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SHORT COMMUNICATION

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On the communicative significance of whistles in wild killer whales (*Orcinus orca*)

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Abstract Killer whales (*Orcinus orca*) use pulsed calls and whistles in underwater communication. Unlike pulsed calls, whistles have received little study and thus their function is poorly known. In this study, whistle activities of groups of individually known killer whales were compared quantitatively across behavioural categories. Acoustic recordings and simultaneous behavioural observations were made of northern resident killer whales off Vancouver Island in 1996 and 1997. Whistles were produced at greater rates than discrete calls during close-range behavioural activities than during long-range activities. They were the predominant sound-type recorded during socializing. The number of whistles per animal per minute was significantly higher during close-range behavioural activities than during long-range activities. Evidently, whistles play an important role in the close-range acoustic communication in northern resident killer whales.

Introduction

Identifying the behavioural context of different vocalization types under natural conditions is a crucial step in the study of animal communication systems. Delphinids produce two types of sounds in underwater communication: burst-pulsed sounds ("calls") and tonal sounds ("whistles"). Whistles play an important role in the acoustic communication of most delphinids studied to date (review in Tyack 1998). However, only a limited number of studies have dealt with free-ranging populations, and hence the social framework in which communication takes place is rather unknown (review in Herzing 2000).

Resident killer whales (*Orcinus orca*) off the coast of Vancouver Island, British Columbia, produce burst-pulsed calls and whistles in underwater communication (Ford 1989). Repertoires of stereotyped calls are group-specific. These "discrete calls" are the predominant sound type during activities when individuals are widely spaced, for example during foraging, suggesting that they are used to maintain contact between members of the social group (Ford 1989, 1991). Ford (1989) reported that whistles are most commonly associated with social interactions and concluded that they are predominantly used as close-range affiliative signals. However, detailed measures of the extent of whistling across different behaviours have not been described. Here we report findings from a systematic study of behavioural correlates of whistle production in wild killer whales off Vancouver Island, British Columbia.

Materials and methods

Data collection

We studied the northern community of resident killer whales off Vancouver Island, British Columbia (50°30′ N, 126°35′ W). Resident killer whales live in matrilines of 2–14 animals and feed primarily on fish. The northern resident community comprised 216 individuals in 33 matrilines (1998 census, Ford et al. 2000). Data were collected from 1 July to 13 October, 1996, and from 11 July to 17 October, 1997 from 20-m motor-vessels during 3–9 h (average 4.5 h) long commercial whale-watching excursions from Telegraph Cove (northern Vancouver Island). The killer whales were observed on 196 field trips (130 days; >200 h observation time). When killer whales were encountered, we identified individuals by natural markings, using binoculars (7X50, 8X50) (Ford et al. 1994). Identifications were confirmed by three land-based observation camps and one visual- and acoustic monitoring station. After identification, we moved at least 500 m ahead and shut off the vessel engine for sound recordings. Most of the animals were recorded approaching the vessel within 500 m. As the animals passed the boat, we stopped recording, moved to another position, and resumed recording. The sounds were recorded with hydro-

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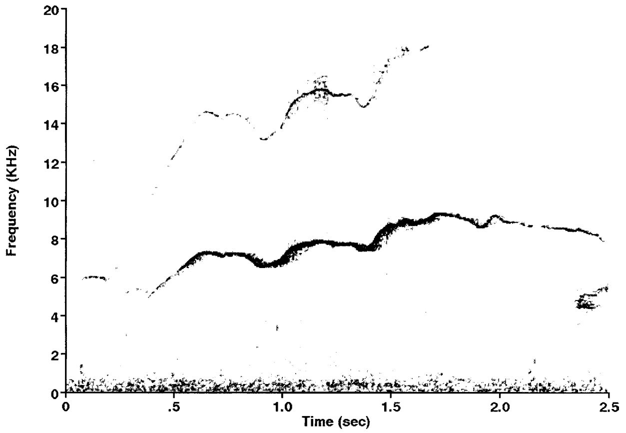

