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ORIGINAL PAPER

Signature whistles in wild bottlenose dolphins: long-term stability and emission rates

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Abstract Whistles are key elements in the acoustic repertoire of bottlenose dolphins. In this species, the frequency contours of whistles are used as individual signatures. Assessing the long-lasting stability of such stereotyped signals, and the abundant production of non-stereotyped whistles in the wild, is relevant to a more complete understanding of their biological function. Additionally, studying the effects of group size and activity patterns on whistle emission rate may provide insights into the use of these calls. In this study, we document the decades-long occurrence of whistles with stereotyped frequency contours in a population of wild bottlenose dolphins, resident in the region of the Sado estuary, Portugal. Confirmed stereotypy throughout more than 20 years, and positive identification using the signature identification (SIGID) criteria, suggests that the identified stereotyped whistles are in fact signature whistles. The potential roles of non-stereotyped whistles, which represent 68 % of all whistles recorded, are still unclear and should be further investigated. Emission rates were significantly higher during food-related events. Finally, our data show a comparatively high overall whistle production for this population, and no positive correlation between group size and emission rates, suggesting social or environmental restriction mechanisms in vocal production.

Keywords Bottlenose dolphins · *Tursiops truncatus* · Acoustic communication · Signature whistles · Long-term stability · Activity patterns · Group size

Introduction

The exchange of information is a vital process in animal societies, and the idea that social complexity is linked to higher vocal complexity has received increasing attention (Bouchet et al. 2013; Freeberg et al. 2012; Maciej et al. 2013).

The ability to remember and recognize other individuals in a group appears to be an advantage in species that live in complex social units (Casey et al. 2015; Moreira et al. 2013; Tibbetts and Dale 2007; Wiley 2013). Naturally, any type of sensory label that may convey information about the presence or motivational state of particular individuals is of enormous potential value, as it may enhance the recognition of kin, mates and allies and facilitate social interactions in open, dynamic animal societies.

The existence of individual identity cues encoded in acoustic communication signals has been reported for several mammalian species, with long-term individual recognition having been considered a key element in social contexts such as cooperation, competition and alliance formation (Casey et al. 2015; Mumm et al. 2014; Sharpe et al. 2013; Wiley 2013).

Bottlenose dolphins are acoustically specialized animals, capable of complex cognitive processes (Bruck 2013; Herman 2010; Marino et al. 2007), which live in dynamic fission-fusion societies (Connor et al. 2000; Wells 2014; Wells et al. 1987). This species presents a diverse repertoire of vocalizations associated with specific behavioural contexts: click trains used in sonar-related tasks (Au 2004; Herzing and dos Santos 2004; Jensen et al. 2009); burst-pulsed sounds emitted during social interactions, and during foraging/

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feeding events (Díaz López and Shirai 2009; dos Santos et al. 1995; Herzing 2000); and narrow-band, frequency-modulated whistles used in a variety of contexts (Acevedo-Gutiérrez and Stienessen 2004; Caldwell and Caldwell 1965; Janik and Slater 1998).

Whistles with stable stereotyped contours have been described as learned, unique, individually distinctive contact calls known as "signature whistles" (Caldwell and Caldwell 1965; Caldwell et al. 1990; Janik and Sayigh 2013; Janik et al. 2006; Janik and Slater 1998; Sayigh et al. 1999). These communication signals, developed through vocal learning, are thought to convey individual identity information and to be used to signal the presence and location of an emitter (Janik et al. 2006; Kershenbaum et al. 2013; King et al. 2013; Sayigh et al. 2007).

Although slight variations in the signature whistles, or their production in multiple loops, have been proximately linked to emotional state expression (Caldwell et al. 1990), the persistence of multi-year stable contours has been noted both in captivity and in the wild (Caldwell et al. 1990; Janik et al. 1994; Sayigh et al. 1990). Moreover, playback experiments have highlighted the importance of such stereotyped stable signals in kin discrimination (Sayigh et al. 1999) and long-term recognition (Bruck 2013).

The ability to recognize "friends or foes", through long-distance communication calls, may help to mediate social interactions in a demanding underwater environment. However, despite the relevance of signature whistles' functions, these signals have been found to represent between 38 and 70 % of all whistle production in the wild (Buckstaff 2004; Cook et al. 2004; Watwood et al. 2005). The role of non-stereotyped whistle emissions is still unclear.

