seek attention. An individual may be able to transfer information non-vocally about the direction to take by attracting the attention of others that in turn can observe the direction in which the lobtailing animal is heading.

The implications of the use of side-flops and upside-down lobtailing are substantial. These behaviours were usually performed by one individual from the school. Since both behaviours are strikingly related to changes in the school's behavioural state (e.g. start/stop a socialising, resting or diving bout), it implies that the change in behavioural state is led by only one or few individuals. However, these cues were not always used to terminate or initiate a behavioural bout. It is possible that dolphins used these non-vocal signals when vocal signals would have been disadvantageous (e.g. non-intentionally alerting prey, predators or conspecifics). For example, transient killer whales (*Orcinus orca*) are much less vocal than resident killer whales because their primary prey (marine mammals) are able to detect their vocalisations (Deecke et al., 2002; Ford et al., 1998). If a school needs to synchronise its activity but cannot communicate the timing of this synchronicity vocally, non-vocal cues are good alternatives, despite probably being energetically more expensive. Moreover, the sound produced by side-flops and upside-down lobtails does not propagate as far as vocalisations would (Finneran et al., 2000). Therefore, it is possible for individuals to convey information to their nearest neighbours by using these behaviours rather than vocalisations.

Using non-vocal signals to avoid unintentional communication to conspecifics implies that dolphin schools within a population could compete for resources. Two distinct social units have been identified in the population (Lusseau and Newman, 2004). In addition, feeding competition has been observed in Doubtful Sound. In three instances, I observed one individual which had a fish in its mouth being actively pursued (chased, pounced and bitten) by several other individuals. On one occasion four males pursued a mother and calf pair and after several minutes of harassment one of the males removed the fish from the mouth of the female (personal observation). If this represents genuine competition for food, it would be advantageous to communicate feeding or socialising motivations to close associates without advertising the information to others to avoid both direct and scramble competition. On the other hand, if direct competitors are not within hearing distance, vocal communication is without competitive cost, and is probably energetically cheaper.

It can be advantageous for a school to follow an individual that has much experience about the location of fish schools in time and space (following the “grand-mother hypothesis” (Whitehead and Mann, 2000)). Similarly, if co-ordination of school activity is necessary to ensure efficient prey capture (Conradt and Roper, 2000), leaving the instigation of activities to one or few individuals can minimise discord and maximise synchrony. However, according to Conradt and Roper’s model this despotic situation is only advantageous if the group size is small and the leader makes less error on the optimal activity duration (Conradt and Roper, 2003). Currently, there is no way of testing these parameters in the field. However, the school size was not smaller when dolphins used side-flops and upside-down lobtails to change behavioural state than when none were performed ($F_{1,93} = 1.96$, $p = 0.2$; $F_{1,93} = 0.36$, $p = 0.55$, respectively). Two hypotheses prevail. Dolphins may use non-vocal communication to avoid advertising decisions outside of their school therefore avoiding scramble or direct competition from conspecifics and avoiding being detected by preys. These communicative behaviours may therefore only be used when necessary (conspecifics close by for example). It is also possible that dolphins shift from a despotic to a democratic decision-making system depending on certain unknown criteria which are related to environmental factors such as prey density or likelihood of being disturbed during a resting bout for example.

Acknowledgements

Data for this study were collected during an impact assessment of dolphin-watching activities which was funded by the New Zealand Department of Conservation. Additional financial and technical support was contributed by the New Zealand Whale and Dolphin Trust, the University of Otago (Departments of Zoology and Marine Sciences and Bridging Grant scheme) and Real Journeys Ltd. I would like to thank my supervisors Liz Slooten and Steve Dawson for their contribution to this research. I would also like to thank the many volunteers that helped me in the field as well as my colleagues Susan M. Lusseau and Oliver J. Boisseau for their numerous contributions to this project. Thanks to Ramon Ferrer-i-Cancho for numerous fruitful discussions on this project and to two anonymous reviewers whose comments improved this manuscript.

Appendix A

Definitions of the behavioural states, abbreviations for each state are given in parenthesis.

