Chapter 5

MEDITERRANEAN COMMON BOTTLENOSE DOLPHIN'S REPERTOIRE AND COMMUNICATION USE

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ABSTRACT

Bottlenose dolphins are an extremely vocal mammalian species and vocal communication plays an important role in mediating social interactions. This study carried out year round from 2005 to 2008 represents the first attempt in the Mediterranean basin to outline the repertoire, production rates of social sounds, and associated behavior of Mediterranean bottlenose dolphins. Data were collected as part of a long term study, in which acoustic recording and behavioral observations (from surface and underwater) were made. Over the 4-year study period, 25 months were spent in the field and the dataset consisted of 35 hours of dolphin observations and simultaneous recordings. The acoustic repertoire observed in this study was extremely diverse. Bottlenose dolphin communication sounds ranged from soft and melodic sounds to harder, almost harsh sounds. The results, showing that vocal emission increased, especially in those activities involving excited depredation or socializing, confirmed that activity and social signals production were related. Moreover, the fact that was observed a positive relation between group size and the production of social signals, confirms that dolphin vocalizations are used for communicative and social purposes. My findings on social signals emission also suggest that burst pulses vocalizations probably play an equally important social signaling role as do tonal sounds. Particularly, "long burst pulsed sounds", in agonistic interactions like those observed during depredation, could be used with the intent to settle rank conflicts and avoid competition between group members. This study also gathered evidence to support the use of whistles as contact calls between mother and calf pairs of dolphins. Although many of these vocalizations have been described in the literature, their association with specific behaviors provides additional contextual information about their potential use as communication signals.

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INTRODUCTION

Bioacoustics research provides important insights into animal behavior. Communication was defined as consisting of exchanges of information between a sender and a receiver using a code of specific signals that usually serve to meet common challenges (e.g. reproduction, foraging) and in group living species, to promote group cohesiveness (Vauclair, 1996). Many animals communicate specific messages accompanied by additional information about their motivation, sex, age, or even their identity (Halliday, 1983). During acoustic communication, an animal transmits information to other individuals using sound signals and thus attempts to influence the behavior of these individuals to its own advantage (Dawkins and Krebs, 1978; Slater, 1983).

Dolphins (family: Delphinidae) are an extremely vocal mammalian family and vocal communication plays an important role in mediating social interactions. Most studies of delphinid vocalizations have concentrated on bottlenose dolphins, *Tursiops truncatus* and *T. aduncus* (e.g. Lilly and Miller., 1961; dos Santos et al., 1990; Smolker et al., 1993; Janik et al.; 1994; Connor and Smolker, 1996; Janik and Slater, 1998; Sayigh et al., 1999; Lammers et al., 2003; Boisseau, 2004; dos Santos et al., 2005).

Classification techniques of the vocal repertoire of dolphins have suffered from nomenclature difficulties (Herzing, 2000). Most dolphin species can produce two primary types of sounds thought to play a role in social interactions: (i) tonal, frequency-modulated whistles, and (ii) rapid repetition rate "burst-pulse" click train (Herman and Tavolga, 1980; Popper, 1980; Schultz et al., 1995; Herzing, 2000; Boisseau, 2004). Whistles are tonal signals that appear to play an important role in maintaining contact between dispersed individuals (McCowan and Reiss, 1995a, Janik & Slater 1998; Janik, 2000a; Acevedo-Gutiérrez and Stienessen, 2004; Watwood et al., 2004; dos Santos et al., 2005). Burst pulsed sounds comprise the majority of conspecific vocalizations, but have received much less attention because they are recorded far less frequently than whistles and thus require high levels of field study effort to build up large samples (Herzing, 2000; Lammers et al., 2003; Boisseau, 2004). These sounds have also been strongly implicated in communication (Caldwell and Caldwell, 1967; McCowan and Reiss, 1995b; Herzing, 2000; Lammers et al., 2003; Boisseau, 2004). Some authors have suggested they are related with courtship, dominance, and/or aggressive behaviors in the same species (Overstrom, 1983; Schultz, 1995; Connor and Smolker, 1996; Veit, 2002), but their occurrence and functional significance are still only poorly understood.

Bottlenose dolphins live in complex fission-fusion societies where communication provides a template for members of a group to gain information about each other in order to interact more effectively (Smolker et al., 1992; Connor et al., 2000). Intraspecific cooperation and high rates of information transfer in highly social species in a changing environment is vital to species success. As the complexity of bottlenose dolphins' social organization is only matched by few species (Connor et al., 2000), their communication system merits a profound investigation, despite the many methodical difficulties that are inherent to their aquatic life.

It was determined that vocalization rates are dependent on a dolphin's behavior, with feeding and socializing having the highest vocalization rates (Jones and Sayigh, 2002; Acevedo-Gutiérrez and Stienessen, 2004; dos Santos et al., 2005). Even with a wealth of

information about bottlenose dolphin vocal behavior, there is a little mention of production rates and the use of conspecific social signals in the wild.