Fig. 1 Spectrogram of a whistle of a northern resident killer whale. DF=48.8 Hz, DT=20.5 ms, FFT size=1,024 points

phones (Bruel and Kjaer 8101 in 1996, Offshore Acoustics in 1997; sensitivity: –180 dB re 1V/μPa or greater) using Sony TCD-D8 (1996) and Sony TCD-D7 (1997) DAT-recorders (20 Hz–20 kHz±1 dB). While recording, we continuously noted the number of animals at the surface, their distance and orientation to the boat, spacing of surfacings, aerial displays. A total of 167 recordings (total length of >40 h) were obtained.

Data analysis

Based on observations of surface behaviour and spacing of surfacings, we grouped the activities of killer whales into five long-range categories where the distance between surfacing individuals exceeded at least several body lengths, and two short-range categories, where the distance between surfacing individuals was less than one body length (modified from Ford 1989; Barrett-Lennard et al. 1996).

Long-range: During *foraging* whales were dispersed over a wide area. Non-directional swimming, irregular diving patterns and varying swimming speeds with short periods of high speed swimming at the surface indicated foraging activities (mean group size 3.8, range 1–6). *Mixed foraging* occurred when animals of more than one matriline were foraging (mean group size 7.1, range 4–10). *Slow-travelling* whales swam in a widely dispersed group on a consistent course at 3–6 km/h (mean group size 4.0, range 1–6). During *mixed slow-travelling*, animals of more than one matriline were present during the recording (mean group size 7.8, range 3–16). *Travelling* whales swam in one or several groups on a consistent course >6 km/h (mean group size 11.2, range 5–20).

Short-range: *Social-travelling* whales swam on a consistent course at 3–6 km/h and engaged sporadically in interactions, such as body contact, or activities such as flipper or fluke slapping (mean group size 9.3, range 5–17). *Socializing* whales grouped together and engaged in social interactions and aerial displays (e.g. breaching, flipper and fluke slapping, chases, rolling over each other, sexual interactions). During socializing, killer whales made little or no consistent progress (mean group size 6.3, range 2–17).

We used the software package RTS, version 2.0 (Engineering Design), for real-time-spectrographic analysis (150 kHz 16 bit A/D converter, sample rate = 50 kHz, frequency range = 0–20 kHz, dynamic range = 42 dB, FFT size = 512 points, DT = 10.2 ms, DF = 98 Hz, overlap = 50%). We classified killer whale sounds into *discrete pulsed calls* that are repetitive, stable over years and pod specific, *variable pulsed calls* that are non-repetitive, and *whistles*. Whistles appear in spectrographic analysis as a narrow-band tone with or without harmonics (Fig. 1). They range in frequency from 1.5 to 18 kHz with most energy around 5–8 kHz. Durations range from 50 ms to 18 s (Ford 1989; Thomsen et al. 2001).

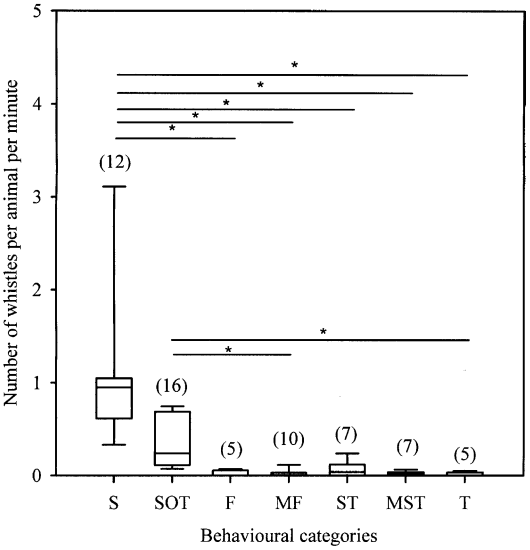

Fig. 2 Number of whistles per animal per minute in different behavioural categories. *Boxes* represent interquartiles. *Vertical lines* represent 90% confidence interval. *Solid horizontal lines* represents the medians. Numbers of matrilines or matriline-associations from which recordings for each behavioural category were analysed are *in parentheses*. Abbreviations: *S* socializing, *SOT* social-travelling, *F* foraging, *MF* mixed foraging, *ST* slow-travelling, *MST* mixed slow-travelling, *T* travelling. *Horizontal lines* show statistically significant differences between samples; * *P*<0.05

