Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*)

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Because cetaceans are difficult to study in the wild, little is known about how they use their sounds in their natural environment. Only the recent development of passive acoustic localization systems has enabled observations of the communication behaviour of individuals for correlation with their surface behaviour. Using such a system, I show that bottlenose dolphins in the Moray Firth, Scotland, produce low-frequency bray calls which are clearly correlated with feeding on salmonids. The production of these calls is followed by fast approaches by conspecifics in the area. In animals which use sound as a foraging tool, it is difficult to distinguish between food calls which have evolved because of their role in attracting conspecifics, and food manipulation or searching calls which may attract conspecifics as a by-product. However, the low-frequency structure of the bottlenose dolphin bray suggests that it evolved because of a role in manipulating prey rather than in attracting conspecifics. This conclusion suggests that dolphins exploit the perceptual systems of their prey to facilitate capture.

Keywords: food calls; *Tursiops truncatus*; dolphin communication

1. INTRODUCTION

Food-related signalling has been described in many animals. Bees (*Apis mellifera*) (von Frisch 1967) and naked mole-rats (*Heterocephalus glaber*) (Judd & Sherman 1996) inform other members of their colonies about the location of food patches. Several birds (Elgar 1986; Marler *et al.* 1986; Brown *et al.* 1991; Heinrich & Marzluff 1991) and primates (Dittus 1984; Chapman & Lefebvre 1990; Elowson *et al.* 1991; Benz *et al.* 1992; Clark & Wrangham 1993; Hauser & Marler 1993) produce calls if they encounter divisible food items. Different possible benefits to the caller have been proposed for this seemingly altruistic behaviour. Food calls could inform closely related kin of food sources and, thus, increase the caller's inclusive fitness (von Frisch 1967; Judd & Sherman 1996). The presence of other animals at the feeding site could increase the caller's food intake (Brown *et al.* 1991) or decrease predation pressure (Elgar 1986). In social groups food calling could increase an individual's social status (Clark 1993) or decrease levels of aggression if others discover the same food source (Hauser 1992). Finally, food calls could be effective in attracting potential mates (Smith 1991).

In animals which use sound for echolocation or to manipulate prey, the distinction between food-related signalling to conspecifics and food-associated calling which attracts conspecifics as a by-product is less clear. Many odontocetes produce sounds while they are foraging because they use echolocation clicks to detect and pursue prey. These echolocation signals are of high frequency and are highly directional and, therefore, are less likely to attract conspecifics. However, this has not been investigated systematically. In bats, echolocation signals can attract conspecifics to a feeding site (Barclay 1982). This attraction could be disadvantageous but unavoidable if other means of detecting prey are not available. Norris & Møhl (1983) argued that dolphins might also be able to debilitate prey with sound. Such sounds would be more likely to attract conspecifics to a feeding site. Loud, low-frequency bangs have been recorded from feeding odontocetes (Marten *et al.* 1988), but we do not know whether they stun prey and/or attract other dolphins.

Information on food-related signalling to conspecifics in cetaceans is sparse. To date, there is no report about such food calls in captivity. However, captive animals are usually fed dead fish which could prevent the animals from giving out food calls. In the wild, it is difficult to identify when an animal is feeding from the surface. Würsig & Würsig (1980) stated that the surface behaviour of dusky dolphins (*Lagenorhynchus obscurus*) suggested that they produce food-related calls which attract conspecifics, but the sounds were not recorded. Some authors have argued that sounds recorded during obvious feeding behaviours, such as bubble-net feeding in humpback whales (*Megaptera novaeangliae*) (D'Vincent *et al.* 1985) and feeding on seals in killer whales (*Orcinus orca*) (Guinet 1992), recruit conspecifics. Killer whales in Norway also produce calls during group feeding on herrings (Similä & Urgate 1993). However, these studies could not show correlations between calling and the approach of non-calling animals since the position of the caller was unknown.

Bottlenose dolphins produce a variety of low-frequency calls which have hardly been studied. One such call is the bray as described by dos Santos *et al.* (1995). In this paper, I investigate the functional significance of braying in the behaviour of wild bottlenose dolphins in the Moray Firth, Scotland, by using a passive acoustic localization method. With this method, it was possible to identify a caller and study the nature and direction of the reactions of other animals when a bray was given.

