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No shallow talk: Cryptic strategy in the vocal communication of Blainville's beaked whales

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ABSTRACT

Communicating animals must balance fitness benefits against the costs of signaling, such as increased predation risk. Cetaceans communicate mainly with sound and near-surface vocalizations can place signalers at risk from shallow-diving

top-predators with acute hearing such as killer whales. Beaked whales are deep divers living in small cohesive groups with little social defense from predation. Little if anything is known about their acoustic communication. Here, eight Blainville's beaked whales were studied with suction cup attached DTags to provide the first report on social communication as a function of diving behavior for any of the 21 ziphiid species. Tagged whales produced two previously unrecorded signals with apparent communicative functions: (1) fast series of ultrasonic frequency modulated clicks (rasps) were recorded from six individuals, and (2) harmonically rich short whistles with a mean fundamental frequency of 12 kHz were recorded from one whale at up to 900 m depth, the deepest whistles recorded from a marine mammal. Blainville's were silent 80% of the time, whenever shallower than 170 m depth and during the prolonged (19 min) silent ascents from vocal dives. This behavior limits the ability of shallow-diving predators to track Blainville's acoustically and may provide a striking example of the evolutionary influence of the risk of predation on animal communication.

Key words: vocal communication, acoustic crypsis, social sounds, deep divers, Cetacea, Ziphiidae.

Animals that communicate must balance the fitness benefits inherent in signaling against the costs, such as energetic expenses related to signal production and increased risk of predation (Bradbury and Vehrencamp 1998). While Zahavi (1975) argues that the cost of signaling may be a critical part of sexual advertisement, animals are expected to minimize costs and maximize benefits for most other communication functions. The extensive evolution of mechanisms for crypsis (Ruxton 2009) suggests that the cost of being detected by predators may exert a substantial selection pressure on communication. Acoustic communication is widespread in marine mammals that exploit the favorable sound transmission properties of water. Toothed whales use echolocation clicks to find food and navigate and often produce a large number of dedicated communication vocalizations in the form of whistles and complex pulsed signals (*e.g.*, Tyack 1986) mostly while socializing near the surface. Reports of marine mammals silencing in the presence of killer whales (*Orcinus orca*) (Thomas *et al.* 1989) suggest that vocalizing whales increase the risk of being detected acoustically by some larger delphinids that prey on many species of marine mammals (Jefferson *et al.* 1991). Among small marine mammals, there seem to be at least two strategies to reduce this predation risk: acoustic crypsis and social defense against predation. The acoustic crypsis hypothesis proposed by Madsen *et al.* (2005a) and Morisaka and Connor (2007) notes that several delphinid species of the genus *Cephalorhynchus*, along with the porpoises and dwarf sperm whales, have converged on producing narrow-band high-frequency clicks for echolocation and communication (Dawson 1991, Clausen *et al.* 2010) at frequencies above the hearing sensitivity of killer whales. The social defense against predation hypothesis proposed by Norris and Dohl (1980) suggests that most other delphinids and sperm whales, which produce sounds easily detected by killer whales, may rely upon their social groups to detect and protect themselves against predation or reduce individual predation risk through dilution.

Little is known about acoustic communication or antipredation strategies in the second largest family of the toothed whales, the deep-diving beaked whales (Ziphiidae). Deployments of acoustic tags on Blainville's beaked whales (*Mesoplodon densirostris*; see Fig. S1) have indicated that these animals apparently are only vocally

active at depth during foraging dives, where they emit numerous echolocation clicks (Johnson *et al.* 2004, Tyack *et al.* 2006) at frequencies within the hearing range of killer whales (Szymanski *et al.* 1999, Johnson *et al.* 2004, 2006). The behavior of these whales, foraging by echolocation at depth and spending very little time at the surface, has been interpreted as an adaptation to reduce predation by killer whales (Aguilar de Soto 2006, Tyack *et al.* 2006, Baird *et al.* 2008) that have limited diving capabilities compared to beaked whales (Baird *et al.* 2005). However, this behavior is also consistent with the mesopelagic and deep benthopelagic niche of Blainville's beaked whales, which makes production of echolocation clicks unnecessary at shallower depths. Nonetheless, given that Blainville's beaked whales are social animals that live in small and cohesive associations, tending to surface and dive together (Aguilar de Soto 2006, Claridge 2006), they would be expected to make communicative sounds especially near the surface to maintain social ties and coordinate activities, as is the case for short-finned pilot whales (Aguilar de Soto 2006) and sperm whales (Weilgart and Whitehead 1993).

The only apparently communicative signals recorded by any means from Blainville's beaked whales are a few burst pulse sounds at 1–6 kHz recorded from a stranded whale (Caldwell and Caldwell 1971), and a 1.5 s whistle and three burst pulses at 6–16 kHz recorded near a surface group of this species (Rankin and Barlow 2007). These few recordings indicate that Blainville's beaked whales are capable of producing sounds near the surface, but little if anything is known about if and when dedicated communication signals are produced in this species. Here, we set out to study the communicative behavior of Blainville's beaked whales in the context of their diving activity. Multisensor acoustic tags were placed on eight whales to record the sounds made by the tagged whale and others nearby, along with information about the activity and overall social context of the tagged whales. We identified two novel types of sound apparently dedicated to social communication: whistles and rapid series of clicks that we named rasps. Surprisingly, all rasps and whistles were recorded in deep dives at depths below 170 m, even though the whales spent only 40% of their time at these depths. We discuss how deep sound communication may form part of a cryptic strategy in Blainville's beaked whales in which acoustic activity may be adapted to reduce predation risk.