This study represents the first attempt in the Mediterranean basin to outline the repertoire, vocal production, and associated behavior of Mediterranean free-ranging bottlenose dolphins. These dolphins have been the focus of a long term study along the north-eastern coast of Sardinia (Italy). The study area provides a unique opportunity to study vocal production of wild bottlenose dolphins because on a year-round, daily basis, groups of dolphins tend to follow predictable spatial patterns foraging and socializing onshore. Additionally, human activities influence the distribution of food resources and dolphins behavior (Díaz López, 2006a,b; Díaz López, 2009), which promote the evolution of social organizations (Díaz López and Shirai, 2008) and individual preferences for the area (Díaz López and Shirai, 2007).

The aims of this study are: (i) to quantify and describe the entire vocal repertoire of these resident bottlenose dolphins, (ii) to examine the behavioral context in which specific social signals are produced, and (iii) to analyze the vocal production rates according to group size and presence of mother-calf pairs within the group.

METHODS

Data Collection

The data analyzed for this study were collected from resident free-ranging bottlenose dolphins in the north-eastern waters of Sardinia (Italy) from 2005 to 2008 (Figure 1). Data were collected as part of a long term study, in which acoustic recording and behavioral observations were made year round. These bottlenose dolphins have been under study since 1991; they are well habituated to human observers and can be recognized individually.

Surveys for dolphins were conducted from a 5-m research vessel, with a 40-hp Yamaha outboard engine. Leaving the harbor, a predefined course was followed until a group of dolphins was sighted. During focal observation sessions selected focal groups were observed for extended periods, often the course of several hours. During this study, we distinguish the term group as either a solitary animal or any aggregation of dolphins in the visual area, usually involved in the same activity, following Díaz López (2006b). The encounter continued until the group was lost; a group was considered lost after 15 min without a sighting (Díaz López, 2006b).

The group size was assessed visually *in situ*, and the data were later verified with photographs and videos taken during each sighting. Observations were considered satisfactory when the visibility was not reduced by rain or fog, and sea conditions were < 3 on the Douglas sea force scale (approximately equivalent to the Beaufort wind force scale). In each encounter, individuals were identified *in situ* based on natural marks, nicks, scars, or unique skin pigmentations on the dorsal fin and surrounding area (Würsig and Jefferson, 1990). Photographs and video recordings were also used to document and verify visible surface and underwater activities. Underwater observations with snorkel gear aided in behavioral sampling.
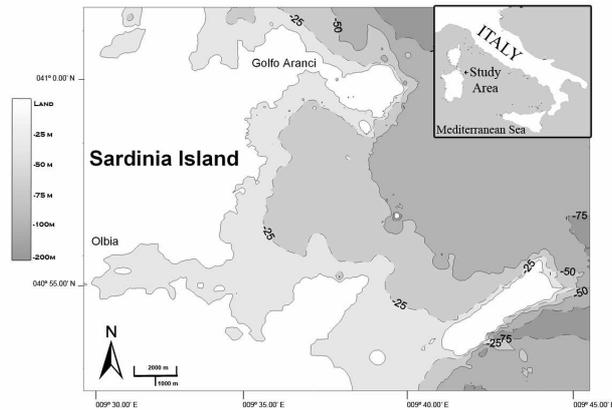
Figure 1. Map of the study area along the north-eastern coast of Sardinia (Italy).

Calves were defined as dolphins two thirds or less the length of an adult they consistently swam beside and slightly behind (Shane, 1990). Adults were those estimated to be longer than 2.5m (Diaz Lopez, 2006a).

In each survey, the first recording sample was collected at least 20 minutes after the initial sighting to allow the dolphins time to habituate to our presence, and no other cetacean species or dolphin group were observed in the vicinity. To record dolphin sounds and behavior, we stationed the vessel within 2 - 50 m of the periphery of the group with the engine off and lowered a hydrophone to a depth that varied between 7 - 9 m.

We used an omni-directional hydrophone, with a frequency response of 0.02 - 100 kHz connected to a preamplifier. Dolphin signals were digitally sampled using a professional 2-channel mobile digital recorded (M-Audio) at a rate of 44 kHz and 16 bites, providing a maximum frequency for all recordings of 22 kHz. This maximum frequency is suitable for detecting and recording most bottlenose dolphin social signals (although not suitable for complete documentation of echolocation clicks and some broadband pulses) (Herzing, 2000; Boisseau, 2004).

Acoustic recordings were collected continuously during focal group observations and monitored via headphones for quality assurance. Observations of surface behavior of dolphins were narrated onto one channel while the hydrophone was recorded simultaneously onto the other channel. Behavioral data were collected using focal group continuous sampling (Altmann, 1974), although during underwater observations was used "*ad libitum*" sampling (Altmann, 1974) to record the dolphins' activity. The more detailed descriptions of underwater behavior and events were later compared with the commentary on the acoustical recording.

Observed behaviors were divided into "predation", "depredation", "traveling" and "socializing". As used herein, predation refers to dolphins preying on free-ranging prey, whereas depredation refers to bottlenose dolphins taking, or attempting to take, prey that are confined in fish farm cages (Díaz Lopez, 2006a, 2009, Figure 2) or that have been caught in fishing nets (Diaz Lopez, 2006b). Traveling involved swimming on a consistent course, with all the members of the group generally spaced within a few body lengths of each other, with rhythmic surfacings followed by shallow dives. Socializing animals were involved in active

surface and underwater behavior that included interactions with other group members (body contact, erection, charge, slapping, intromission, petting, etc.) and aerial activity.