The identification of stereotyped and non-stereotyped whistles and their context of emission in wild populations is a critical step towards a better understanding of such distinctive calls. However, to single out signature whistles in free-ranging dolphin groups can be challenging given the difficulty of pinpointing the emitters of each call. The recently proposed signature identification (SIGID) method for bout analysis has proved to be effective in the identification of signature whistles in field recordings of bottlenose dolphins (Janik et al. 2013; King and Janik 2013; Kriesell et al. 2014). Additionally, the use of the photo-identification technique in small groups of dolphins has been proposed as a possible strategy to identify the whistling animals (Lima and Le Pendu 2014).

In the Sado estuary (Portugal), the acoustic behaviour and the social structure of a well-known small resident group of approximately 30 bottlenose dolphins has been studied for more than two decades (Augusto et al. 2012; dos Santos et al. 1995) and the occurrence of stable stereotyped whistles has been previously reported (dos Santos et al. 1990; dos Santos et al. 2005).

In this study, we investigate the effects of activity pattern and group size on the emission rates of stereotyped and non-stereotyped whistles. Furthermore, we positively identify signature whistles for the first time in this population, using the SIGID method (Janik et al. 2013), and document the long-term occurrence of stable stereotyped contours.

Methods

Field recordings were made in the Sado estuary, Portugal, and adjacent coastal waters (approximate location of the Sado mouth is 38° 29′ N, 8° 55′ W).

All data were collected from an 8.40-m-long inboard motorboat during daylight hours (1000 to 1800), from April 2011 to October 2014 with sea state ranging from 0 to 3 Beaufort. Whenever a group of dolphins was detected, and after a 15-min habituation period, the boat was positioned approximately 500 m ahead of the group's position, with the engines and all boat devices turned off, and the hydrophone was placed at a depth of at least 3 m. Acoustic samples were collected for periods of time that lasted from 1 to 10 min (mean duration=1.50 min±0.98), when the animals were within a 500-m radius.

Acoustic measurements were carried out using a factory-calibrated recording system: a Cetacean Research Technology hydrophone, model C55 (effective sensitivity of −165 dB re 1 V=1 μPa, frequency response of ±3 dB in the 0.020- to 44-kHz band and +3/−13 dB in the 0.009- to 100-kHz band, polarized by a 9-V battery) connected by a 15-m cable to a Fostex FR-2 digital recorder. High-pass filter at 100 Hz was chosen to avoid self-noise generated by the recording platform and low-frequency vibrations. Recordings were made, at a sampling rate of 192 kHz and with a 24-bit resolution, with the recording level fixed at the calibrated settings and the trim level at −26 dB. All recordings were stored on Compact Flash memory cards as time-stamped wave files. The geographic location of each recording was given by a Garmin Foretrex 301 portable GPS.

Photographs of surface behaviour and dorsal fins were collected with a digital Nikon D70S and/or a Canon EOS 400D (both with 70–300-mm zoom lenses).

Behavioural context was ascribed according to the following categories (based on Dos Santos et al. 2005): (1) travelling—linear position of a tight group moving between areas, with no aerial behaviours; (2) foraging/milling—zigzag movements of a subdivided group, occasionally with dives longer than 1 min and aerial activity; (3) surface feeding—spread out individuals, groups surfacing more than 10 m apart, with only very short dives and abundant movements at the surface, including captures, prey leaping or prey toss; and (4) social interactions—active surface and aerial behaviours, with physical contacts and no prey detectable, sometimes with synchronous movements.

Resting behaviour, with the animals floating at the surface in tight units, was also observed in four occasions, but these samples were excluded from the analyses.

Group size was estimated by direct counting of the animals by two observers and subsequently averaging the counts. Group composition was determined by photo-identification techniques and using the photo catalogues of the Sado population (see www.projectodelfim.pt).

Additional data

For the whistle classification task and long-term stability assessment, the whistles' categories created in 1990 and 2005 were used. Details of the recording equipment and methodology are given in dos Santos et al. (1990, 2005).

