Social calls in humpback whale mother-calf groups off Sainte Marie breeding ground (Madagascar, Indian Ocean)

Anjara Saloma[*,1,2,3], Maevatiana N. Ratsimbazafindranahaka[*,1,2,3], Mathilde Martin[1], Aristide Andrianarimisa[2], Chloé Huetz[1], Olivier Adam[1,4], Isabelle Charrier[1]

[1] Institut des Neurosciences Paris-Saclay, Université Paris-Saclay, CNRS, Saclay, France
[2] Département de Zoologie et Biodiversité Animale, Université d'Antananarivo, Antananarivo, Madagascar
[3] Association Cétamada, Barachois Sainte Marie, Madagascar
[4] Institut Jean Le Rond d'Alembert, Sorbonne Université, Paris, France

[*] First authors that equally contributed to the work

Corresponding author:
Maevatiana N. Ratsimbazafindranahaka
Institut des Neurosciences Paris-Saclay (NeuroPSI), UMR 9197 CNRS
Campus CEA Saclay, 151 route de la Rotonde, 91400 Saclay, FRANCE
Email address: maevatiana.ratsimbazafindranahaka@universite-paris-saclay.fr

Abstract

Humpback whales (*Megaptera novaeangliae*) use vocalizations during diverse social interactions or activities such as foraging or mating. Unlike songs produced only by males, social calls are likely produced by all types of individuals (adult males and females, juveniles and calves). Several studies have described social calls in the humpback whale's breeding and the feeding grounds and from different geographic areas. We aimed to investigate for the first time the vocal repertoire of humpback whale mother-calf groups during the breeding season off Sainte Marie island, Madagascar, South Western Indian Ocean using data collected in 2013, 2014, 2016, and 2017. We recorded social calls using Acousonde tags deployed on the mother or the calf in mother-calf groups. A total of 21 deployments were analyzed. We visually and aurally identified 30 social call types and classified them into five categories: low, medium, high-frequency sounds, amplitude-modulated sounds, and pulsed sounds. The aural-visual classifications have been validated using Random Forest (RF) analyses. Low-frequency sounds constituted 46% of all social calls, mid-frequency 35%, and high frequency 10%. Amplitude-modulated sounds constituted 8% of all vocalizations, and pulsed sounds constituted 1%. While some social call types seemed specific to our study area, others presented similarities with social calls described in other geographic areas, on breeding and foraging grounds, and during migrating routes. Among the call types described in this study, nine call types were also found in humpback whale

40 songs recorded in the same region. The diversity of the social calls recorded in mother-calf
41 groups highlights the importance of acoustic interactions in the relationships between the mother
42 and the calf and between the mother-calf pair and the escorts.