METHODS

Data Collection

Blainville's beaked whales were studied using suction cup attached DTags (Johnson and Tyack 2003) that sample sound simultaneously with orientation and depth of the whale. Tags with a single hydrophone, used in 2003, had an acoustic sampling rate of 96 kHz and a –10 dB bandpass response from 500 Hz to 47 kHz. Stereo DTags, used since 2004, have two hydrophones separated by 2.5 cm with a –10 dB response from 500 Hz to 81 kHz. Dynamic range was about 85 dB (2003) and 90 dB (2004+) at 30 kHz with respect to a 20 kHz noise bandwidth. None of the analyzed sounds came close to clipping the recording system. Nonacoustic sensors were sampled at 50 Hz and decimated to 25 Hz or 5 Hz for postprocessing.

Data were collected during five field efforts performed from 2003 to 2008 off El Hierro (Canary Islands, Spain). An observation post on a high cliff was used for sighting whales, while tagging and photo-identification were performed from a

4.5 m inflatable boat. Tags were attached to the backs of whales using a 5 m hand-held carbon fiber pole. The tags weighed ~ 20 g in water and measured $20 \times 10 \times 3.5$ cm³, amounting to less than 0.8% of the frontal cross-sectional area of a Blainville's beaked whale. Wilson *et al.* (1986) found that noninvasive attached devices with cross-sectional areas between 2.3% and 10% of the cross-sectional area of African penguins (*Spheniscus demersus*) did not affect their foraging and swimming behavior, while larger devices did. Tags used here were well below the relative cross-sectional area of the smallest devices tested by Wilson *et al.* and thus we assume that they had little impact on the behavior of tagged whales. However, the act of tagging may have a short-term effect due to the close approach of the boat and the initial contact of the suction cups with the skin. The behavior of the whales at the moment of tagging was monitored visually. Reactions of the whales to tagging attempts comprised alteration of swimming course, increase of speed and changes in distances between the members of a group. Tagged whales that were followed visually from land seemed to resume normal behavior as soon as the tagging boat separated from the group.

No young or mother-calf pairs were approached for tagging and no more than three approaches were performed to any whale in a day. The short surfacing time of Blainville's beaked whales (2 min average, Tyack *et al.* 2006) prevented *in situ* recognition of all individuals and an *a posteriori* examination of photographs showed that three whales were tagged more than once in different years, resulting in seven individuals sampled in 12 tag deployments (Table 1). We classified the whales following Claridge (2006) as: adult male (with exposed teeth and abundant scars), adult female (no exposed teeth, some markings and accompanied consistently by a young), and indeterminate (whales that could be subadult males without exposed teeth or adult/subadult females without associated young). Smaller animals were classified as calves or juveniles if they were $< 1/2$ or $2/3$ of the length of the adult, respectively.

Data Analysis

Tag data were analyzed using custom scripts in Matlab 6.5 (MathWorks Inc., Natick, MA). Acoustic data were evaluated both aurally and *via* spectrograms (512 FFT Hann window, 50% overlap) to locate vocalizations produced by the tagged whale or by other nearby animals. Although beaked whales are the most frequently sighted species in the study area, groups of delphinids are occasionally observed. Clicks from Blainville's beaked whales were identified and discriminated from dolphin clicks based on the temporal and spectral characteristics of Blainville's beaked whale clicks and on their production patterns (Johnson *et al.* 2006). Dolphin clicks and whistles in the recordings occurred consistently in bouts and were faint, making them readily distinguishable from Blainville's beaked whale sounds. Three types of click sounds were identified from tagged whales: usual echolocation clicks, rapid series of clicks (buzzes) associated with prey capture attempts (Johnson *et al.* 2004), and audibly distinct burst-pulse sounds (which we named rasps). Clicks from the tagged whales were differentiated from clicks made by nearby conspecifics using (1) the received level and the angle of arrival of the vocalizations to the stereo hydrophones, and (2) the low-frequency energy associated with clicks produced by tagged whales, which is absent in clicks recorded in the far field (Johnson *et al.* 2006, 2009). The interclick interval (ICI) of clicks within rasps was measured using

Table 1. Whale: tagged individual indicating its photo-ID catalog code (<http://www.cetabase.info>) and if it is: ♂ adult male, ♀ adult female; *Ind*: indeterminate or *young*. * Male 4 did not have erupted teeth, but the pronounced bulging of the lower jaw clearly indicated its sex. Some whales were tagged more than once and in each tagging occasion they were given a different tag code. Tag code: formed by the last two digits of the year (2003–2008) and the Julian day of the tag deployment followed by a letter indicating the consecutive order of tag in the day. Group composition indicates the number of *total* of whales and number of whales of each different size/sex class in the group. The number of hours of acoustic tag records during day and nighttime (before/after sunset). Percent of time vocal: percent of time spent in the vocal phase of the dives. The number of vocal dives: number of vocal dives recorded during the day and at night for each tag deployment and for each individual whale. The last four columns indicate the number of vocal dives containing rasp or whistles from tagged whales (*rasp*, *whistle*) or from untagged conspecifics (*nt rasp*, *nt whistle*) during the day and at nighttime; na: no data are available, *i.e.*, the tag deployment did not contain night dives.