Acoustic analyses

For acoustical analyses, only recordings with no vessels within a 2-km radius of the dolphin groups were considered. In order to identify, categorize and count all the vocal elements present in each sample, recordings were first inspected by two trained independent observers, aurally and visually, using Adobe Audition CS5.5 (Adobe Systems Inc., San Jose, CA) with Hamming windows of 512 points. Tonal, narrow-band, modulated signals were classified as "whistles" and selected for further analyses.

Spectrograms of all whistles with clear and complete frequency modulation contours were plotted and labelled using Raven Pro 1.4 (Cornell Lab of Ornithology, Ithaca, NY) with Hann windows of 512 points and a frequency resolution of 93.8 Hz and 50 % overlap.

Whistles were then classified according to their fundamental frequency contour, using visual classification (a reliable method, broadly used in animal communication studies, see Janik 1999) based on key frequency modulation aspects: start and end frequency and inflection points.

The first step of the classification process was to identify whistles with stable contours that occurred repeatedly in our dataset, which were classified as stereotyped whistles (SW). The remaining whistles, with variable contours, were classified as non-stereotyped whistles (NSW).

Secondly, each SW was compared with templates of known whistle types present in a catalogue of stable whistle contours recorded in the Sado region since 1987 (dos Santos et al. 1990, 2005). Whenever a whistle matched a known category, it would be classified as such. For whistles that could not be assigned to any of the categories present in the catalogue, new mutually exclusive categories were created.

Whistle classification was independently carried out by three experienced observers and subsequently discussed and cross-validated.

The SIGID method (Janik et al. 2013) was adopted in order to identify signature whistles. For each SW category, the whistles' emission sequence was analysed and inter-whistle interval measured. If 75 % or more of the whistles in each category occurred within 1 to 10 s of each other, that category would be positively identified as a signature whistle. The SIGID criteria were only applied in categories with at least five whistles.

Statistical analyses

For the analyses of whistle occurrence, emission rates were obtained by dividing the number of whistles by the number of minutes of each sample and by group size. Correlations between group size and the emission rates were calculated (Pearson product-moment correlation).

Lilliefors (Kolmogorov-Smirnov) tests were used to test for normality, and Levene tests were used to test for homogeneity of variances. A Mann-Whitney *U* test was performed to compare the emission rate of SW and NSW.

Kruskal-Wallis tests were performed to compare the emission rate according to the behavioural state identified during sampling ("surface feeding", "foraging/milling", "social interactions" or "travelling"). Post hoc tests for pairwise comparisons were used to identify the main differentiating activities (Dunn tests for SW and NSW).

All statistical analyses were performed using IBM SPSS Statistics 21 (IBM Inc.).

Results

From the acoustic signals collected from 2011 to 2014, a total of 1715 whistles were extracted for further analyses (see Table 1).

Of all the selected whistles, 32 % were clearly identified as stereotyped whistles (SW = 550 whistles). The remaining 1165 whistles presented variable frequency-modulated contours and were considered non-stereotyped whistles (NSW).

The whistles classified as SW were ascribed to 27 contour categories (Table 2). The SW categories exhibit long-term stability: whistle types "AP", "CA1" and "KE" were recorded during the three periods of data collection (see Fig. 1), and 11 other whistle types were previously identified in the 1990s. The 13 new contour categories comprise 51 % of all SW whistles recorded from 2011 to 2014.

The SIGID criteria for bout analysis (Janik et al. 2013) allowed a positive identification as signature whistles of 12 stereotyped whistle types in our dataset (Fig. 2).

Table 1 Summary of data collection

Data collection	Sample size (N)	Recordings (min)	Extracted whistles (N)
April to November 2011	127	164	923
April to August 2013	84	116	274
March to October 2014	72	123	518

Emission rates

Although the number of animals present during recordings varied between 2 and 24, no correlation was found between the group size and the emission rate of whistles ($r_{\mathrm{P}}=-0.068$, $N=271$, $P=0.271$).

The mean overall whistle rate recorded in the Sado estuary was 0.56 whistles/min/dolphin. Non-stereotyped whistles were more abundant than stereotyped whistles in our recordings (68 % of all the good-quality whistles), and significant differences were found when comparing their emission rates (SW—0.15 whistles/min/dolphin; NSW—0.41 whistles/min/dolphin; Mann-Whitney U test: $U=46\,348$, $N=541$, $P<0.01$).