The definition and duration of each behavioral category was attempted *a posteriori* following data analysis strictly based on objective, non-discrete parameters, including specifically observed behavioral events, area, dive duration, swimming direction and speed, contact among individual dolphins, presence of fishing gears, and other variables (Díaz López, 2006b). Units of behavior (events) transcribed included tail stock dive, regular dive, flukes up dive, fast surfaces, body contact, chasing fish, breaching, leaps, slapping, belly up, floating, erection, defecation, charge, petting, belly to belly, biting nets, and rolling.

Figure 2. Bottlenose dolphin attempting to take fish confined in a fish farm cage.
(Photo: Díaz López, B.)

Vocal Repertoire Qualitative Analyses

The acoustic recordings were played back on a PC computer as spectrograms and waveforms using SPECTOGRAM 6.2.3 program. A 1024-point Hamming window was used to plot all sonograms. We set frequency resolution at 43.1 Hz, the display frame duration was 3 ms, and the dynamic range was -90 dB.

We identified communication signal types based on visual and aural analysis. This simultaneous visual and aural monitoring allowed for a more complete analysis of the recordings; weak sounds could be categorized with spectrographic images and faint images with aural inputs (Acevedo-Gutiérrez and Stienessen, 2004).

Two additional lines of evidence make us nearly certain that these sounds were produced by bottlenose dolphins. First, the amplitude of these sounds corresponded closely to the proximity of individuals; in particular, the highest-amplitude sounds always occurred with bottlenose dolphins alongside our boat position. Secondly, throughout the entire study period, these distinctive sounds were never detected in the absence of bottlenose dolphins. We were unable to ascertain which dolphin produced a sound; thus, for this study, we employed the inclusive definition of a dolphin focal group to account for all individuals producing sounds.

Because vocal repertoire of bottlenose dolphins varied from acoustically simple to complex, social signals were initially divided into three acoustic structural categories based in the shape of the spectrogram and signal duration. This classification was based in part on previously reported categories (Boisseau, 2004) and partly on arbitrary interpretation: "tonal signals", "short burst pulsed vocalizations" (impulsive emissions shorter than 200ms with most energy below 5 kHz), and "long burst pulsed vocalizations" (single or a sequence of pulses longer than 200ms). Even though qualitative categorization of this kind is arbitrary, it allows a reduction of the acoustical data. Although characteristics within the same signal category varied slightly, this variation was generally small compared with those among different social signal categories.

Within these three categories, signal types were transcribed by noting the date, time, and the type of vocalization. Afterwards, a group size and a behavioral category were assigned to each vocalization type as a result of the photo-identification and behavioral analysis respectively.

Statistical Analysis

The duration of a recording can influence the total number of sounds for that sample. It is expected that the positive correlation between the two will decrease as sample time increases. Partial correlations were calculated between the sampling duration and number of social signals in order to determine threshold where the correlation was no longer significant. All samples beneath the threshold were discarded.

For the analysis of the signals production, emission rates were calculated, dividing the total number of social signals counted by the number of minutes recorded.

We hypothesized that social signal production would vary with behavioral activity. To test this hypothesis we used discriminant function analyses. Discriminant function analysis identifies a linear combination of quantitative predictor variables that best characterize the differences among groups. For the purposes of this study, discriminant analysis was used in a descriptive sense for revealing major acoustic differences between the groups. Variables are combined into one or more discriminant functions. Based on these discriminant functions, the classification procedure assigns each vocalization to its appropriate group (correct assignment) or to another group (incorrect assignment). The larger the standardized coefficients for each type of sound in each discriminant function, the greater the contribution of the respective type of sound to the discrimination between groups. To follow the assumptions of the discriminant analysis the predictors were Log_{lo} transformed and the residuals were examined. Equality of the means of the groups was tested by a multivariate analysis of variance MANOVA.

The Kruskal Wallis test was performed on data to test the equality of medians of several univariate samples (Zar 1998). If the test shows significant inequality of the medians, a Tukey's post-hoc contrast was performed. The Spearman rho non parametric rank-order test was used to test for correlation between variables.

All the statistical tests and mathematical analysis were performed with PAST (Hammer et al., 2001) software package. Statistical significance was tested at the $P < 0.05$ level. The data are presented as means $\pm$ SE .

RESULTS

Over the 4-year study period, 25 months were spent in the field and the dataset consisted of 35 h of observations and simultaneous recordings. Vocal production and recording length were significantly correlated (Spearman' s rho correlation $r = 0.47$, $P < 0.001$, $n = 343$) up until 9 minutes in length. As such, 220 acoustical recordings greater than 9 minutes in length were used for the remaining analysis and 123 short recordings were therefore discarded (remaining samples: Spearman's rho correlation $r = 0.18$, $P = 0.14$, $n = 220$). The mean duration of the selected acoustical recordings was 18.9 ± 1.6 min.