Introduction

44 Cetaceans use acoustic communication in many social contexts such as predator alert, foraging
45 cooperation, mating, and parental care (Tyack, 1999). Humpback whales are cetaceans known
46 for their complex, highly structured, and organized songs produced by males in breeding areas
47 (Payne & McVay, 1971) but they also generate 'social sounds'. 'Social sounds' is a general
48 expression for all sounds produced outside male songs (Payne, 1978). Social sounds include non-
49 song vocalizations called 'social calls' and sounds generated by active surface behaviors
50 (breaching, tail or pectoral fins slapping, etc.). Humpback whales' social calls have been the
51 subject of several studies, both in feeding or breeding grounds, as well as on migration routes
52 (Jurasz & Jurasz, 1979; D'Vincent, Nilson & Hanna, 1985; Silber, 1986; Cerchio & Dahlheim,
53 2001; Dunlop et al., 2007; Zoidis et al., 2008; Stimpert et al., 2011; Rekdahl et al., 2013; Epp et
54 al., 2021; Epp, Fournet & Davoren, 2021; Indeck et al., 2021). These social calls vary from low
55 to high-frequency calls and differ in their general structure (cries, grumbles, snorts, pulses,
56 grunts, etc.) (Silber, 1986; Dunlop et al., 2007; Rekdahl et al., 2013). They are produced by the
57 same sound generator as for songs, located inside the respiratory system (Adam et al., 2013).
58 Individuals in all group compositions produce social calls: lone adults, singletons, multiple
59 animals, pairs, and mother-calf pairs accompanied or not by escorts (Dunlop, Cato & Noad,
60 2008). Unlike songs, social calls have been described as variable through time, interrupted by
61 silent periods, apparently unpredictable, and not showing the rhythmic, consistent and
62 continuous temporal pattern of songs (Tyack, 1981; Silber, 1986).
63   Social calls in adult humpback whales were first described as ranging from 50 Hz to over 10
64 kHz with fundamental frequencies below 3 kHz (Silber, 1986). These social calls were reported
65 to be produced when whales are predominantly in groups of three or more adults, in surface-
66 active groups including both females and males (Silber, 1986). The first recording of humpback
67 whale calves' social calls was performed by Zoidis et al. (2008) using a technique involving a
68 two-element hydrophone array. It has been suggested that calves' vocal repertoire is limited and
69 vocalizations are simple in structure, short, predominantly composed of low frequencies, and
70 have a relatively narrow frequency bandwidth (Zoidis et al., 2008).
71   Up to now, the biological functions of social calls remain unclear. Visual observations from
72 surface activity suggested that social calls could serve either as a sign of aggression among males
73 competing for the "principal escort" status (Tyack, 1983; Baker & Herman, 1984; Silber, 1986)
74 or, in some specific breeding competitive contexts, depending on sex and group composition,
75 among adults as a deterrent to dissuade approach from other whales of same or opposite sex
76 (Tyack, 1983).
77   Mother-calf pairs constitute the only stable social association on breeding grounds in
78 humpback whales. Calves are born in a rich acoustic environment filled with songs and social
79 calls. Recent acoustic studies on the social calls of humpback whales investigated vocal

80 production from mother-calf pairs (Dunlop et al., 2007; Fournet, Szabo & Mellinger, 2015;
81 Recalde-Salas et al., 2020; Indeck et al., 2021) with an attempt to assign social calls to females
82 or calves. Identifying the sound source remains a real challenge (Saddler et al., 2017; Indeck et
83 al., 2021), and thus further investigations are needed to assign accurately social call types to
84 mothers or calves.
85   The social calls of humpback whales in the South Western Indian Ocean remained poorly
86 documented. This present study aimed to investigate the repertoire of social calls recorded by
87 suction-cup acoustic tags (Acousonde 3B) attached to female humpback whales or their calf off
88 Sainte Marie island, Madagascar, South Western Indian Ocean, during four breeding seasons.
89 Our goal was to complement the knowledge of acoustic communication in poorly documented
90 yet critical social groups such as mother-calf groups and to complement the global catalog of
91 humpback whale calls.

Materials & Methods
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Study area
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94 We collected acoustic data during winters 2013, 2014, 2016, and 2017 in the coastal waters off
95 Sainte Marie island, Madagascar, South Western Indian Ocean (Between latitudes 17° 19' and 16°
96 42' South, and longitudes 49° 48' and 50° 01' East), where mother-calf pairs come in these
97 relatively calm and shallow waters (Trudelle et al., 2016).

Data collection and tagging procedure
98

99 We used Acousonde 3B (www.acousonde.com) attached to females or calves via four suction
100 cups, a non-invasive attachment system, to record sounds. We deployed tags from a 6.40-m rigid
101 motorboat using a 5-m handheld carbon-fiber pole. The boarding team consisted of staff
102 experienced in successfully approaching mother-calf pairs: one operator, photographer, note-
103 taker, and tagger.
104   For each spotted group with mother-calf pair, approaches similar to touristic boats, complying
105 with Madagascar's Code of Conduct for whale watching activities (Inter-ministerial decree
106 March 8th, 2000), were adopted: the boat's speed was reduced gradually at 800 m distance from
107 the spotted group. The observation area for mother-calf groups was set at a 200 m radius around
108 them. We used this distance to observe the groups before tag deployment. We noted the group
109 composition: lone mother-calf pair (MC) or mother-calf pair accompanied by one or several
110 escorts (MCE). Behavioral observations and photo-identification were obtained concurrently for
111 each group, and the calf's relative age was estimated using the angle of furling of its dorsal fin
112 (Huetz et al., in press; Cartwright & Sullivan, 2009): C1 (neonate) – calf presenting some folds,
113 scars, and skin color that tends to be light grey dorsally and white ventrally and with less than
114 44° dorsal fin furl (Faria et al., 2013), C2: very young but non-neonate calves having more than
115 45° but less than 72° dorsal fin furl, and C3: older calves that have unfurled dorsal fins (> 72°).
116 Depending on the opportunity and on how the group behaved, we tagged the calf or the mother
117 using either a passive or active approach, as described in Stimpert et al. (2012) and Huetz et al.
118 (in press).