Whale	Tag code	Group composition:				Number of hours of hours day/night	Percent of time vocal	Number of vocal dives day/night	Number of vocal dives (day/night) with				
		Number of tot	♂	♀	Ind				Young	rasp	nt rasp	whistle	nt whistle
♂ 1 MDH1	03_284a	5	1	1	2	1	17	40,604	40,794	40,544	3/2	0/0	40,543
	05_294b	3	1	0	2	0	4.7/3	40,602	40,602	40,602	0/0	40,543	0/0
	08_137a	4	1	0	3	0	9/9.7	40,606	40,606	40,577	3/5	4,0544	40,543
Ind 1 MdH15	03_298a	2	0	0	2	0	40,602	40,574	0/na	0/na	0/na	0/na	0/na
	04_287a	5	1	2	0	2	9.6/0	40,663	10/ 4	2/na	4/na	0/na	0/na
♀ 1 MdH22	05_294a	3	1	0	2	0	40,602	40,574	2/na	0/na	0/na	0/na	0/na
	08_289a	6	0	3	1	2	8.3/9.7	40,605	40,605	0/0	0/0	0/0	0/0
♂ 2 MdH6	05_277a	5	1	2	0	2	40,724	40,602	40,663	0/na	1/na	0/na	0/na
	08_136a	4	1	1	1	1	40,602	40,574	2/na	2/na	0/na	0/na	0/na
♀ 2 MdH43	05_285a	2–3	0	0	2–3	0	5/3.7	40,575	40,543	40,543	0/0	0/0	0/0
♂ 3 MdH74	08_142a	4	1	1	1	1	1.9/0	40,574	1/na	1/na	0/na	0/na	0/na
	08_148a	2	0	0	2	0	6.2/0	40,574	0/na	1/na	1/na	0/na	0/na

a supervised click detector, *i.e.*, an energy detector whose results were monitored manually by inspecting the envelope and spectrogram of the signal.

Occasional whistles were found in a context that indicated that they were produced by Blainville's beaked whales. The whistles were quite distinct in duration and production pattern from delphinid whistles (see Results) and were found at times when characteristic bouts of delphinid clicks and whistles were not audible. A subset of the Blainville's beaked whales whistles were classified as produced by the tagged whale as they were recorded with a consistent angle of arrival, similar to that of the tag whale clicks. A supervised contour extractor was used to parameterize the fundamental frequency of the whistles that were recorded with sufficient signal to noise ratio.

Acceleration Rate during Rasps and Buzzes

Rapid movements have been associated with rapid click series or buzzes in several echolocating species (Miller *et al.* 2004, Johnson *et al.* 2004, 2007, Aguilar de Soto *et al.* 2008) including beaked whales, supporting the idea that these sounds represent prey capture attempts. To test for possible differences in the behavioral contexts of rasp and buzz production, we computed the root-mean-square (RMS) acceleration rate or jerk of tagged whales as a proxy for rapid motion while different types of sounds were produced. Acceleration rate was approximated by differentiating the signal from each axis of the three-axis accelerometer, decimated to a 25 Hz sampling rate. The magnitude of the resulting three-axis acceleration rate vector was computed at each sample and the RMS value of the magnitude was taken over the duration of each rasp and buzz.

RESULTS

Tags provided a total of 102 h of combined acoustic and movement data, 69 of which were during the day (*i.e.*, before local sunset). Tagged whales were vocal during a mean of 18% of the tag recordings and only vocalized when deeper than 170 m, during the vocal phase of 47 deep dives (*i.e.*, all dives deeper than 450 m) (Fig. 1). The silence of the whales when shallower than 170 m is particularly striking given that Blainville's beaked whales spend some 60% of their time shallower than this depth (Fig. 1). The most common vocalizations produced by all whales were series of frequency modulated (FM) echolocation clicks, interspersed with buzzes marking prey capture attempts (Johnson *et al.* 2004, 2006; Madsen *et al.* 2005*b*). In addition to these echolocation sounds, whales occasionally produced tonal whistles and short bouts of clicks with a repetition rate that resembled that of buzzes but with a markedly different aural impression. These click sequences (Fig. 2) were tentatively distinguished from buzzes and named "rasps." Examples of sound files of whistles and rasps are provided as supporting information. In the following, we first describe the acoustic characteristics of rasps and whistles and second their patterns of occurrence.

Differences between Rasps and Buzzes

Buzzes are composed of short unmodulated clicks that are easily distinguished from the longer FM clicks in regular echolocation (Johnson *et al.* 2006). Analysis

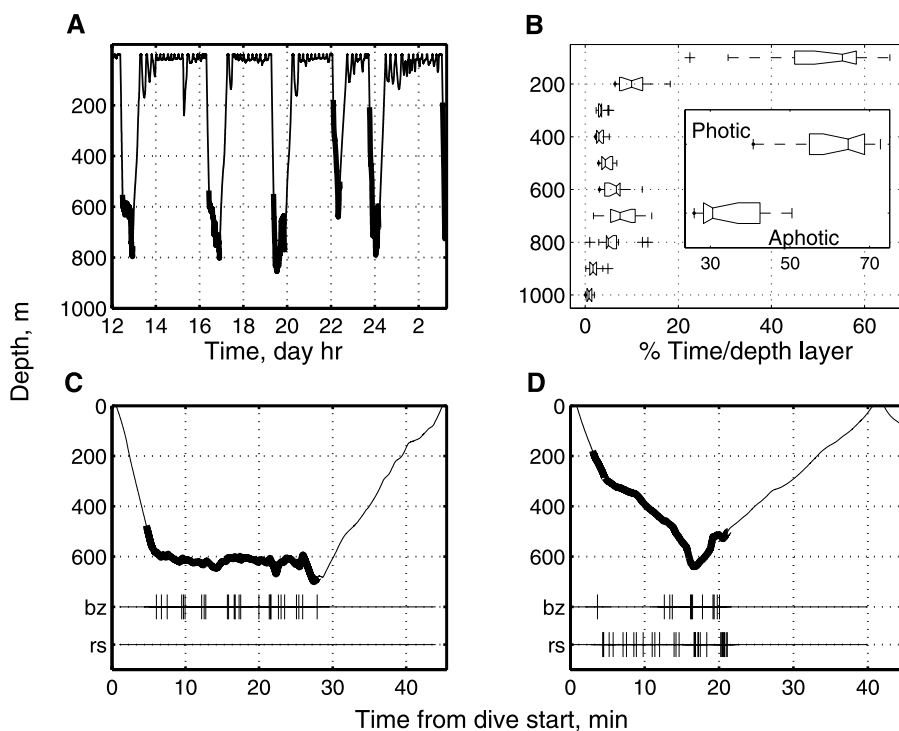


Figure 1. (A) Dive profile of a tagged Blainville's beaked whale showing with a thickened line the time during which the whale is vocally active. (B) Proportion of time spent by all tagged whales at each 100 m depth layer from 0 to 1,000 m depth. The box shows the proportion of time spent in the photic and aphotic layers (shallower and deeper than 200 m depth, respectively) by all whales. (C and D) Occurrence of raps and buzzes, noted as vertical lines, in a typical foraging dive with numerous buzzes and few or no raps (C) and in a vocal dive with an atypical high number of raps and less buzzes than average (D).