Vocal Repertoire of Free-Ranging Bottlenose Dolphins

From the selected 220 acoustic recordings, 7713 separate vocalizations were categorized aurally and visually into three structural categories "tonal" (3503 vocalizations), "short burst pulsed vocalizations" (1748 vocalizations), and "long burst of pulses" (2462 vocalizations).

Within these three classes, 14 signal types were transcribed based in part on previously reported vocalizations and partly on novel interpretation (Figure 3): creaks (Lilly and Miller, 1961), screeches (dos Santos et al., 1995), buzzes (Herzing, 1996), chokes (Boisseau, 2004), gulps (dos Santos et al., 1995), coughs (Boisseau, 2004), yelps (Wood, 1953), quacks (Lilly and Miller 1961), pops (Connor and Smolker, 1996), brays (dos Santos et al., 1995), croaks, cries, twitters and whistles (summaries in Herzing, 2000).
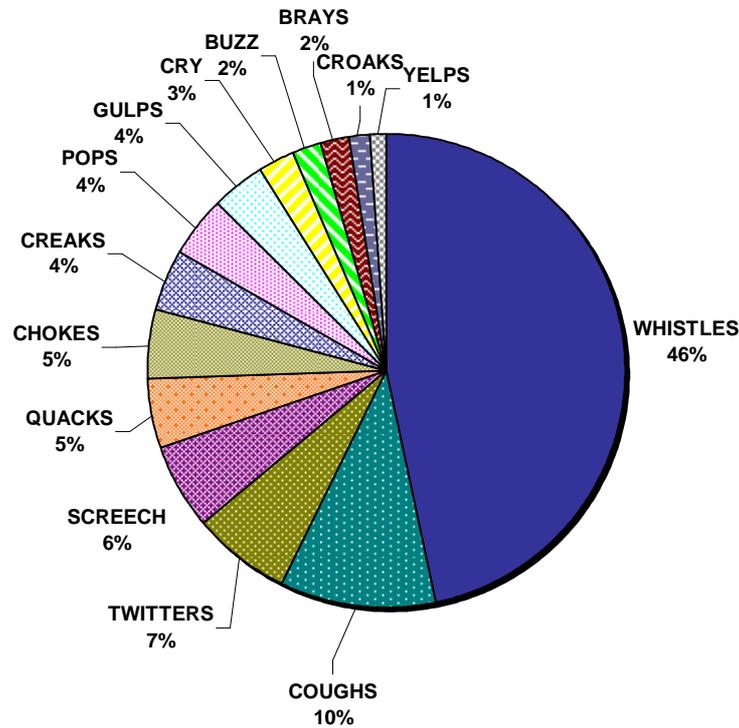
Figure 3. Proportions of social signals recorded in various contexts during focal group sampling.

"Tonal sounds" were the most frequent vocalizations given by bottlenose dolphins. Results from visual classification showed that this class could be divided into two separate types: whistles and twitters. Whistles are the most common vocalization (3072 vocalizations), they are long (longer than 200 ms) and have most energy between 4 and 23 kHz (Figure 4). Twitters are less frequent (431 vocalizations), they are short (usually less than 200 ms), and of lower frequency (most energy below 4 kHz, Figure 5).
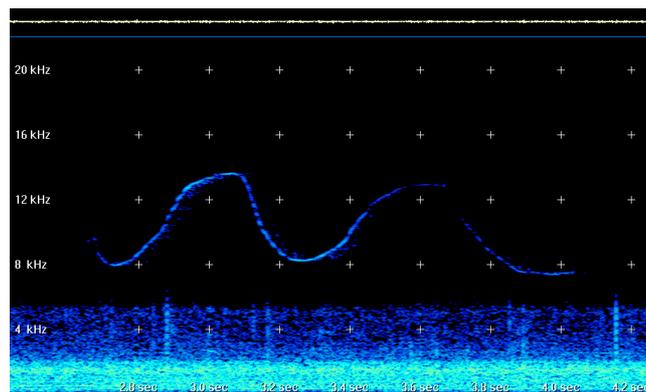

Figure 4. Spectrogram and waveform of bottlenose dolphin's whistle recorded in Sardinia (Italy). FFT = 1024, display frame duration = 2 ms.
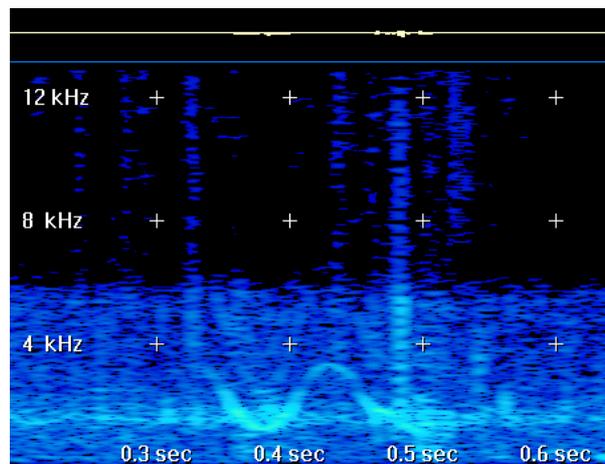
Figure 5. Spectrogram and waveform of bottlenose dolphin's twitter recorded in Sardinia (Italy). FFT = 1024, display frame duration = 1 ms.