119 We did not follow the animals after tag deployment to avoid further disturbance of their
120 behavior. The tags were retrieved after few hours or the following day when they detached
121 themselves from the animals. Our tagging processes lasted 21 minutes on average and never
122 exceeded 30 minutes (i.e., our maximum duration to tag a whale). All methods were carried out
123 following relevant local guidelines and regulations, and the Fisheries Resources Ministry,
124 Madagascar, approved all experimental protocols (Research and Collect permits #44/13-
125 MPRH/SG/DGPRH, #43/14-MRHP/SG/DGRHP, #28/16- MRHP/SG/DGRHP, and #26/17-
126 MRHP/SG/DGRHP). This present study complies with the European Union Directive on the
127 protection of animals used for scientific purposes (EU Directive 2010/63/EU).

128 **Vocal repertoire and acoustic analysis**
129 We downloaded the audio files from the tags as *.MT files, converted them to *.WAV format
130 using GoldWave software (GoldWave Inc.), and analyzed them using Avisoft SASLab Pro
131 version 5.207 (Avisoft Bioacoustics). We produced spectrograms of the acoustic recordings
132 using 1024-point Fast Fourier Transform, 75% overlap, and Hamming window.
133 Calls that are clearly audible and distinguishable were aurally and visually identified,
134 classified, and then compared with social call catalogs available in the literature (Dunlop et al.,
135 2007; Dunlop, Cato & Noad, 2008; Zoidis et al., 2008; Stimpert et al., 2011; Rekdahl et al.,
136 2013, 2017; Fournet, Szabo & Mellinger, 2015; Epp, Fournet & Davoren, 2021; Indeck et al.,
137 2021). Call types qualitatively similar to call types described in these catalogs were given the
138 same name. New names were given for the remaining call types based on onomatopoeia as these
139 new call types' behavioral context or biological function are still unknown and the main acoustic
140 structure can be common to several call types (e.g., several call types can be low-frequency
141 upsweep calls). Additionally, we used 16 recordings of male songs collected off Sainte Marie
142 island during the same field seasons (2013, 2014, 2016, and 2017) to determine if some social
143 calls were similar to males' song units.
144 For each identified social call, we measured several temporal and spectral characteristics. We
145 determined each call's start- and end-time on the oscillogram to determine its total duration (Dur,
146 s). From the averaged spectrum, we manually measured the fundamental frequency (F0, Hz). We
147 also performed automatic measurements on the averaged spectrum, such as the peak frequency
148 (Fmax, Hz), the energy quartiles as the frequency below which 25% (Q25), 50% (Q50), and 75%
149 (Q75) of the total energy occurred, and the frequency bandwidth within which the total energy
150 fell within 12 dB of the peak frequency (Bdw, Hz). On the spectrogram, we measured the
151 frequency excursion (Fexc, Hz) as the difference between the higher and lower frequencies
152 where applicable. Fexc (Hz) was measured on the first visible frequency band for harmonic-
153 structured calls. For calls presenting pulsed structure, we measured the pulse rate (PR, in Hz)
154 using the pulse train analysis function in Avisoft SASLab Pro (PR was considered to be zero for
155 calls without a pulsed structure). Similar to Dunlop et al. (2007), we categorized social calls as
156 either low-frequency sounds (LF), mid-frequency harmonic sounds (MF), high-frequency
157 harmonic sounds (HF), amplitude modulated sounds (AM), noisy and complex sound (NC), or
158 pulsed sounds (PS). LF corresponds to calls with peak frequency below 160 Hz. MF corresponds

159 to calls with a peak frequency ranging from 170 to 550 Hz. HF corresponds to calls with a peak
160 frequency above 700 Hz. AM corresponds to sounds consisting of a combination of long
161 harmonic and amplitude modulated components with peak frequency ranging from 20 to 300 Hz.
162 NC corresponds to broadband calls or harmonic calls with additional noise-like features. PS
163 corresponded to low-frequency sounds repeated rhythmically.