of rasp clicks from nontagged whales received apparently on-axis in the tag (*sensu* Møhl *et al.* 2003, Johnson *et al.* 2006) showed that their characteristics were similar to those described for FM clicks and clearly different from those of buzz clicks. Working on the hypothesis that the audibly distinct raps were composed of FM clicks rather than buzz clicks, we examined the click type in each high repetition click sequence recorded from tagged whales ($n = 1,413$) and untagged conspecifics ($n = 687$). Click characteristics were compared against the duration and time-frequency (Wigner-Ville) distribution reported for FM and buzz clicks (Johnson *et al.* 2006). Classification of clicks from tagged whales was then checked with an additional spectral test (Appendix S1). The characteristics of clicks in sequences recorded from nontagged whales vary widely, presumably depending on the aspect of the vocalizing whale with respect to the tag. Most of these sequences had at least some clicks that could be clearly classified as buzz or FM, but 7% of sequences could not be classified due to low received level and likely off-axis recording aspect, and these were not included in further analysis.

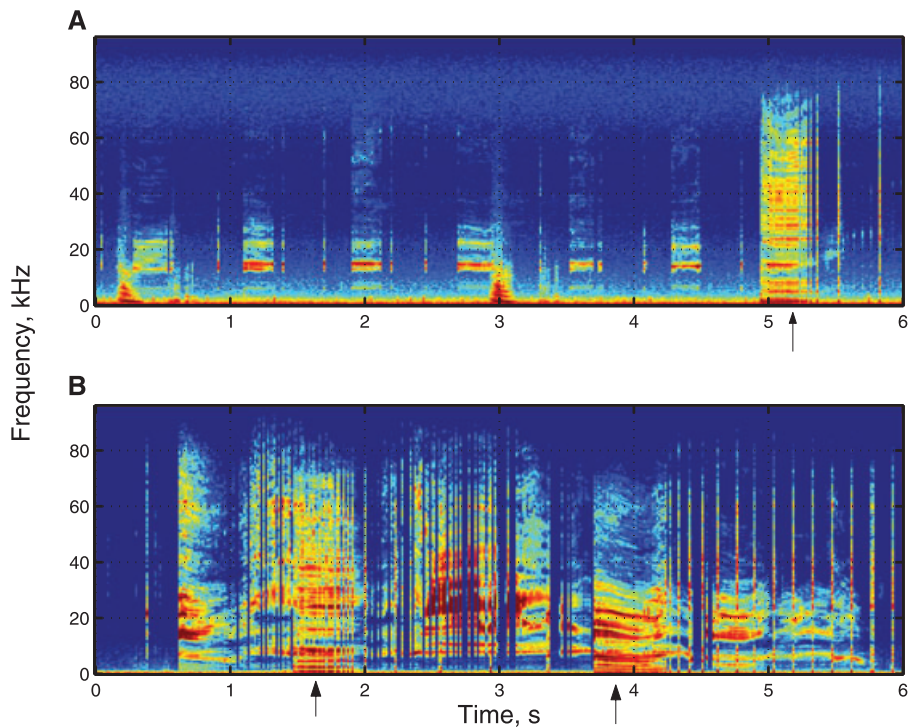


Figure 2. (A) Spectrogram (Hamming 1,024 FFT, 512 overlap) of a series of rasps from a nontagged whale occurring right before the tagged whale (male 2) emits a rasp and starts regular clicking. (B) Spectrogram of a seeming vocal interaction occurring 2 min after the sounds in the upper panel, with clicks and rasps produced by the tagged whale and by very close conspecifics. Rasps from the tagged whale are indicated by arrows.

Having distinguished buzzes and rasps based upon their click properties, we tested whether rasps, such as buzzes, were associated with increased movement, consistent with prey capture attempts (Miller *et al.* 2004). The RMS acceleration rate during rasps and buzzes from each tagged whale was compared to that during a control set of intervals starting 10 s before each rasp and buzz, and with the same duration. The acceleration rate during rasps ($n = 152$) was similar to the acceleration rate during preceding control intervals for seven of the eight tag deployments containing rasps (Wilcoxon rank test, mean $P = 0.5$, $P > 0.06$ in seven cases and $P = 0.02$ in one case). In contrast, the acceleration rate during buzzes ($n = 1,261$) was significantly higher than the acceleration rate both in preceding control intervals and during rasps (Wilcoxon rank test, all $P < 0.000004$ and $P < 0.006$, respectively) in seven of the eight tag deployments with rasps. In one tag deployment on male 1, the tag was attached near the tailstock and recorded similarly high acceleration rate signals during swimming in and out of buzzes. The same male was tagged on two other occasions and the difference in acceleration rate between buzzes and rasps was highly significant in those tag recordings.