2. METHODS

The study was conducted in the Kessock Channel of the Moray Firth, Scotland. The Moray Firth contains a resident

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Proc. R. Soc. Lond. B (2000) **267**, 923–927
Received 4 January 2000   *Accepted* 26 January 2000

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population of around 130 bottlenose dolphins (Wilson *et al.* 1999). Underwater sound recordings and localizations were conducted using a passive acoustic localization system (Janik *et al.* 2000). This method uses the difference in the time of arrival of a sound at different hydrophones to calculate the source position. Three HTI SSQ94 hydrophones (High Tech, Inc., Gulfport, MS, USA) were arranged in a triangle (side lengths 208, 503 and 560 m) in the channel. Each transmitted its signals using a Micron TX-101 VHF radio transmitter (Audio Engineering Ltd, London) to a recording and observation point on the north shore. Each radio transmission was received with a Yaesu FRG 9600 receiver (Yaesu Musen Co., Tokyo) and recorded on a Fostex 380S multitrack tape recorder (Fostex Corp., Tokyo). The frequency response of this system was 50 Hz– 18 kHz ± 3 dB. To determine the difference in the time of arrival of a sound at each pair of hydrophones, the signals were cross-correlated using SIGNAL software (Beeman 1996). All source locations which would result from a specific time difference at the receiving hydrophones fell along one calculated hyperbola in the study area. Thus, the intersection of the three calculated hyperbolas indicated the position of the signalling dolphin. Data were only taken from an area where the localization error was < 13 m (for details see Janik *et al.* 2000).

Only braying was considered in this study. To investigate the responses of other dolphins, their behaviour in relation to the position where a bray was localized was monitored from the surface. Brays are usually produced in bouts by one dolphin, so I only used the first bray in a series. A single bray which was separated from others by more than 1 min or a bout in which separate brays were less than 1 min apart were considered a braying event. Throughout, I use the term caller for the dolphin which emitted the first bray and the term non-caller for other dolphins. Nevertheless, other dolphins could have brayed occasionally or produced other calls in response to a bray, but this was not investigated.

Observations of the dolphins' surface behaviour were carried out from a point on the north side of the channel 30 m above water level and 145 m from the nearest hydrophone. From this point the whole area could be monitored for the surface behaviour of all dolphins. Observational data on the position, direction and behaviour of each surfacing dolphin were recorded using continuous sampling on a separate channel of the multi-track cassette tape recorder and on the audio track of a Sony camcorder which monitored part of the area. The analysis included both audio and video recordings. By combining human observations with data from the video camera the whole study area could be monitored continuously. All instances of the following behaviour patterns were noted.

(i) Fast swimming. A dolphin surfaces, creating white caps due to its speed. The direction of fast swimming was noted. Porpoising (i.e. shallow forward leaps of not more than one body width above the surface which sometimes occurred when a fast swimming dolphin surfaced) was also included in this category.

(ii) Leaping. The whole animal leaves the water in any other way than porpoising. Cases in which only the fluke stayed in the water were also counted as leaps.

(iii) Feeding. A fish was seen either in a dolphin's jaws or swimming away from it at the surface. Only fast swimming fishes were seen, as they sometimes broke the surface during their escape.

(iv) Surfacing. Only the back of a dolphin breaks the surface.

All these behaviour patterns were mutually exclusive except for feeding. I could not identify individuals, thus a series of surfacings could have been by one or several dolphins.

To investigate whether dolphins were attracted to braying, I compared the location and direction of all fast swims in relation to the source position of a bray. I noted which landmark on the south shore the animal was seen in front of to determine the position of an observed dolphin. This limited the possible position of an individual to somewhere on a straight line between the observation point and a given landmark. The positions of landmarks were taken from admiralty charts of the area (scale 1:2500). To determine a dolphin's distance from the observation point, the channel was divided into three distance areas, one close to each shore and one in the middle of the channel. Each area was 175 m wide, so that the whole channel between the hydrophones was covered. Thus, for each surfacing there was a straight line in one of the three areas in which the dolphin could have been. The position of each surfacing was compared to the location of the caller by using that point on the straight line closest to the caller's position as determined by acoustic localization. This is the most conservative estimate of non-caller–caller distance. To avoid observer bias, I did not attempt to estimate the distance of a surfacing dolphin from the observation point more accurately. The sound source position was only determined in a post-hoc analysis, so the source location was unknown by the observer which further avoided bias.