We selected 87 recordings which were not masked by boat noise to any great extent and in which the behaviour of the majority of observed animals could be classified clearly into one of the seven behaviour categories. We divided them into 3-min sample intervals and then systematically selected every second 3-min sample interval from each recording. Thus, a total of 177 (3-min) samples were selected. For each sample we counted the number of discrete calls, variable calls and whistles, and calculated the proportion of each for every recording. In addition the number of whistles per animal per minute was calculated for each recording. Observations in the field indicated that whistles had a range of detectability of approximately 500 m (Thomsen et al. 2001). To correct for situations when whales were widely spaced, and individuals were out of acoustic range of the hydrophone, the number of whistles was divided by the number of animals within approximately 500 m. To avoid pseudoreplication, multiple recordings of a particular matriline or of one particular matriline association from the same behaviour category were pooled. Number of whistles per animal and minute were compared across the seven behaviour categories with a Kruskal-Wallis *H*-test. If means differed we performed a multiple comparison following Dunn's method (Zar 1984).

Results

A total of 7,202 sounds were counted. Of these, 889 were whistles, 4,856 were discrete calls and 1,457 were variable calls. The predominant sound type in all long-range behaviour categories was discrete calls. At close ranges, the proportion of discrete calls decreased considerably, whereas the proportion of variable calls and whistles increased. Whistles were on average the predominant sound type during socializing (Table 1). The mean number of whistles per animal and minute had the

Table 1 Relative frequency of occurrence (%) of whistles, discrete calls and variable calls during activities of seven behavioural categories. First number in parentheses indicates the sample size for each behavioural category (number of different matrilines from which recordings were analysed), second number indicates number of recordings analysed, third number indicates the number of 3-min samples analysed

Behavioural category/ sounds	Socializing (12/15/33)	Social-travelling (16/18/49)	Foraging (5/17/31)	Mixed foraging (10/10/21)	Slow-travelling (7/14/22)	Mixed slow-travelling (7/8/14)	Travelling (5/5/7)
Whistles	43%	26%	3%	6%	6%	2%	2%
Discrete calls	29%	54%	94%	85%	85%	89%	96%
Variable calls	28%	20%	3%	9%	9%	9%	2%

highest value during socializing (1.33±0.5 SE, *n*=12) followed by social-travelling (0.38±0.3 SE, *n*=16), slow-travelling (0.08±0.03, *n*=7), foraging, mixed foraging, mixed slow-travelling and travelling (all 0.02±0.01, *n*=5, 10, 7, 5, respectively) (Fig. 2). The mean number of whistles per animal and minute during socializing was significantly higher than during every other behaviour category excluding social-travelling (*H*-test, *H*=45.14, *df*= 6, *P*<0.001; Dunn's method, *P*<0.05). The number of whistles per animal and minute during social-travelling was significantly higher than during mixed foraging and travelling (Dunn's method, *P*<0.05) (Fig. 2).

Discussion

Our study demonstrates quantitatively that whistles in northern resident killer whales are mostly associated with close ranges between individuals. This is particularly the case during socializing, when whistles are the predominant sound type. On the other hand, whistles are only sporadically emitted during long-range exchanges when whales are dispersed. This confirms Ford's (1989) qualitative observation that whistles are produced primarily during close-range, social interactions among killer whales.