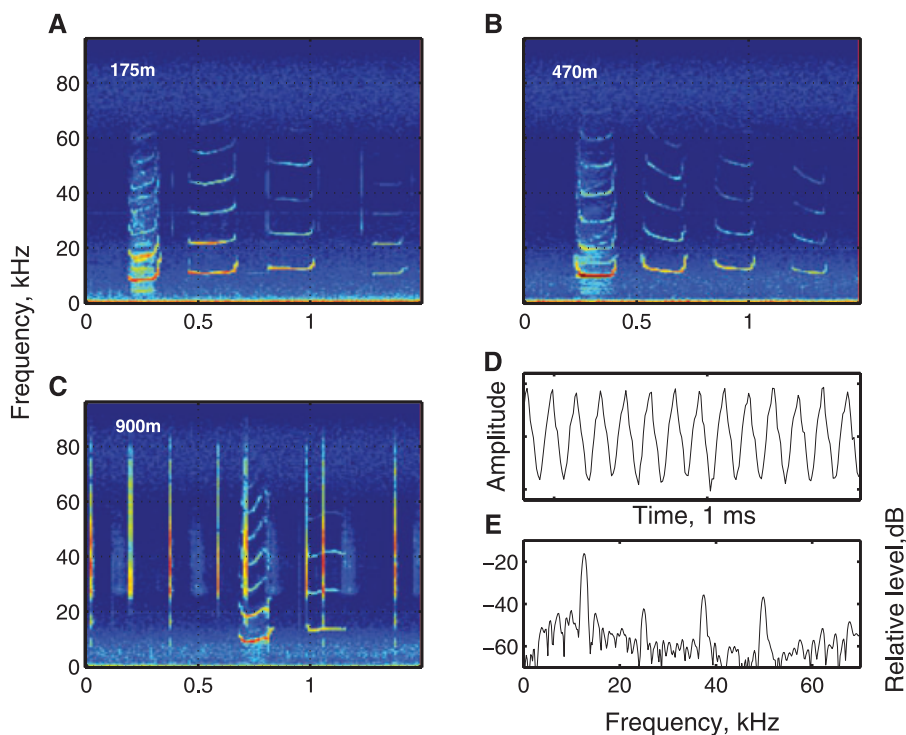


Figure 3. (A–C) Spectrograms (1,024 Hamming, 512 overlap) of three series of stereotypical whistles produced by a tagged Blainville’s beaked whale (male 1). The depth of the whale at the time is indicated in each panel. The whistles produced at 900 m depth coincided with clicks from two untagged whales and bottom echoes produced by these clicks. (D) Waveform of 1 ms of the second whistle in B showing that the signal is a continuous tone. (E) Spectrum (1,024 FFT) of 2 ms of the same whistle showing the harmonics of the whistle as peaks in the relative received level.

Characteristics of Rasps and Whistles

Rasps from tagged whales, averaged over individuals, had a median duration of 0.6 s and contained a median of 87 clicks (interquartile range, IQR, 43 clicks, $n = 13,130$ clicks from 144 rasp for which clicks were easily detected). The median ICI was 5.3 ms (IQR 1.7 ms), with the ICI tending to be higher at the beginning of rasps. Rasps tended to occur as isolated bursts of clicks but we also recorded nine bouts of rasps, each lasting 2–11 s and composed of 3–18 accelerating series of clicks, similar to isolated rasps, interspersed by a few usual FM clicks with ICI up to 0.15 s. Individual rasp clicks did not appear to differ from regular FM clicks in duration, modulation or level, although precise comparison is complicated by on-animal recording effects in the case of clicks from tagged whales and continually varying recording aspect for clicks from untagged whales (Johnson *et al.* 2009).

Whistles recorded from tagged whales were highly stereotyped in duration (mean 0.2 s, SD 0.03) and frequency (Fig. 3), with little frequency modulation: the 5–95 percentiles of whistle fundamental frequency averaged 11.4 and 13.4 kHz,

respectively. The same percentiles were 11.8 and 13 kHz in 19 whistles from untagged whales recorded with enough signal to noise ratio. Whistles contained harmonics up to the limit of the tag recording bandwidth (about 80 kHz). The waveform and spectrum of whistles (Fig. 3) were consistent with a tonal rather than burst-pulse sound. All tagged whale whistles occurred in seven short series lasting 0.5–1.8 s and containing 2–7 whistles each, separated by an average of 0.3 s of silence. The RMS received level at the tag of the first whistle in each series tended to be higher than that of the following whistles, with a mean difference of 6 dB (–3 to 18 dB). The source level (SL) of all focal whistles, back-calculated from the signal at the tag assuming spherical spreading over the 2 m separation between the tag and the sound source, ranged from 123–149 dB re 1 μ Pa RMS at 1 m. The separation between the tag and the sound source was estimated from field photos of the tagged whale. This SL approximation does not consider any potential effects of the whale tissues close to the receiver, which may introduce a bias (Madsen *et al.* 2006).

Occurrence of Rasps and Whistles

Rasps and whistles were recorded only during deep dives and the low number of dives from individual tagged whales makes it difficult to evaluate the factors that influence the production of these sounds. The individual with the longest cumulative tag record (three tags summing 42 h over 5 yr) is male 1 and all of the whistles were recorded in tag deployments on this whale. Whistles attributed to the tagged whale ($n = 28$) were produced in four dives over two tag deployments, at a mean depth of 450 m (170–900 m). Whistles judged to be from untagged whales ($n = 23$) were recorded at 500 to 700 m depth in two dives performed by the same male in two different tag attachments (Table 1, 2). All whistles recorded from the tagged whale occurred within 1 min of the whale starting to produce usual echolocation clicks (start of clicking, SOC) in the descent of foraging dives. The few whistles recorded from untagged whales were dispersed throughout the vocal phase of the dive in which they were recorded. Whistles from tagged and untagged whales did not cooccur in a dive but were closely associated with rasps, with all whistles occurring within 1 min of rasps (Fig. 4).