If the position of a fast swim was less than 50 m from the caller the behaviour pattern was counted as occurring at the position of the caller. Otherwise, the direction of fast swimming was noted as either towards the caller (decreasing distance to caller's position) or away from the caller (increasing distance to caller's position). All statistical tests were two-tailed and were calculated by using the SPSS statistical package, v. 7.5 (Norusis 1997).

3. RESULTS

Figure 1 shows a waveform and spectrogram of a bray call. In July 1996, I recorded 132 braying events in 51 h 15 min of observations with dolphins present. This yielded a rate of 2.58 braying events per hour. The number of dolphins present varied from three to over 15. To investigate whether braying could be food related, I investigated what other behaviour patterns were observed during feeding. Twenty-five feeding events were found in this sample. Three additional feeding events were observed in other *ad libitum* samples in 1996. The fishes taken by the dolphins in these events were relatively large. Only two fish species of the observed size and shape are common in the Kessock Channel in the summer, salmon (*Salmo salar*) and sea trout (*Salmo trutta*). Using one-zero sampling, I noted whether braying, fast swimming or leaping occurred in the area during 1 min before and after feeding (figure 2). As a comparison for this test, another 28 randomly chosen 2-min periods were examined for the occurrence of all the registered behaviour patterns. Fast swimming (Cramer's V-test $V = 0.5$ and $p < 0.001$) (Siegel & Castellan 1988) as well as braying ($V = 0.57$ and $p < 0.001$) occurred significantly more often during feeding than during non-feeding periods while leaping, a behaviour often associated with socializing, did not ($V = 0.19$ and n.s.). Braying was associated with 93% of all feeding events, while fast swimming only occurred in 71% of cases. However, fast movements
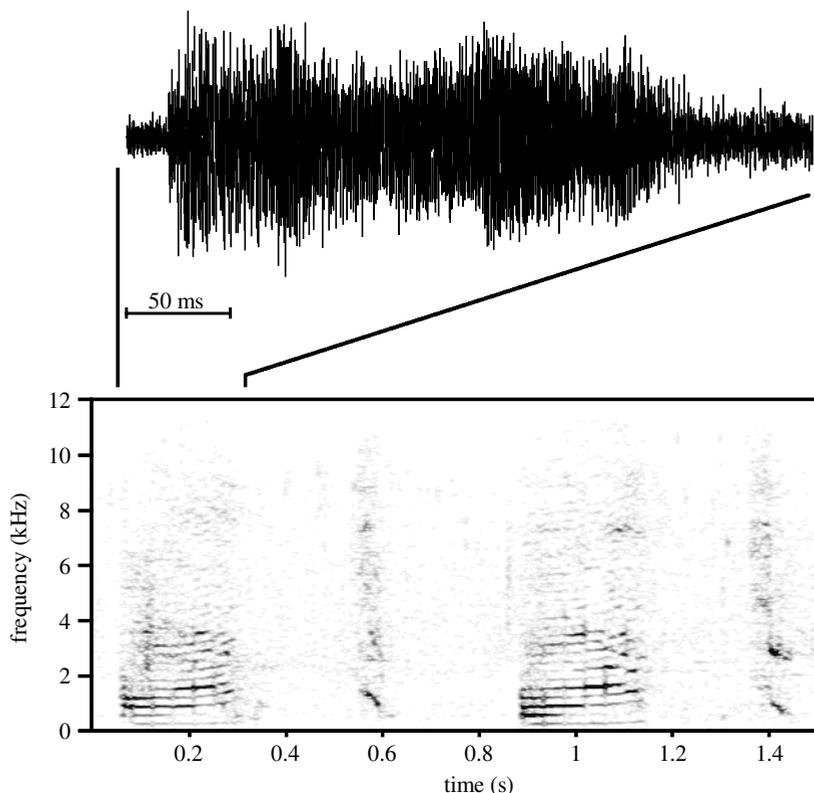
Figure 1. Spectrogram of two brays from a bottlenose dolphin and the waveform of the first element. Each bray consists of two parts, a long multiband part and a short downsweep. The upper part shows the waveform of the first element of the first bray. Note the separate clicks in the waveform indicating that a bray is a burst-pulsed sound. Sampling rate 24 kHz, fast Fourier transform (FFT) length 512, frequency resolution 60 Hz, time resolution 2.7 ms and overlap between FFTs 87.5%, calculated using floating point arithmetic.

could only be observed if they occurred at the surface. Thus, fast movements could be more common than this during foraging, but simply occur fully submerged.