Mann (1999) points out that group sampling in cetaceans is not without problems, since not all individuals can be observed at all times. However, due to their size and conspicuousness, killer whales are comparably easy to identify, even at greater distances. Therefore, in most cases, we were able to identify and observe individuals at each surfacing. Nonetheless, we cannot rule out the possibility that submerged individuals behaved differently from the rest of the group. Future studies will attempt underwater sound *and* underwater behavioural recordings in order to overcome these methodological problem. Another problem might be that whistles are too faint and therefore do not travel far enough to be detected from foraging whales. According to Miller (2000), whistles of northern resident killer whales have an average source level of 140 dB re 1V/μPa at 1 m (range 129–148 dB). Given these source-levels, and our recording conditions, it is very likely that most of the whistles were detected at 500 m range. It is true that some fainter whistles could have been missed from whales foraging at 500 m distance, especially when animals were facing away from the microphone. However, since most recordings were at closer ranges, with animals facing the hydrophone, this problem is reduced. Finally, the variation in whistle rates across behaviours was of such a magnitude that the problem of differential detectability is probably negligible.

It has been hypothesized that in some delphinids, for example the bottlenose dolphin (*Tursiops truncatus*), some whistles serve as individual signatures which function as cohesion signals (Caldwell et al. 1990). If whistles in killer whales serve such a function, we would expect them to be most common when animals are widely spaced, for example during foraging or travelling. As shown, the opposite is true. The significant increase in whistles during socializing and social-travelling indicates that they play an important role in close-range communication among killer whales. Many behaviours that take place at close-ranges appear to be affiliative in nature (Jacobsen 1986; Osborne 1986; Ford 1989). Socializing individuals obviously transmit and receive a variety of information related to these interactions through the tactile, visual and acoustic channel. Whistles could play an essential role in this information transfer. In a future report (F. Thomsen et al., unpublished data) we shall look at the structure of whistles in detail and draw further conclusions on the possible functions of whistles in close-range acoustic communication in wild killer whales.

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References

Barrett-Lennard LG, Ford JKB, Heise KA (1996) The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. Anim Behav 51:553–565

Caldwell MC, Caldwell DK, Tyack PL (1990) Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In: Leatherwood S, Reeves RR (ed) The bottlenose dolphin. Academic Press, San Diego, pp 199–234

Ford JKB (1989) Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Can J Zool 67:727–745

Ford JKB (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can J Zool 69:1454–1483

Ford JKB, Ellis GE, Balcomb KC III (1994) Killer whales: the natural history and genealogy of *Orcinus orca* in British Columbia and Washington State. UBC Press, Vancouver

Ford JKB, Ellis GE, Balcomb KC III (2000) Killer whales: the natural history and genealogy of *Orcinus orca* in British Columbia and Washington State, 2nd edn. UBC Press, Vancouver

Herzing D (2000) Acoustics and social behavior of wild dolphins: implications for a sound society. In: Au WWL, Popper AN, Fay RR (eds) Hearing by whales and dolphins. Springer, Berlin Heidelberg New York, pp 225–273

Jacobsen JK (1986) The behavior of *Orcinus orca* in the Johnstone Strait, British Columbia. In: Kirkevold BC, Lockard JS (eds) Behavioral biology of killer whales. Alan R. Liss, New York, pp 135–187

Mann J (1999) Behavioural sampling methods for cetaceans: a review and critique. Mar Mammal Sci 15(1):102–123

Miller PJO (2000) Maintaining contact: design and use of acoustic signals in killer whales, *Orcinus orca.* PhD dissertation, Massachusetts Institute of Technology, Woods Hole Oceanographic Institution

Osborne RW (1986) A behavioral budget of Puget Sound killer whales. In: Kirkevold BC, Lockard JS (eds) Behavioral biology of killer whales. Alan R. Liss, New York, pp 211–249

Thomsen F, Franck D, Ford JKB (2001) Characteristics of whistles from the acoustic repertoire of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. J Acoust Soc Am 109:1240–1246

Tyack P (1998) Acoustic communication under the sea. In: Hopp SL, Owen MJ, Evans CS (eds) Animal acoustic communication. Springer, Berlin Heidelberg New York, pp 163–219

Zar JH (1984) Biostatistical analysis (2nd edn). Prentice Hall, Englewood Cliffs, N.J.