State	Definition
Travelling (TR)	School is moving steadily in a constant direction (faster than the idle speed of the observing vessel). Swimming with short, relatively constant dive intervals. The school spacing varies
Resting (REST)	School is moving slowly in a constant direction (slower than the idle speed of the observing vessel). Swimming with short, relatively constant, synchronous dive intervals. Individuals are tightly grouped
Milling (MI)	No net movement. Individuals are surfacing facing different directions. The school often changes of direction as well. Dive intervals are variable but short. The school spacing varies
Diving (DIVE)	Direction of movement varies. School dives synchronously for long intervals. All individuals perform “steep dives”, arching their back at the surface to increase their speed of descent. The school spacing varies. Diving most likely represented the “feeding” category in other studies (Shane, 1990)
Socialising (SO)	Many diverse interactive behavioural events are observed such as body contacts, pouncing, and hitting with tail. Individuals often change their position in the school. The school is split in small sub-schools that are spread over a large area. Dive intervals vary

Appendix B

Definition of behavioural events (adapted from Schneider, 1999).

Event	Code	Definition
Active surfacing	AS	Rapid surfacing with spray, a major part of the back is visible during the surfacing
Bubble-blow	BB	Exhaling underwater, producing a stream of bubbles
Bite	BI	One dolphin bites another
Change of direction	CD	The focal school change of travelling direction by more than 45° and less than 180°
Chase	CH	Two dolphins actively surfacing following one another
Eye-out	EO	Dolphin lifts its head above water until its eye is exposed
Fart blow	FB	Dolphin exhales above water with its blowhole contracted producing a fart-like sound
Forced blow	FOB	Dolphin forcefully exhales above water produce a loud ‘chuff’ sound
Headbutt	HB	Two dolphins jump simultaneously and hit their heads together
Headbutt miss	HBM	Similar to headbutt but without visible or audible contact between the two dolphins
Head flop	HF	Dolphin jumps, clearing partially its body out of the water, and land on its side
Horizontal jump	HJ	Dolphin clears its body out of the water, keeping its body in a horizontal position, and re-enters the water head first
Lobtail	LT	Forcefully slaps the water surface with the tail
Pounce	PN	One dolphin forcefully nudges another with its beak/shoulder/back
Side flop	SF	Dolphin jumps clearing its entire body out of the water and lands on its side
Sharking	SH	Dolphin swims horizontally at the water surface with its dorsal fin visible above water
Snaggle	SN	Dolphin floats stationary at the water surface, its body horizontally flexed. Dolphin holds breath and contracts melon

Appendix B (*Continued*)

Event	Code	Definition
Spy-hop	SP	Dolphin stands vertically in the water with body partially out of the water
Throat flop	TF	Dolphin jumps and lands on its throat
Tail out	TO	Tail fluke is lifted clear out of the water, dolphin does not arch its back while surfacing (does stays at the surface), and tail re-enters the water without splashing
Tail-out dive	TOD	While surfacing dolphins arch its back and increase its angle of re-entrance. The tail is lifted out of the water and dolphin dives vertically
Tail-out jump	TOJ	Dolphin jumps out of the water with its fluke lifted clearly into the air
Tail slap	TS	Dolphin hits another with its tail fluke
Tail-stock dive	TSD	While surfacing dolphins arch its back and increase its angle of re-entrance. Only the tail peduncle is lifted out of the water and dolphin dives vertically
Twisted jump	TWJ	Dolphin twists itself around the longitudinal axis while leaping and re-enters the water head first or belly first
Twisted surface	TWS	Dolphin twists itself around the longitudinal axis while surfacing actively and re-enters head first
Upside-down lobtail	ULT	Dolphin is upside-down stationary at the surface, belly pointing upwards, and forcefully slaps the water surface with its tail
Vertical jump	VJ	Dolphin leaves the water vertically, clears its entire body out of the water, and re-enters the water head first in a vertical position
Weak lobtail	WLT	Dolphin hits the water surface with its tail fluke. Dolphin does not move its tail-stock during the hit, only the tail moves vertically
Rubbing	RUB	Dolphin rubs on a shallow pebble beach
Startled		While surfacing dolphin shakes its entire body in an involuntary movement
Mirror		One dolphin swims under another and strokes it with its pectoral fins
Back-flop	BF	Dolphin jumps and lands on its back
Turnaround	TA	The focal school change of direction by 180°
Carry weed	WE	Dolphin carries algae on its beak, fin, flippers or tail fluke

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