The rest of the proposed repertoire are burst pulsed vocalizations. In the "short burst pulsed sounds" class are single burst intrinsically short (less than 200ms) (Figure 6). Within this class, 6 different signal types were detected: chokes, gulps, coughs, brays, quacks, and croaks. The remaining vocalizations are the "long burst pulsed sounds" class, these are the longest social signals in the proposed repertoire (longer than 200ms) and they are composed of a single or a sequence of pulses (Figure 7). Within this class, 6 different signal types were detected: buzzes, creaks, screeches, yelps, pops, and cries.
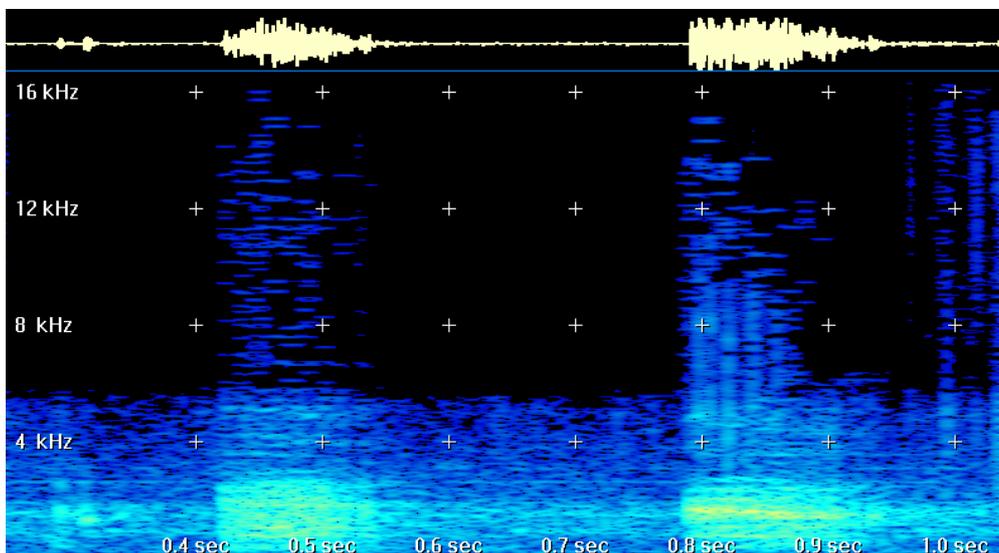

Figure 6. Spectrogram and waveform of bottlenose dolphin's "short burst pulses" recorded in Sardinia (Italy). FFT = 1024, display frame duration = 1 ms.
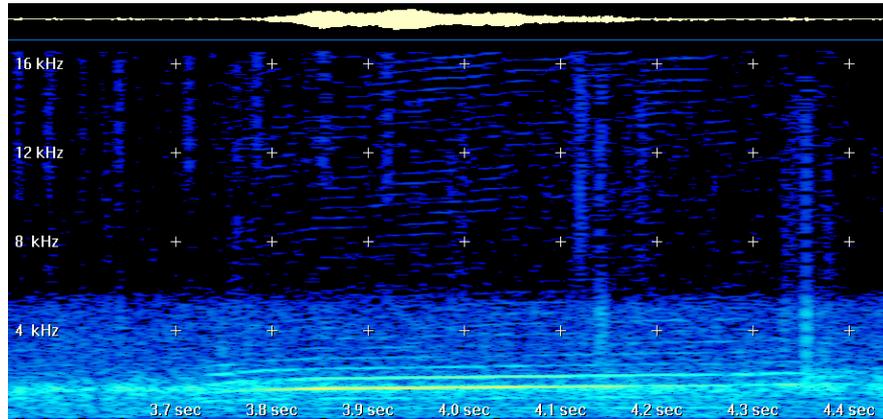
Figure 7. Spectrogram and waveform of bottlenose dolphin's "long burst pulse" recorded in Sardinia (Italy). FFT = 1024, display frame duration = 1 ms.

Vocal Production of Social Signals

The total emission rate resulted in a mean number of 4.52 ± 0.5 social signals per minute. Table 1 shows the mean emission rate according to activity patterns. The emission of the different acoustical classes which were recorded in the study area was not random, "short burst pulsed sounds" were recorded less often than "tonal" and "long burst pulses" vocalizations (Kruskall Wallis test, Hc = 32.9, $p<0.001$).

Table 1. Mean emission rate (*number of social signals per minute*) according to activity patterns.