If brays indicate feeding, fast swims could either be chases of fishes at the caller's position or rapid approaches by conspecifics attracted by the bray. However, if braying indicates social interactions which involve chases between individuals, one would expect them to occur at the caller's position. Fast swimming in 15 s periods before and after the first bray occurred in association with 36% of all braying events in July 1996, but the exact position of the caller was unknown for the 1996 data set since only one hydrophone could be used.

In the second phase of this study, I investigated whether fast swimming was observed before and after a bray occurred at the caller's position or whether it involved other dolphins approaching or avoiding the caller using passive acoustic localization. Only fast swimming could indicate a dolphin's movement since I could not identify individuals. In 25 cases between 14 July 1995 and 21 September 1995 fast swimming was observed in at least one of these periods and the first bray could be localized acoustically (total observation time 37 h 45 min). I also counted the total number of fast swims (figure 3a). However, since it was unclear whether one or more dolphins were responsible for the fast swimming, tests were conducted on the one-zero sampling data. Fast swimming at (binomial test $p < 0.05$) as well as towards the caller's position (binomial test $p < 0.001$) increased significantly after a bray (tables 1 and 2). Fast swimming

away from the caller's position was rare (once before a bray and twice after a bray) and its rate did not change after a bray (binomial test n.s.) (figure 3b). However, not all dolphins in the area reacted with an approach. Even animals near the caller's position sometimes did not react, but continued to surface without any acceleration.

4. DISCUSSION

This study demonstrates how important it is to use acoustic localization in the study of dolphin communication. If only one hydrophone had been used, one could have easily concluded that the surface-active dolphins also produced brays. However, the result presented here shows that braying is a food-related call and that it leads to an approach by conspecifics. Thus, most of the surface behaviour displayed was by non-braying dolphins in order to reach the caller's position. The fewer observations of fast swims at the position of the caller could be due to two factors. First, feeding on large fishes is likely to involve fast swims at the caller's position. In fact, fast swims before braying were more likely to occur at the caller's position than in any other location. Second, all surfacings within 50 m of the caller were considered to be at the caller's position and the distance between a caller and a non-caller was determined in a very conservative way. Thus, this distance could have been underestimated in many cases. Some dolphins that were considered to be at the caller's position could actually have been non-calling animals nearby which were also attracted and fast swimming.
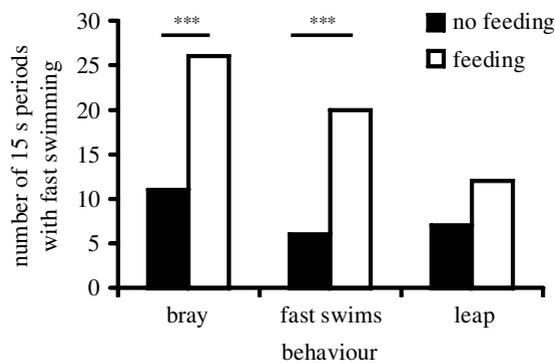
Figure 2. Occurrence of braying, fast swims and leaping in periods when feeding was observed compared with control periods. $n = 28$ for each condition (Cramer's *V*-test ***$p < 0.001$).
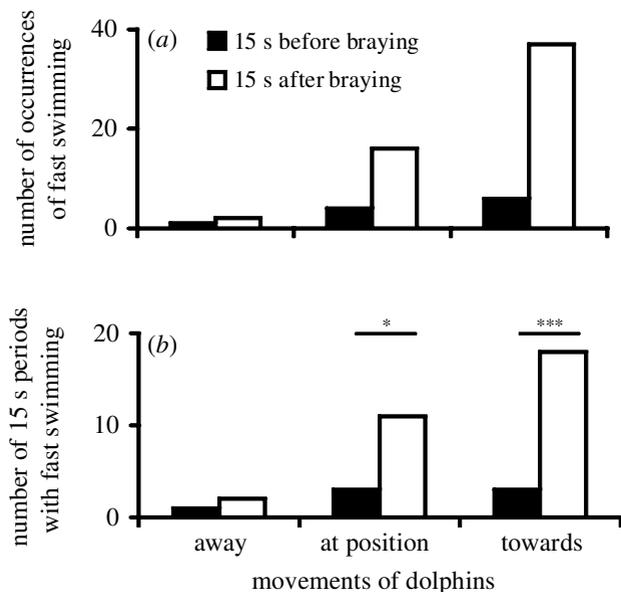

Figure 3. Frequency of fast swimming before and after a bray. The bray occurred at time 0 s. (*a*) Total number of fast swimming surfacings. A test was not conducted since it was not clear how many animals accounted for surfacings. (*b*) Number of 15 s periods which contained fast swimming (one-zero sampling). An asterisk indicates a significant difference (binomial test *$p < 0.05$ and ***$p < 0.001$).