164  To validate our aural-visual classification of calls by categories and by types (Thiebault et al.,
165 2019; Indeck et al., 2021), we performed Random Forest (RF) analyses using the *randomForest*
166 package in R (Liaw & Wiener, 2002). We calculated the global accuracy of the RF classification
167 of calls by categories and by types (defined as accuracy = 1- OOB, where OOB stands for out-of-
168 bag error, the misclassification error rate) and computed the Gini index, which gives the
169 importance of the variables used for the classification. We only included acoustic variables that
170 were primarily measurable for most of the calls: Dur, Fmax, Q25, Q50, Q75, and PR. We
171 included only call types for which we had at least six exemplars. The number of variables to be
172 randomly selected at each split was set at 2 (as we had only six variables), and the number of
173 trees grown was set at 500. We used a balanced RF design to maintain equal sample sizes of
174 each category or type in the classification and avoid the over-representation of the most
175 represented classes (Chen, Liaw & Breiman, 2004). In this design, each tree of the RF is built
176 with the same number of calls per category or per type (i.e., the smallest number of calls for a
177 given category or type).

178 **Received level**
179 We measured the received level (in dB re 1µPa RMS) of the most common and aurally and
180 visually easily identifiable call types using the Root Mean Square (RMS) function in Avisoft
181 SASLab Pro. We considered only ten good quality calls with a signal-to-noise ratio above 10 dB
182 and without overlap for each selected call type.

183 # Results
184 **Tag deployments**
185 We performed 62 successful tag deployments (35 on calves and 27 on mothers) during the four
186 years of data collection. Acoustic data were usable for 21 deployments (21 different mother-calf
187 groups): seven deployments on mothers and 14 deployments on calves (Table 1). The other
188 deployments were not analyzed due to the high background noise level or their short durations
189 (less than 30 minutes). Background noise was mainly present when the tag was placed in a
190 higher position close to the dorsal fin and thus often out of the water, especially on calves for
191 which surfacing activities occurred very often. Of the 21 studied groups, we identified 12 as MC
192 and 9 as MCE. Three groups had C1 calf, three had C2 calf, and 15 had C3 calf. We detected
193 social calls in all of the studied groups.

194 **Social call classification**
195 A total of 2033 social calls were clearly distinguishable. Aural-visual characteristics allowed the
196 classification of these calls into 30 call types representing five of the six main categories

197 suggested by Dunlop et al. (2007) (Table S1): low-frequency sounds (LF), mid-frequency
198 harmonic sounds (MF), high-frequency harmonic sounds (HF), amplitude modulated sounds
199 (AM), and pulsed sounds (PS). We did not find any call corresponding to the noisy and complex
200 sound (NC) category. Eleven call types were qualitatively similar to previously described call
201 types and 17 were new (Table S1).
202   Regarding our classification validation using RFs, 757 social calls representing 17 call types
203 were eligible for the analyses. These call types were: 100 Hz, bass, boom, gru, snort, burp,
204 thowp, wop, downsweep, woohoo, trumpet, heek, whoop, squeak, ascending shriek, trill, and fry.
205 The RF showed a global accuracy of prediction of 93% for classifying the calls into the five
206 defined main categories (OOB error rate = 7%, Table 2). The acoustic variables showing the
207 highest importance for the classification were Q25, Fmax, and PR (Gini index: 10.24, 10.18, and
208 6.93 respectively, Table 2). Most call categories showed low individual classification error rates.
209 For classifying the calls by types, the RF showed a global accuracy of prediction of 77% (OOB
210 error rate = 23%, Table 3). The acoustic variables showing the highest importance for
211 classification were Fmax, Q25, and Dur (Gini index: 32.10, 31.78, and 26.94 respectively, Table
212 3). Of the 17 calls included in the RF analysis, only four call types showed exceptionally high
213 error rates ($\geq$ 50%): gru, snort, thowp, and wop. These call types may share features with other
214 call types (short, harmonic, and low-to-medium frequency calls).