Activity patterns

For both stereotyped and non-stereotyped whistles, the lowest emission rates were observed during “travelling” (SW=0.09 whistles/min/dolphin, NSW=0.2 whistles/min/dolphin).

Table 2 Contour types classified as stereotyped whistles (SW) and identified as signature whistles

	1987 and 1988 (dos Santos et al. 1990)	1992 and 1999 (dos Santos et al. 2005)	2011–2014 (this study)	Whistles with a bout interval of 1–10 s (SIGID criteria)
AP[a]	•	•	•	80 %
AP3		•	•	NA
CA1	•	•	•	44 %
CA3		•	•	68 %
CA4[a]		•	•	80 %
CE[a]		•	•	85 %
CM[a]		•	•	82 %
CM2[a]			•	78 %
CM3[a]			•	100 %
CM4			•	50 %
CO		•	•	30 %
DE[a]		•	•	90 %
DS			•	44 %
HP[a]			•	92 %
KE[a]	•	•	•	79 %
LE			•	73 %
MC		•	•	60 %
ME[a]			•	83 %
ME2			•	57 %
RA[a]		•	•	76 %
SO2			•	25 %
UL			•	50 %
UP			•	59 %
US		•	•	65 %
VU		•	•	NA
VU2[a]			•	87 %
WA			•	44 %

Following the SIGID criteria, whistles with more than 75 % of its occurrence within 1–10 s of each other were positively identified as signature whistles

[a] Signature whistles

• Whistle type identified a in the dataset

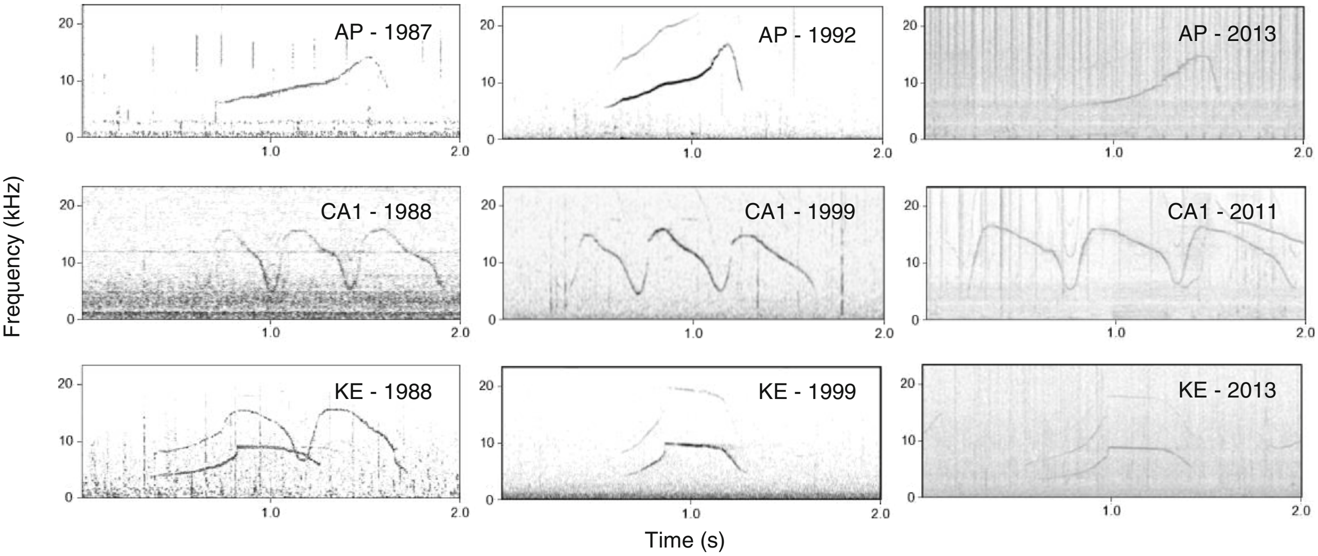

Fig. 1 Representative spectrograms of long-term stability in stereotyped whistles recorded in the Sado region, Portugal

Significant differences were found in the emission rates of both stereotyped and non-stereotyped whistles according to the activity patterns (SW—Kruskal-Wallis test: H_3=19.072, P<0.01, N=272; NSW—Kruskal-Wallis test: H_3=39.744, P<0.01, N=269).