ACOUSTICAL CLASSES BEHAVIOURS	TONAL SOUNDS	SHORT BURST PULSES	LONG BURST PULSES	TOTAL
SOCIAL	7.68 ± 2.31*	2.70 ± 0.91*	4.41 ± 1.29*	13.15 ± 2.78*
TRAVEL	1.39 ± 0.43	0.98 ± 0.45	0.13 ± 0.64	3.57 ± 0.72
PREDATION	1.23 ± 0.22	0.56 ± 0.18	1.53 ± 0.43	2.83 ± 0.54
DEPREDATION	3.17 ± 0.64*	1.05 ± 0.33*	2.62 ± 0.69*	5.94 ± 1.15*
TOTAL	2.24 ± 0.29	0.90 ± 0.16*	2.12 ± 0.32	4.52 ± 0.51

Means $\pm$ standard errors (SE) are given for all measured variables. Asterisk indicates significance level.

The number of dolphins present varied from 1 to 17 (mean of 4.48 ± 0.2 dolphins). Groups were composed of either adults (76%) or adults and immatures (24%). A positive relation was observed between the number of dolphins in each group and the number of social signals in that recording (Spearman' s rho correlation $r = 0.41$, $P < 0.001$, $n = 220$, Table 2). Solitary bottlenose dolphins did not produce any vocalization (n = 12).

The number of mother-calf pairs within a group was significantly related to the vocal emission rate (Spearmans rho test = 0.25, p < 0.001, n= 52). Mean emission rate across all behavior categories for groups of adults was 3.8 ± 0.5 vocalizations per minute compared with

6.8$\pm$1.2 vocalizations per minute for groups with mother-calf pairs (Kruskall Wallis test, Hc = 13.1, $p <$ 0.001, Table 3).

Table 2. Spearman' s rho correlation between the number of dolphins in each group and the different social signals in that recording.

Acoustical classes	Spearman' s rho correlation value	Significance level
TONAL SOUNDS	0.30	p<0.001
SHORT BURST PULSES	0.30	p<0.001
LONG BURST PULSES	0.35	p<0.001
TOTAL	0.41	p<0.001

Table 3. Mean emission rate (*number of social signals per minute*) across all behavior categories for groups of adults and groups with mother-calf pairs.

ACOUSTICAL CLASSES Group composition	TONAL SOUNDS	SHORT BURST PULSES	LONG BURST PULSES	TOTAL
Adults	1.65$\pm$0.26[a]	0.82$\pm$0.19 [a]	2.01$\pm$0.39 [a]	3.79$\pm$0.53 [a]
Mother-calf pairs within the group	4.16$\pm$0.84[b]	1.15$\pm$0.30 [b]	2.49$\pm$0.54 [b]	6.88$\pm$1.25 [b]

Means $\pm$ standard errors (SE) are given for all measured variables. Different superscripts in the same column indicate significance difference.

Use of Conspecific Social Signals

Out of all the behavioral categories, predation was most commonly observed (40% of samples), followed by depredation activities (30% of samples), socializing (16% of samples), and traveling (14% of samples).

To test for acoustical distinctiveness among behaviors of bottlenose dolphins, we first conducted a discriminant function analysis with behavior as the grouping variable. As shown in the Table 4, the discriminant analysis correctly identified 110 of 220 recordings; moreover the probability of correctly classifying social behaviors was the highest (71%). The variable that displayed the strongest discriminant power in the model was the emission of "long burst pulses", when this vocal signal was excluded the percentage of correctly predicted classifications decreased drastically (79 of 220 recordings). Multivariate analysis indicated that the activities were indeed significantly different from one another (MANOVA F = 3.45, d.f$_1$ = 9, d.f$_2$ = 648, p < 0.001), attributed to differences in sounds production. The highest emission rate was observed while animals were engaged in social activities such as body contact, etc. In the same way, dolphins engaged in depredation produced more frequently social signals than dolphins traveling or dolphins engaging in predation (Table 1).

Bottlenose dolphin group size remained constant among behaviors (Kruskall Wallis test, Hc = 4.8, p= 0.20). Table 6 shows correlations between social signals and group size in each of the activity pattern categories. During socializing a positive relation was expected between the number of dolphins in each group and the number of social signals in that sample; however, significant correlation was only found between group size and the number of "tonal sounds" recorded (Spearman' s rho correlation r = 0.72, *P < 0.01*). The highest correlation

between vocalizations and number of dolphins in each group was observed during depredation (Spearman' s rho correlation $r = 0.86$, $P < 0.001$).

Table 4. Classification success of the discriminant analysis for the four behavioral categories, with three variables in the model ("tonal sounds", "short burst pulses", and "long burst pulses").

Behavioral categories	TOTAL N	Correctly identified	Percent correct
SOCIAL	35	25	71%
TRAVEL	30	5	16%
PREDATION	89	57	64%
DEPREDATION	66	9	13%
TOTAL	220	110	50%

The number and percentage of behaviors correctly classified are displayed.

Table 5. Bottlenose dolphins mean group size with relation to behavioral categories.

Behavioral categories	Means $\pm$ standard error (SE)
SOCIAL	8.7$\pm$1.3
TRAVEL	5.9$\pm$0.71
PREDATION	4.3$\pm$0.27
DEPREDATION	3.8$\pm$0.28
TOTAL	4.5$\pm$0.2

Table 6. Spearman' s rho correlation between the number of dolphins in each group and the different social signals in that recording.