Low-frequency sounds (LF)
216 LF was the most represented category (46%, N = 925/2033). Eleven call types were within the
217 LF category: 100 Hz sound, bass, boom, gru, snort, burp, guttural, thowp, wop, bark, and drum
218 (Fig. 1). Bass and wop were the most common LF calls (heard in eight groups each), followed by
219 100 Hz and thowp (seven groups), gru and snort (six groups), and by boom (four groups). The
220 remaining LF calls were rare (head in two groups for drum and only one group for guttural, burp,
221 and bark). Burp, bark, and drum were only heard in MC groups. The remaining LF calls were
222 heard in both MC and MCE groups. Bass was a harmonic sound with a fundamental frequency
223 below 40 Hz on average. Bass can sometimes be masked by background noise. Wop and thowp
224 were brief harmonic upsweep sounds similar in frequency but different in duration. The 100 Hz
225 call was a long, relatively flat call. Gru was a short harmonic sound like snort but with more
226 spaced harmonics. Snort can be produced in sequences. Boom was a harmonic sound produced
227 either in sequence or alone. Boom was frequently produced in series with 100 Hz following a
228 well-defined order (100 Hz – boom – boom – 100 Hz). Guttural appeared to be a "composite
229 call" consisting of one gru and one heek (MF) without silence between the two. Drum was a very
230 short call always produced in series, and burp was a short harmonic sound with several close
231 harmonics. Bark was a short harmonic sound with ascending frequency modulation.

Mid-frequency harmonic sounds (MF)
233 MF was the second most represented category (35%, N = 718/2033). Eight call types were within
234 the MF category: groan, downsweep, woohoo, trumpet, heek, whoop, wiper, and creak (Fig.2).
235 Heek was the most common MF call (heard in nine groups), followed by whoop (seven groups),

236   downsweep and woohoo (five groups), and by trumpet (three groups). Groan, wiper, and creek
237   were uncommon (heard in one group only). Groan, wiper, and creak were only heard in MC
238   groups. The remaining MF calls were heard in both MC and MCE groups. Heek was a short MF
239   call with a variable frequency modulation pattern (ascending, descending, or modulated). In
240   some instances, heek was produced with gru (LF), with a short silence separating the two
241   vocalizations to constitute a "combined call." Whoop was a long upsweep call starting with a flat
242   part and fast ascending frequency. Downsweep was a long call showing a descending frequency
243   slope with well-spaced harmonics. Woohoo was a long-duration call (i.e., several seconds)
244   showing a variable frequency-modulated pattern. Trumpet was a call produced alone or
245   associated with gru or slight snort. Downsweep, woohoo, and trumpet were found in humpback
246   whale songs recorded around the study site. Groan was a long harmonic call. Wiper was a short
247   harmonic sound with a U-shape frequency modulation pattern, always produced in series (four to
248   five repetitions) but with a random temporal pattern. Creek was a composite call constituted by
249   two different successive sounds without silence, and it showed the widest frequency bandwidth.

250   **High-frequency harmonic sounds (HF)**
251   HF was the third most represented category (10%, $N = 202/2033$). Two social calls were within
252   this category: squeak and ascending shriek (Fig. 3). Both were quite common: squeak was heard
253   in seven groups, and ascending shriek was heard in four groups. Squeak and ascending shriek
254   were heard in both MC and MCE groups. Squeak was a very short call with frequencies above 1
255   kHz, and ascending shriek was one of the longest social calls with the highest frequencies
256   amongst all. Both squeak and ascending shriek were also found in humpback whale songs
257   recorded around the study site.