Rasps were more common than whistles, being emitted by six of the seven tagged whales (Table 1) in 20 of the 47 dives in the data set. The mean depth of rasps ($n = 152$) from tagged whales was 494 m (170–900 m, per dive data in Table 2). Rasps from untagged whales ($n = 496$) were detected in 21 dives by four individuals at a mean tag depth of 560 m (180–1,280 m). In total, 30 deep dives contained rasps from tagged or untagged whales. The time delays between the nearest pairs of signals within a dive are shown in the survivor plot of Fig. 4. More than 65% of pairs of rasps performed within the same dive occurred within 10 s of each other, whether the pairs were produced by tagged whales, untagged whales, or from tagged/untagged whales. Excluding two atypical dives with numerous rasps, which are discussed below, most dives contained only a few rasps and 75% of the 88 rasps produced by tagged whales in these dives occurred in bouts within 2 min before or after SOC. Rasps from untagged whales also tended to associate with SOC of the tagged whale, with a median absolute delay of 3 min (IQR 12 min). Only in one dive were rasps recorded after the end of echolocation clicking during the ascent but these rasps ended within 2 min of the end of regular clicking. The silent ascents from deep dives lasted on average 19 min (SD 4 min, $n = 40$ dives).

Table 2. Number of rasps and whistles produced in dives containing these signals and depth of the tagged whales when these sounds were recorded. Whale and tag code: as in Table 1. Dive: consecutive number of dive containing rasps or whistles for each tag deployment. The number of rasps and whistles from tagged animals (rasps, whistles) and untagged animals (nt rasps/whistles) and depth of the tagged whales at the time that these signals were recorded.

Whale	Tag	Dive	Number of rasp	Number of nt rasp	Number of whistle	Number of nt whistle	Depth rasp, m (mean, range)	Depth nt rasp (mean, range)	Depth whistles (mean, range)	Depth nt whistles (mean)
♂ 1	03_284a	1	0	1	0	0	—	410	—	—
		2	0	3	0	0	—	677 (549–714)	—	—
		3	0	22	0	0	—	391 (297–507)	—	—
		4	33	87	0	16	473 (268–640)	544 (353–640)	—	521
		5	3	1	0	0	199 (198–200)	706	—	—
		1	2	0	0	0	551 (549–553)	—	—	—
		2	4	0	0	0	536 (508–587)	—	—	—
		3	7	0	0	19 (4 s)	483 (455–507)	—	464 (438–510)	—
		4	2	0	0	4 (1 s)	187 (184–188)	—	175	—
		1	2	1	0	0	592 (576–606)	1282	—	—
♀ 1	04_287a	2	0	1	0	0	—	793	—	—
		3	10	19	0	0	587 (530–843)	825 (471–931)	—	—
		4	7	16	0	0	243 (192–458)	279 (180–408)	—	—
		5	1	25	3 (1 s)	0	171	478 (446–541)	176	—
		6	12	13	2 (1 s)	0	828 (795–899)	497 (358–900)	898 (898–899)	—
		7	0	3	0	0	—	789 (765–825)	—	—
		8	3	21	0	7	593 (551–628)	602 (502–707)	—	678
		1	0	1	0	0	—	443	—	—
		2	1	0	0	0	876	—	—	—
		3	0	2	0	0	—	540 (539–540)	—	—
♂ 2	05_294a	4	1	1	0	0	738	560	—	—
		5	11	6	0	0	463 (394–519)	442 (402–528)	—	—
		1	1	0	0	509	—	—	—	
		2	2	0	0	0	477 (457–498)	—	—	810
		1	0	1	0	0	—	—	—	—
		1	26	241	0	0	598 (324–740)	—	—	—
		2	3	30	0	0	384 (370–400)	—	—	—
		4	14	0	0	0	361 (232–713)	—	—	—
		1	9	0	0	0	419 (371–452)	—	—	—
		2	0	1	0	0	—	460	—	—
♀ 2	05_285a	1	0	0	0	—	—	—	—	—
		4	14	0	0	0	—	—	—	—
♂ 3	08_142a	1	9	0	0	—	—	—	—	—
		2	0	1	0	0	—	—	—	—
♂* 4	08_148a	1	0	1	0	—	—	—	—	—
		2	0	1	0	0	—	—	—	—