For the stereotyped whistles, the highest emission rates were obtained during "social interactions" (0.29 whistles/min/dolphin). Pairwise comparisons revealed significant differences between "surface feeding" and "travelling" (P<0.01) and "foraging/milling" and "travelling" (P=0.019) (Fig. 3).

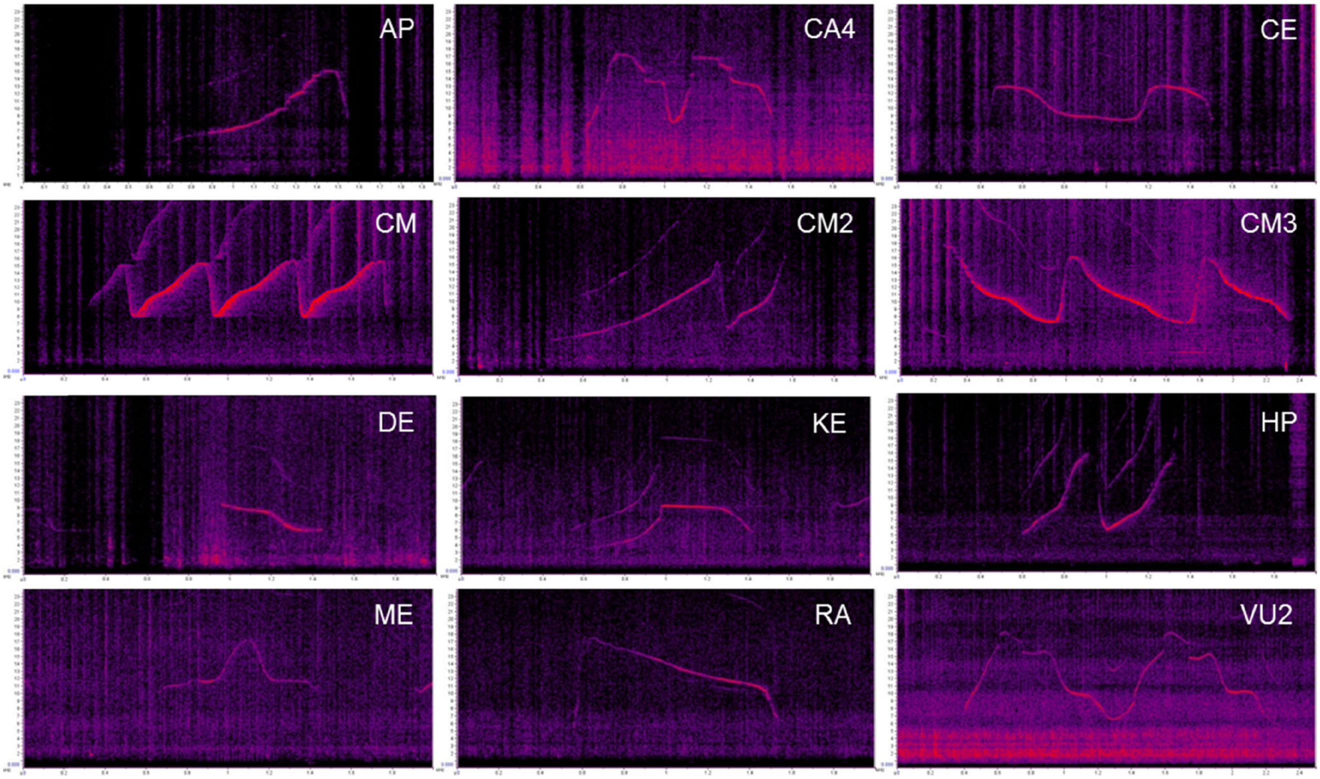

Fig. 2 Stereotyped whistle contours positively identified as signature whistles using the SIGID method. Spectrograms with 512-point Hann windows and a frequency resolution of 93.8 Hz