258   **Amplitude modulated sounds (AM)**
259   AM was the fourth most represented category (8%, N = 167/2033). Five social calls were within
260   the AM category: door, whine, trill, bug sound, and AM grunt (Fig. 4). AM grunt and trill were
261   the most common MF calls (heard in six and five groups, respectively). The remaining calls were
262   relatively uncommon since they were heard only in one group each. Door was heard in a MC
263   group. Whine and bug were found in MCE groups only. Trill and AM grunt were heard in both
264   MC and MCE groups. Trill, door, whine, and bug are long calls ranging from one to five seconds
265   duration with a peak frequency ranging from 100 to 400 Hz. They were produced in bouts of
266   random durations. AM grunt was short and, while commonly produced alone, it was sometimes
267   associated with LF calls such as gru or snort. Whine, trill, and bug were also found in humpback
268   whale songs recorded around the study site.

269   **Pulsed sounds (PS)**
270   PS was the least represented category (1%, $N = 21/2033$). Four social calls were classified in this
271   category: fry, bubble sound, moped, and gloop (Fig. 5). These calls consisted of a repetition of
272   very short, low-frequency sounds, and they were pretty uncommon. Fry was heard in two groups
273   and the remaining PS calls were heard in only one group each. Fry was heard in both MC abd

274   MCE groups. Bubble sound was heard in a MC group. Moped and gloop were only found in
275   MCE groups.

Received level

277   Five call types were selected for the calculation of the received level: three LF (100 Hz, bass,
278   and boom), one AM (trill), and one MF sound (heek). The received level ranged from 132 to 154
279   dB re 1μPa RMS with an average of 141 dB re 1μPa RMS ($N = 50$, 10 per call type; Table 4).

Discussion

281   Humpback whales' vocal activity is well known for its diversity and complexity at individual,
282   group, and population levels. Social calls occur in all group compositions, in both breeding and
283   foraging grounds as well as on migratory routes (Dunlop et al., 2007; Dunlop, Cato & Noad,
284   2008; Zoidis et al., 2008; Stimpert, 2010; Rekdahl et al., 2013; Fournet, Szabo & Mellinger,
285   2015; Recalde-Salas et al., 2020; Epp et al., 2021; Epp, Fournet & Davoren, 2021; Indeck et al.,
286   2021). The aural-visual analysis allowed us to identify 30 social calls distributed into five main
287   call categories (LF, MF, HF, AM, PS) for mother-calf groups off Sainte Marie island. Our RF
288   analyses showed a relatively high precision that demonstrates our aural-visual classification's
289   robustness.
290   We could not establish if sounds were produced either by the mother or the calf or by any
291   nearby conspecifics (i.e., escort) in our acoustic recordings. Indeed, the accelerometer data of the
292   tag (Goldbogen et al., 2014) could not be used to assign caller identity as the sampling rate used
293   was 10 Hz, and even if our sampling rate was higher than 10 Hz, the close spatial proximity
294   between a mother and her calf makes such methodology unreliable (Saddler et al., 2017). On the
295   other hand, received levels alone are insufficient for assigning caller identity as most calls may
296   show low amplitude levels, and several animals may be present around the tagged animal
297   (Stimpert et al., 2020). The calls described in the present study are thus considered as the
298   acoustic output of mother-calf groups (including possible escort). Further investigations are still
299   needed to assign each recorded social call to an individual. We are currently planning to explore
300   the possibility of using simultaneous deployment on the mother and the calf to determine the
301   caller's identity. Combining the received level of the same call on two different tags and the
302   vertical distance between the mother and her calf (obtained from the diving profile) may allow
303   the attribution social call to the corresponding individual.
304   Nine call types out of 30 we aurally and visually identified were similar to song units
305   recorded during other days off the Sainte Marie island between 2013 and 2017 and were detected
306   even in groups identified as MC, except for whine and bug sound. Assuming that mother-calf
307   group composition did not change through the recordings' duration, the detection of sounds
308   similar to song units in groups composed only of a female and a calf (MC groups) suggests that
309   female humpback whales (or even calves) are able produce sounds with similar acoustic features
310   as males' song units.
311   Some social calls recorded in mother-calf groups off Sainte Marie island presented qualitative
312   similarities to those described in other geographic areas during the breeding, feeding seasons, or