The distinct approach reaction in the 15 s after a bray suggests that this sound was the indicator of a feeding event to other dolphins. Furthermore, brays are rarer than other dolphin sounds. Whistles and clicks are used in many different contexts and occurred at high rates throughout the recording sessions in this study (Janik *et al.* 2000). This relative rarity could mean that brays are used exclusively during feeding. It would be interesting to know how context specific the use of brays is because braying also occurred several times in the randomly selected control periods. However, the controls in this study were the times in which feeding could not be observed from above the surface and it is possible that submerged feeding occurred during these periods. In fact, the small amount of feeding observed at the surface suggests that most feeding occurred under water.

Table 1. *Changes in the occurrence of fast swimming at the caller's position before and after brays*

	fast swimming after brays	
fast swimming before brays	no fast swims	fast swims
no fast swims	2	9
fast swims	1	13

Table 2. *Changes in the occurrence of fast swimming towards the caller's position before and after brays*

	fast swimming after brays	
fast swimming before brays	no fast swims	fast swims
no fast swims	7	15
fast swims	0	3

However, is this call used to signal conspecifics or to manipulate prey behaviour? The hypotheses brought forward for other animals are less likely in dolphins. Because fishes are very mobile and it is unlikely that other dolphins will find the same food spot at the same time, explanations which involve the avoidance of increased aggression by other group members can be discarded. Furthermore, dolphins do not have many predators, so that a decrease in predation pressure due to the presence of more individuals does not seem a likely reason for food calling. Four other hypotheses could explain braying.

(i) Brays could attract closely related kin. Female bottlenose dolphins tend to associate with their kin (Wells *et al.* 1987). However, dolphins have very fluid association patterns and the probability that other unrelated individuals are also attracted is high.

(ii) Attracting conspecifics is a strategy for increasing the feeding success of the caller. In swallows, a caller benefits from the presence of other individuals because insect swarms disperse more slowly if more animals are present (Brown *et al.* 1991). In dolphins, the approach of conspecifics could chase fishes back towards the caller and, thus, increase its probability of a catch.

(iii) The caller could benefit by an increase in its social status. This is a possibility which we know little about, since the dynamics of status in dolphin societies are virtually unknown. In this and the other hypotheses mentioned so far, the bray would be a signal to conspecifics, as has been suggested for food calls in other species.

(iv) However, another possible function of brays could be to change prey behaviour. The structure of a bray suggests that it has not evolved as a long-distance signal to conspecifics. Most of its energy is below 2 kHz. Even though low frequencies travel further under water, the hearing sensitivity of dolphins is low in this frequency range (Johnson 1967). An alternative explanation is that brays either stun a fish or change its behaviour so that it is easier to catch. Salmon can be disorientated by exposure to low-frequency sound (VanDerWalker 1967). The mechanism of this effect

is not understood. Possibly acceleration in water affects the swim bladder or lateral line system, the sound hits the resonant frequency of the fish or parts of it, the sound pressure level overloads the hearing of the fish or the sounds actually cause tissue damage. It has been argued that high-frequency clicks are less likely to stun prey because the sound pressure levels required would be too high (Zagaeski 1987; Marten *et al.* 1988). However, if it is not the pressure but another parameter which elicits the reaction, clicks might still stun prey. Marten *et al.* (1988) argued that low-frequency sounds are likely candidates for prey stunning because they fall in the auditory range of fishes and last long enough to over-load their hearing. Stunned fishes have been observed in association with noisy tail slaps by killer whales, but it was not clear whether the sound or contact with the tail was responsible (Similä & Urgate 1993). Further studies are needed to investigate the possibility of manipulating prey with sound.

Looking at the facts from this study it seems more likely that brays are used to manipulate prey behaviour rather than attract conspecifics. Thus, dolphins seem to exploit the perceptual system of their prey to facilitate capture. If true, the attraction of conspecifics would be a by-product of braying.

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