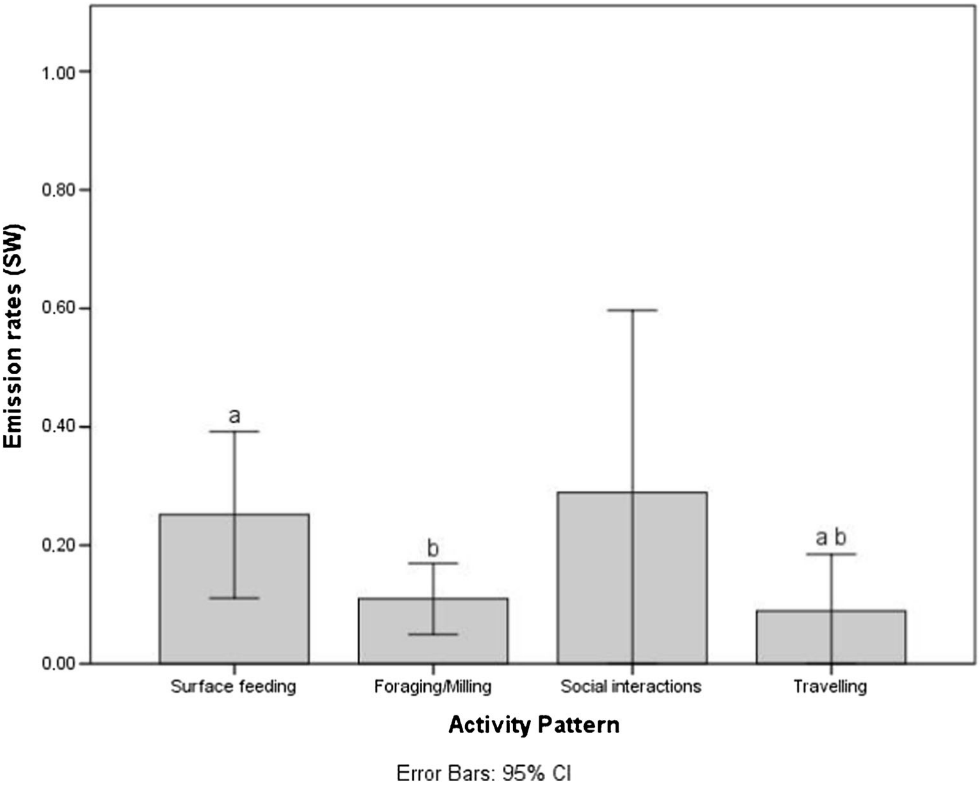

Fig. 3 Emission rate (whistle/min/dolphin) of stereotyped whistles according to the activity pattern. Significant differences: "surface feeding" and "travelling" (*a*) and "foraging/milling" and "travelling" (*b*). *Error bars* 95 % CI

For non-stereotyped whistles, the highest emission rates were recorded during "surface feeding" (0.61 whistles/min). Pairwise comparisons revealed significant differences between "surface feeding" and "travelling" ($P<0.01$) and "foraging" and "travelling" ($P<0.01$) (Fig. 4).