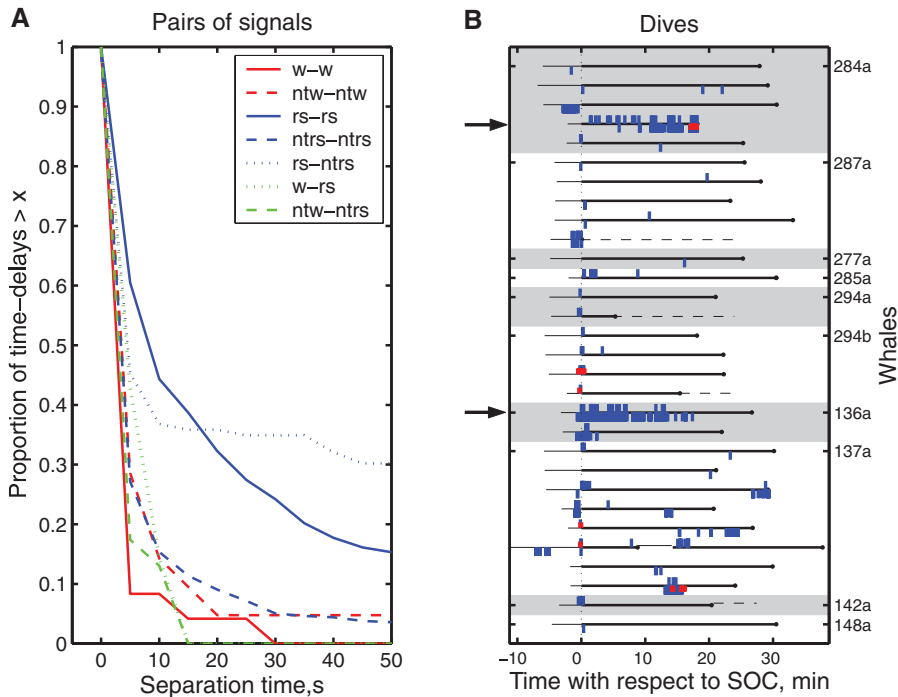


Figure 4. (A) Survivor plot of the time delays between pairs of consecutive signals recorded within each dive. Legend: w and rs, and ntw and ntrs are whistles and rasps from tagged and untagged whales, respectively. The y-axis is the proportion of pairs of signals that are separated by at least the time in the x-axis. Most signals occurred within 7 s of another signal irrespective of type. Whistles from tagged and untagged whales never coincided within a dive and are not plotted. (B) Occurrence of rasps and whistles from tagged or untagged whales in dives with either sound ($n = 30$). Each black horizontal line represents the time from the start of a dive to the end of the vocal phase. Four incomplete dives are plotted finishing as a dashed line. The vocal phase in each dive is indicated by a thicker line. Tag deployment ID is given on the right and time 0 is set to the start of regular clicking (SOC) in each dive. Blue and red bars above the dive line: rasps and whistles from tagged whales, respectively; blue and red bars below the dive line: rasps and whistles from untagged whales, respectively. All tagged whales whistles occur near SOC. Two dives marked with an arrow are atypical in that they contain a very large number of rasps.

Two atypical dives (marked with an arrow in Fig. 4B) contained many rasps from tagged and untagged whales (three and two times more rasps from tagged whales, and three and eight times more rasps from untagged whales, than the maximum in any other dive). These atypical dives also contained the lowest number of foraging buzzes of any dive performed by the same whale (12 and 22 buzzes, when the median number of buzzes per dive of the two whales was 26 and 27, respectively). Rubbing sounds indicating physical contact among whales were not detected in atypical dives. Apart from these two atypical dives, the presence of rasps or whistles in a dive did not seem to affect foraging. The number of buzzes in dives with and without rasps in 10 tag deployments (*i.e.*, excluding the two deployments with atypical dives) was

compared after removing from the buzz count of each dive the mean for all dives in the tag deployment and results were similar (Wilcoxon rank test $P = 0.4$; $n = 17$ and 22 dives with and without rasps, respectively).

In seven of the 47 vocal dives, the audio recording terminated due to a full memory before the end of the dive but after the tagged whales descended below 600 m depth. These incomplete dives were included in the analysis of presence/absence of tagged whale rasps/whistles because in all complete dives with these sounds, some rasps and whistles were recorded during the descent phase of the dive before the whale reached a depth of 600 m. Unless the occurrence pattern of rasps and whistles in the six incomplete dives is radically different from that in complete dives, errors incurred by including incomplete dives in presence/absence analyses should be small. Incomplete dives increased the sample size of dives containing rasps and whistles from tagged whales by 20% and 50%, respectively.

DISCUSSION

Animals living in cohesive social groups need to communicate in order to coordinate their activities and maintain social ties (Bradbury and Vehrencamp 1998). Communication signals are transmitted using the most appropriate media available in the habitat of each species modulated by the risk of detection by predators. Blainville's beaked whales live in apparently small populations with site fidelity (McSweeney *et al.* 2007, Baird *et al.* 2009, Schorr *et al.* 2009, Aguilar Soto *et al.* 2010), forming small groups that often dive synchronously, and reappear synchronously at the surface even after long foraging dives (Aguilar de Soto 2006, Claridge 2006). These animals would appear then to have a strong need to communicate near the surface to orchestrate reunions and foster cohesion among group members. Whales are only able to see each other at relatively short ranges through seawater and even less in the deep ocean or at night. Beaked whales may separate by hundreds of meters both at the surface and when foraging (Zimmer *et al.* 2005, Aguilar de Soto 2006), and sound is the only sensory cue available to maintain group cohesion at these distances. Surprisingly, we show here that Blainville's beaked whales that live in small cohesive groups not only spend more than 80% of their life in silence, both during day and night, but they seem to only vocalize during deep dives. The DTags used in this study had a recording bandwidth of 48 kHz or 80 kHz (used to collect 18 and 84 h of data, respectively) meaning that higher frequency vocalizations might be missed. However, tags on vocalizing animals have invariably recorded low-frequency noise associated with sound production, irrespective of the frequency range of the sounds when recorded away from the animal (Tyack 1986, Johnson *et al.* 2009). The absence of any sounds that could indicate high-frequency vocalizations in tagged whales suggest that these sounds do not occur and we conclude that all tagged whales were silent at depths shallower than 170 m.

In contrast with their silent near-surface behavior, Blainville's beaked whales are vocal at depth and emit apparent communication signals in the form of rasps and whistles at depths up to 900 m. These sounds are produced most often around the beginning of the vocal phase of deep dives, when the whales, after diving together, separate to forage at depth (Aguilar de Soto 2006), suggesting that rasps and whistles might serve a coordinating function as whales disperse. During the vocal foraging phase of the dives, the whales produce FM clicks and buzzes that, in addition to their echolocation function, may communicate positional and foraging information

to nearby eavesdroppers, as reported in Hector's dolphins, sperm whales, and bats (Barclay 1982, Dawson 1991, Madsen *et al.* 2002, Fenton 2003, Dechmann *et al.* 2009). Given the availability of echolocation sounds at depth, it remains a puzzle what kind of additional information is transmitted by rasps and whistles and why this information is only necessary in some of the deep foraging dives.