Behavior	Acoustic class	Spearman' s rho correlation value	Significance level
SOCIAL	Tonal sounds	0.72*	p<0.01
	Short burst pulsed sounds	0.79	P=0.27
	Long burst pulsed sounds	0.63	P=0.61
	TOTAL	0.94	P=0.06
TRAVEL	Tonal sounds	0.38	p=0.53
	Short burst pulsed sounds	0.04	P=0.12
	Long burst pulsed sounds	0.01	P=0.09
	TOTAL	0.38	P=0.05
PREDATION	Tonal sounds	0.24*	p<0.01
	Short burst pulsed sounds	0.25*	p<0.05
	Long burst pulsed sounds	0.29*	p<0.05
	TOTAL	0.74*	p<0.001
DEPREDATION	Tonal sounds	0.40*	p<0.001
	Short burst pulsed sounds	0.53*	p<0.001
	Long burst pulsed sounds	0.48*	p<0.001
	TOTAL	0.86*	p<0.001

Asterisk indicates significance level.

Likewise, correlations between social signals and number of mother-calf pairs within the group in each of the activity pattern categories were only significant during depredation feeding activities (Spearman' s rho correlation $r = 0.36$, $P < 0.01$).

CONCLUSION

As part of the ongoing effort to investigate the acoustic repertoire of Mediterranean free-ranging common bottlenose dolphins, this study focused on the emission rates and the use of conspecific social signals. Thus, to be able to assess the functional significance of social signals it is important first of all to investigate the context in which they are used.

Categorization of vocalizations within a species' repertoire is essential in order to facilitate insight into functionality, social relevance, and geographical variation (Boisseau, 2004). Bottlenose dolphin social signals have been categorized as either tonal or pulsed sounds (e.g., Herman and Tavolga, 1988, Herzing, 2000). Results from this study are in broad agreement with this general classification. However, a new division of the burst pulsed sounds category, based on the duration of these signals and not aurally, into "short" and "long" burst pulses, is also suggested to further discriminate the burst pulsed social signals.

Vocal Repertoire of Free-Ranging Bottlenose Dolphins

The Sardinian common bottlenose dolphin vocal repertoire consists of 14 audibly distinct social signals that differ from each other in their acoustical structure and duration. This vocal repertoire is similar to the vocalizations given by other dolphin populations (e.g. New Zealand (Boisseau, 2004); Portugal (dos Santos et al., 1990); Australia (Connor and Smolker, 1996; Schultz *et al.*, 1995); Bahamas (Herzing, 1996)).

The acoustic repertoire observed in this study is extremely diverse. Bottlenose dolphin communication sounds ranged from soft and melodic sounds to harder, almost harsh sounds. For example, the vocalizations in this study had wildly differing durations ranging from the most diminutive twitters to the long and most extravagant screeches and yelps. The complexity of this vocal repertoire, in conjunction with a fission-fusion society (Díaz López & Shirai, 2008), suggests the possibility that these animals are communicating potentially complex information using these vocalizations (Lammers et al., 2003; Janik & Slater, 1998).

However, repertoire size is difficult to measure in any species when calls are classified solely by ear or acoustic features. Any classification method for animal calls involves decisions by humans on the parameters to be used. Terms such as "screeches," "gulps", "brays", "quacks", "yelps", and more… commonly used to describe and distinguish burst pulsed sounds can result in misleading conclusions, as they primarily describe the subjective impressions experienced by human listeners (McCellan and Small, 1965). Playback experiments on grunts and on the alarm calls of primates (Fischer, 1998; Rendall et al., 1999; Fischer et al., 2001; Fischer and Hammerschmidt, 2001) have shown that the animals themselves distinguish between different call subtypes in ways that are not initially apparent to humans. Therefore, the number of audibly distinct social signals given by Sardinian bottlenose dolphins may not be very meaningful. Additionally, the way the vocalizations are

analyzed, and the authors tendency to split or lump, also affects the interpretation of repertoire size. Further validation is needed to find out which method represents the best approximation to how dolphins themselves classify social signals. As a start, forming classes on the basis of structural characteristics, would lead to more meaningful comparative discussions between authors.

Vocal Production and the Use of Conspecific Social Signals

It is of great interest to understand how behavior affects the properties of the social signals and how variations could be related to motivational states or other useful communicative functions.

The results, showing that emission rates increased, especially in those activities involving excited depredation or socializing, confirmed that activity and social signals production were related. In other words, when bottlenose dolphins are more excited, especially in social or depredation episodes, the social signals production increased. Bottlenose dolphins engaging in predation and traveling were quieter in general. Thus, there may be more advantages in quiet traveling or predation because controlled echolocation might facilitate navigation, detection of other dolphin groups, or detection of potential prey patches (dos Santos and Almada, 2004).

This study also shows that solitary bottlenose dolphins did not produce social signals. Moreover, the fact that was observed a positive relation between group size and the production of social signals, particularly during feeding or socializing, confirms that dolphin social signals are used for communicative and social purposes. The highest emission rate observed while animals were engaged in depredation or social activities cannot be explained by an increase in the number of dolphins because group size remained constant among behaviors.