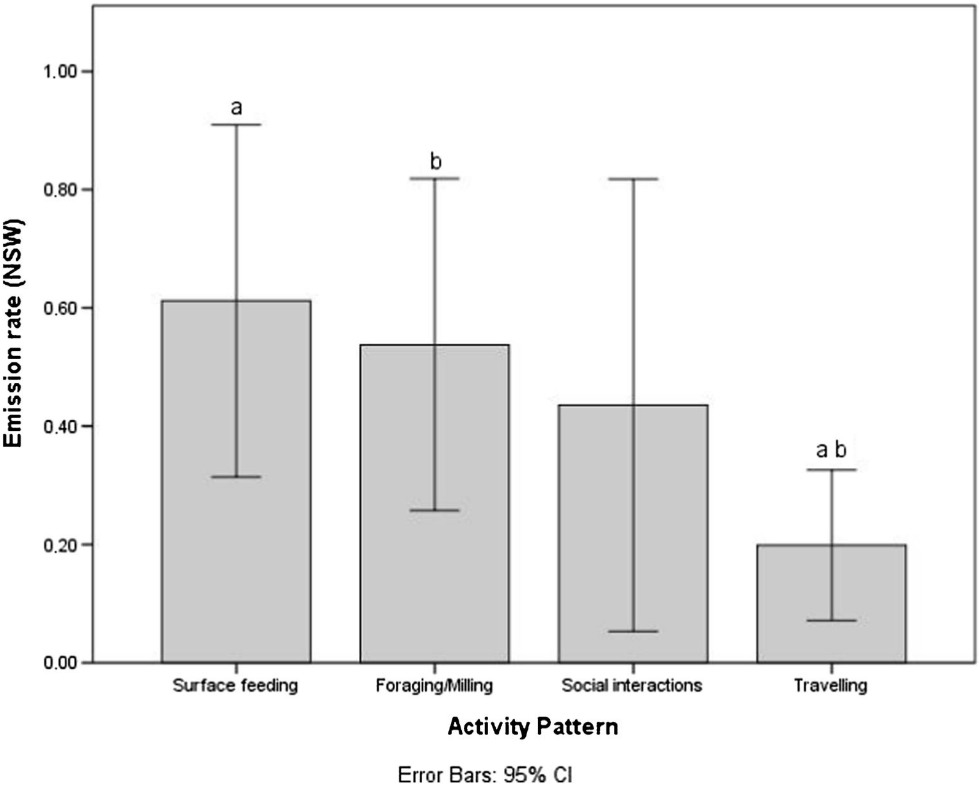

Fig. 4 Emission rate (whistle/min/dolphin) of non-stereotyped whistles according to the activity pattern. Significant differences: "surface feeding" and "travelling" (*a*) and "foraging/milling" and "travelling" (*b*). *Error bars* 95 % CI

Discussion

Long-term occurrence of stereotyped whistles

Long-lasting, acoustically stable signals have been indicated as fundamental units for long-term individual recognition in socially complex societies (Bruck 2013; Jouventin and Aubin 2002; Pitcher et al. 2010). In this study, we document the decades-long occurrence of whistles with stereotyped frequency contours in the resident population of bottlenose dolphins from the Sado region (first recorded in 1987 and 1988, see dos Santos et al. 1990). In a context of considerable frequency contour variability, a number of stable contours were maintained during more than two decades, highlighting the importance of stereotyped whistles in the acoustic repertoire of these free-ranging dolphins. These stable acoustic signals likely serve as individual identity labels that enable long-term social recognition, as suggested by Bruck (2013) and Sayigh et al. (1990).

In our analyses, the occurrence of well-defined stereotyped contours represents approximately one third of all whistle emissions, a figure close to the lower limit documented for the occurrence of signature whistles in other studies (Buckstaff 2004; Cook et al. 2004; Watwood et al. 2005).

Despite the long-term occurrence of several stereotyped whistle types, only 12 contours were positively identified as signature whistles using the SIGID criteria. As its proponents admit, the SIGID criteria are conservative and therefore can miss out about half of the signature whistles in an emission dataset (Janik et al. 2013). Thus, the number of signature whistles in this population may well be underestimated.

It should be noted that during the sampling period, the resident population consisted of 27 individuals (the exact number of observed stereotyped whistle contours). Interestingly, 13 of the individuals in the current population were already present in 1999 (the exact number of stereotyped whistle contours then identified and still observed). Hence, it is possible that all the identified stereotyped whistles are, in fact, individual signature whistles.

Emission rates

The overall whistle production in the Sado estuary was slightly higher than the majority of the emission rates reported for other populations (Cook et al. 2004; Díaz López 2011; Jones and Sayigh 2002; Quick and Janik 2008; Watwood et al. 2005). In small resident populations, lower whistle rates have been explained by the familiarity between group members and habitat characteristics (e.g. Jones and Sayigh 2002). In Sado, despite the small size, the known stability of the population and its residency patterns (Augusto et al. 2012), that was not the case. As suggested by several authors (Buckstaff 2004; Esch et al. 2009), increase in the overall emission rate may be related to environmental disturbance. Thus, in areas with persistent human pressure, such as the Sado estuary (Luís et al. 2014), high levels of whistle emission might be an adaptive response that promotes group cohesion in the presence of multiple stressors (e.g. boat traffic, fishing activities).