The production of whistles and rasps in coincidence with the vocal foraging phase of dives may suggest a foraging function for these sounds, but this does not seem to be the most parsimonious explanation. Whistles have been described to serve for communication in many cetacean species (Tyack 1986) and the acoustic characteristics of whistles are not well suited for echolocation. Although rasps superficially resemble buzzes, their occurrence and the movement patterns of the tagged whales while producing rasps strongly suggest that they do not have a foraging function: rasps are not associated with an increase in acceleration rate, while buzzes consistently are due to their involvement in prey acquisition attempts (Johnson *et al.* 2004). There are numerous buzzes throughout the vocal phase of foraging dives, but rasps are scarce (mean occurrence rate in complete dives is 2.5 rasps/dive *vs.* 23 buzzes/dive) and tend to occur early in dives, about when whales begin regular clicking to search for prey. Rasps also often occur in bouts involving tagged and untagged whales. Thus, rasps do not correspond to the typical pattern of long-range prey search followed by a capture attempt (Madsen *et al.* 2005*b*), and both contextual and movement data suggest that the most likely function of rasps is communication.

Although rasps and whistles are produced at the start of, or during, the echolocation phase of foraging dives, vocal communication, and the activities potentially related to it do not seem to interfere with foraging in most cases. However, two dives performed by two different whales contained numerous rasps including lengthy overlapping bouts of rasps from the tagged and nearby untagged whales. These dives also contained far fewer buzzes than did other dives by the same whales, indicating a reduced foraging rate. The atypical dives were performed by two adult males diving in groups with females and young. It is tempting to suggest that they might relate to courtship encounters or to agonistic interactions. Sexually dimorphic Blainville's beaked whales form harem-like social groups typically comprising one adult male and several females (Claridge 2006, McSweeney *et al.* 2007, Aguilar Soto *et al.* 2010), and intermale combat is thought to produce the extensive scarring on adult males (Mead 1989, MacLeod 1998). No evidence was found in the tag sound recordings for direct physical contact during the atypical dives, although a larger data set would be required to evaluate this hypothesis.

The restriction of Blainville's beaked whales whistles to deep waters may help to explain why whistles are so rare (28 whistles from tagged whales in 102 tag-hours) in comparison with other odontocetes, such as dolphins, that often produce a cacophony of whistles. Whistle production requires more air than clicks (Ridgway and Carter 1988), given the three orders of magnitude greater duration of whistles (Elsberry 2003), and Blainville's beaked whales are vocal at depths where a greatly reduced air volume is available for sound production (Madsen *et al.* 2002). In the only two experiments that address tonal sound production at depth, Jensen *et al.* (2011) observed that pilot whales tended to produce shorter and lower amplitude whistles at depth, while Ridgway *et al.* (2001) reported that only one of two belugas trained to whistle did so at a depth of 300 m. Here, we show that Blainville's beaked whales can whistle at depths up to 900 m, which, to our knowledge, is the deepest whistle reported for any marine mammal. The influence of depth on whistle characteristics could not be tested because the majority of whistles were recorded between

400 and 500 m depth, where air volume varies less than 3%. However, pressure effects may drive the uniformly short duration of Blainville's beaked whale whistles (0.2 s), less than half of the average whistle duration in other cetacean species (Rendell *et al.* 1999). A limited air volume may also cause the reduction in level of whistles produced in series. Ridgway *et al.* (2001) proposed that air recycling would be necessary to produce consecutive whistles at depth, but Blainville's beaked whales may choose instead to let whistles fade in amplitude within a series.

If the SL of rasps is similar to that of FM clicks, as it appears to be, rasps may serve for both intra- and intergroup communication. Whales vocalizing at depth may be audible to other deep receivers at substantial ranges, especially given the usual deep-water sound speed profile that tends to focus sound transmission in a deep water channel (Medwin and Clay 1998). Blainville's beaked whales clicks have been detected at ranges of up to 6.5 km by bottom-mounted hydrophones in quiet conditions (Ward *et al.* 2008), showing that animals emitting these deep echolocation calls are far from cryptic. We often observe different groups of beaked whales foraging within the study area off El Hierro (some 70 km²) and all of this area is potentially within the active space of Blainville's beaked whales rasps. Acoustic signals are used to announce presence in territories by numerous animals of different taxa (Brenowitz 1982) and this may be one function of rasps requiring a different sound from the usual pattern of echolocation FM clicks.

Restricting acoustic communication to deep dives seems to have little benefit for coordinating social interactions in Blainville's beaked whales groups. However, by only communicating at depth and performing long, silent ascents (Tyack *et al.* 2006), these whales reduce the risk of being intercepted by shallow water predators. Blainville's beaked whales live in small groups and so likely do not benefit from the social defenses against predation enjoyed by cetaceans living in larger associations (Norris and Dohl 1980). Silence at shallow depths may then be the best option to avoid predators such as killer whales that commonly prey on cetaceans (Jefferson *et al.* 1991). Killer whales are shallow divers (Baird *et al.* 2005) with a cosmopolitan distribution that are known to prey on beaked whales (Notarbartolo di Sciara 1987) and have been observed in the study site off El Hierro. Although both rasps and whistles may be detectable by predators near the surface, Blainville's beaked whales typically move a considerable horizontal distance during their prolonged silent ascents (Tyack *et al.* 2006). Thus, even though they broadcast their position during dives, it would be difficult for potential predators near the surface to track them acoustically. For Blainville's beaked whales that live in cohesive associations and coordinate their activities (Aguilar de Soto 2006, Claridge 2006), keeping silent near the surface is an unexpected behavior and strikingly in contrast with that of other toothed whales. The development of such a cryptic strategy would be explained if relatively low levels of predation may have significant demographic consequences on the apparently small local populations of this deep-diving whale.

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SUPPORTING INFORMATION

The following supporting information is available for this article online:

Appendix S1. Additional method to discriminate buzz and rasp clicks.

Figure S1. Blainville's beaked whale.

Blainville_whistles.wav. Whistles from Blainville's beaked whales recorded with DTAG off EL Hierro.

Blainville-rasps.wav. Rasps from Blainville's beaked whales recorded with DTAG off EL Hierro.