These observations coincide well with those reported for other wild bottlenose dolphin populations. In a study of coastal bottlenose dolphins from different populations in the North Carolina and Florida coastal waters, Jones and Sayigh (2002) found significant variations in the vocal emission rates. Generally, whistling increased with dolphin group size and was especially common in social interactions. Cook et al. (2004) also reported that whistles increase with group size in Florida and that whistles were more frequent in socializing episodes than in traveling.

The tonal sounds emission rate found in this study, although quite variable, showed a mean of 2.24 tonal sounds per minute. Adjusting the data presented by dos Santos et al., (2005) in Portugal and Jones and Sayigh (2002) in Florida, it is apparent that their whistles emission rates are on the same order of magnitude than the tonal emission rates given by Sardinian bottlenose dolphins engaging in travel or predation. Acevedo-Gutiérrez and Stienessen (2004) obtained similar whistling rates for "non-feeding" dolphins in Costa Rica.

Dolphins engaging in social and depredation behaviors emitted tonal sounds at the higher rate of 7.7 and 3.2 sounds per minute respectively. These values were on the same order than the data observed by Acevedo-Gutiérrez and Stienessen (2004) in Costa Rica for dolphins feeding in the presence of competing sharks. In captivity, during experimental tests characterized by high excitement contexts, two studies obtained higher whistles emission rates (Tyack, 1986; Janik et al., 1994). Although, one has to be careful in extrapolating results

from studies on captive dolphins to wild ones. Data from captive individuals can give us some information on characteristics of vocalizations, but the emission rate and the function may be very different in the wild. These types of studies conducted with animals in captivity or with animals enclosed in large nets in natural environment are questionable because this potentially changes the animal's behavior.

My findings on social signals emission suggest that there were no differences between "tonal sounds" production and "long burst pulses" production. Consequently, as concluded by Lammers et al. (2003) in spotted and spinner dolphins, burst pulses vocalizations probably play an equally important social signaling role as do tonal sounds.

Previous studies on burst pulses production did not find such clear differences in production rates among activities as those presented here. The existing literature is vague because burst pulses have been traditionally discussed in terms of their sonic properties (Herman and Tavolga, 1980; Popper, 1988; Overstrom, 1983; Herzing, 1996; Van Parijs and Corkeron, 2001). The frequent incidence of "long burst pulsed sounds" in social and depredation contexts considered with their rare frequency in controlled echolocation contexts (travel and predation) strongly suggests that their primary function is likely communicative.

These results are consistent with results observed in other bottlenose dolphin populations. The production of burst pulsed sounds reported by Schultz et al. (1995) was mainly correlated to socializing behaviors. But they were not able to observe if these sounds were used in more affiliative or more agonistic contexts. Likewise, other studies reported that burst pulsed sounds were associated to aggressive and agonistic behaviours (Defran and Pryor, 1980; Overstrom, 1983; McCowan and Reiss, 1995; Blomqvist et al., 2004).

Recordings coupled with underwater visual observations of Sardinian dolphins confirmed that "long burst pulsed sounds", in agonistic interactions like those observed during depredation, could be used with the intent to settle rank conflicts and avoid competition between group members. Because entangled fish is not mobile and it is possible that other dolphins will find the same food spot at the same time, explanations which involve the avoidance of competition with other group members can be concerned about. Furthermore, an increase in competition pressure due to the presence of more individuals seems a likely reason for avoidance vocalizations. These avoidance vocalizations were usually enough to discourage competitors. The absence of fights, between the dolphins engaging in depredation contexts during underwater observations, supports this hypothesis. Detailed descriptions of agonistic vocalizations were presented for many other mammalian taxa, including canids (e.g. Brady, 1981), seals (e.g. Phillips and Stirling, 2001), and specially primates (e.g. Green, 1975, Gouzoules et al.,1984; Gouzoules and Gouzoules, 1990; Fischer and Hammerschmidt, 2002).

Mother-Calf Pairs within the Group and Vocal Production

The existence of a relationship between the number of mother-calf pairs within a group and the vocal emission rate was consistent with information conveyed by vocalizations of other bottlenose dolphins studied in this respect. This pattern, noted by Sayigh et al. (1990) and Smolker *et al.* (1993), gathered evidence to support the use of tonal vocalizations as contact calls between mother and calf pairs of dolphins. They also showed that stereotyped or signature whistle patterns were used to call calves back to within visual range of the assumed

mother. These observations also support the individual recognition/group cohesion hypothesis. On the other hand, McCowan and Reiss (1995) noted that burst pulsed sounds could be interpreted to function as aggressive contact vocalizations towards infants. So it is possible then, in the presence of calves, adults engaging in depredation activities increase the production of burst pulsed sounds as aggressive contact vocalizations towards the calves.

Although many of these vocalizations have been described in the literature, their production rate and association with specific behaviors provide additional contextual information about their potential use as communication signals. These findings demonstrate how dynamic and complex bottlenose dolphin vocal behavior is and how important it is to consider many factors in analysis. Further observational and experimental research is needed to determine precisely how complex both the structure and function of dolphin vocal signals are.

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