For species that live in complex societies, the number of recorded calls often correlates positively with the number of individuals present during a sampling period (Borker et al. 2014; Hofmeyr-Juritz and Best 2011; Payne et al. 2003; Radford and Ridley 2008). That pattern has been previously reported for bottlenose dolphins (Jones and Sayigh 2002) but does not occur in all populations (dos Santos and Almada 2004; dos Santos et al. 2005; Quick and Janik 2008). In this study, high levels of whistle rates were observed both for small and larger groups, with the number of whistles per dolphin decreasing as the group size increases. Similar results have been previously reported for the Moray Firth population (Quick and Janik 2008). Environmental conditions, such as high levels of background noise, may be related to this particular pattern. In a noisy habitat, like the Sado estuary, each individual may limit its vocal emissions as the group size increases to avoid overlapping and facilitate an optimal transmission of the emitted signals, especially if a high number of communication calls are produced. It might also be a socially transmitted, variant pattern found in some populations, possibly improving communication efficiency as the group size increases.

Activity patterns

Emission rates of both stereotyped and non-stereotyped whistles varied with ongoing dolphin activities, as found in other studies of wild bottlenose dolphin populations (Acevedo-Gutiérrez and Stienessen 2004; Cook et al. 2004; Jones and Sayigh 2002; Díaz López and Shirai 2009; Quick and Janik 2008).

The lowest whistle rates were obtained during “travelling”. In fact, for approximately half of our “travelling” samples, whistle rates were zero regardless of group size. Due to its hydrographic and physiographic features, the Sado estuary is a challenging navigation area where echolocation and passive vigilance may be more important than communication during “travelling”, especially when the groups are moving in or out. Further studies should address the role of environmental variables such as depth, estuary width and bottom topography in whistle production.

Regarding specifically stereotyped whistles, the highest emission rates were obtained during “social interactions”. Several studies have reported higher rates of whistle emission during socialization, as a consequence of increased arousal or to maintain contact with other group members away from the interaction (Cook et al. 2004; dos Santos et al. 2005; Quick and Janik 2008). In the Sado estuary, social interactions occur in small groups as short sporadic events that include synchronized leaps and physical contact. Considering the strong social bonds between the individuals that compose this small, stable, resident population, the high emission of stereotyped whistles during social interactions could be seen either as affiliative, indicating a motivation to reunite or an "invitation" for other animals to join the social event, or signaling aggression.

Emission rates of stereotyped whistles were significantly higher during "surface feeding" and "foraging/milling". Recent studies highlight the role of synchronous calling during cooperative behaviour (Herzing 2015; King and Janik 2015). Furthermore, the matching of signature whistles has been presented as a regulator of individual spacing during intensive feeding bouts (King and Janik 2015). At our study site, surface feeding episodes are mostly cooperative, aroused events that include prey herding. It should also be noted that in the Sado estuary, visibility is usually reduced to less than 5 m. Following the "ranging hypothesis" (Hopp and Morton 1998), a higher emission rate of stereotyped whistles may be explained by the need of knowing the exact location of each individual during a coordinated hunting activity.

Despite the relevance of stereotyped whistles in the acoustic communication of bottlenose dolphins, we must emphasize that non-stereotyped whistles represented 68 % of all the analysed whistles and the role of such calls is still unclear. Alarm calls and food-related calls are among the most common acoustic signals produced by mammals and birds (Clay et al. 2012; Hollén and Radford 2009). In our study, emission rates of non-stereotyped whistles were significantly higher during "surface feeding" and "foraging/milling", suggesting a possible role of these signals as food-related cues or they may just signal an aroused context. Given the observed excitement during feeding events, non-stereotyped whistles could be simply expressions of emotion. Nonetheless, these signals may also provide information regarding food location, quantity and/or quality, as it has been reported for other species that live in complex social groups, such as ravens and chimpanzees (Clay et al. 2012). Further studies are needed to fully unravel the detailed function of non-stereotyped whistles and their relevance in the acoustic repertoire of bottlenose dolphins.

In conclusion, stereotyped whistles of bottlenose dolphins clearly have a special role as stable signature calls, with key relevance during events that require group coordination, such as feeding and foraging. Such identity labels are critical for long-term social recognition and social memory, facilitating cooperation and differential affiliation patterns based on past interactions. The decades-long occurrence of several whistle contours in this population seems to support this notion.

Although non-stereotyped whistles are particularly abundant in food-related events, their specific roles require further research.

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