313   migrating routes and were assumed to be the same call type. Those calls included snort, thowp,
314   wop (also known as whup), bark, groan, trumpet, squeak, ascending shriek, trill, and AM grunt
315   (Dunlop et al., 2007; Dunlop, Cato & Noad, 2008; Zoidis et al., 2008; Stimpert et al., 2011;
316   Rekdahl et al., 2013, 2017; Fournet, Szabo & Mellinger, 2015; Epp, Fournet & Davoren, 2021;
317   Indeck et al., 2021). Given the wide range of contexts within which these calls were detected
318   (different group types, from breeding areas to feeding areas), these social calls are probably
319   among the most common in humpback whales, and they may have important social roles. These
320   social calls may constitute a global repertoire shared by humpback whales around the world.
321   Further studies are needed to determine their behavioral context and roles, especially for mother-
322   calf pairs.
323   Social calls were detected even in mother-calf groups with neonate calf (C1 class), suggesting
324   that vocal exchanges between mother and calf occur very soon right after birth. Such vocal
325   interactions may be a way to reinforce the calf's social bond with the mother and to imprint the
326   calf's voice on the mother. Calves have been reported to vocalize, and they can produce series of
327   grunts, predominantly low-frequency sounds with a relatively narrow bandwidth (Zoidis et al.,
328   2008). In our acoustic recordings, one call type, heek, is very similar to the amplitude modulated
329   frequency sounds described by Zoidis et al. (2008), and thus, heek may be potentially assigned to
330   calves.
331   We identified calls that can be combined or mixed with a given call type. Such a combination
332   has not been previously described in humpback whales. Composite or concatenated calls have
333   only been documented for few species (Koren & Geffen, 2009; Ouattara, Lemasson &
334   Zuberbühler, 2009; Jansen, Cant & Manser, 2012, 2013; Déaux, Charrier & Clarke, 2016).
335   Concatenated calls often have different biological functions than calls produced separately, as
336   shown for the bark-howl vocalizations in dingo (*Canis familiaris dingo*) (Déaux, Charrier &
337   Clarke, 2016).
338   Compared to the East-Australian catalog (Dunlop et al., 2007) for which recordings were
339   performed on migrating humpback whales of different group compositions (i.e., with or without
340   calves), our repertoire contained fewer main categories (5 versus 6), a similar number of call
341   types (30 versus 34, with eight shared call types), and a lower proportion of social calls also used
342   in songs within the studied area (nine out of 32 in Madagascar versus 22 out of 34 in Eastern
343   Australia; Dunlop et al., 2007). A repertoire with 16 call types has been described for the
344   Southeast Alaskan humpback whales, with three calls likely shared with our repertoire (Fournet,
345   Szabo & Mellinger, 2015). Newfoundland's (Canada) repertoire consisted of 13 calls types and
346   shared only one call type with our repertoire. A standardized comparative study using the same
347   recording methods among these different areas is needed to accurately determine if a given call
348   type is really unique to a population/area, as well as to confirm if the described call types are
349   indeed new ones or a variation of one (previously described) call type. Our results, however,
350   along with these previous descriptions of the repertoire of the humpback whale, support the
351   existence of a highly diversified repertoire of social calls in a humpback whale. Our results also
352   suggest that there is likely as much call diversity in mother-calf groups as in other social groups.

353 Other acoustic studies focusing on mother-calf pairs also support the occurrence of such
354 diversity (Indeck et al., 2021).

355   Regarding our analysis on received levels, we found that calls recorded in mother-calf groups
356 were produced at a low amplitude level, as found previously (Tyack, 1983). The received levels
357 ranged from 132 to 145 dB re 1μPa RMS, which is low compared to the estimated received level
358 from singers of 149-169 dB re 1μPa (Au et al., 2006). Our results are consistent with a recent
359 study on mother-calf pairs in Australia (136 to 141 dB re 1μPa RMS; Videsen et al., 2017). Such
360 low-amplitude vocal production in a mother-offspring pair is quite common in mammals, such as
361 in pinnipeds (walrus; Miller, 1966; Charrier, Aubin & Mathevon, 2010), sheep (low-pitch bleats;
362 Sèbe et al., 2010), and cats (purring sounds; Peters, 2002). Low amplitude level in the context of
363 mother-offspring interactions is not surprising as the communication between the mother and her
364 calf is short- to medium-range, and the purpose is likely to maintain social contact and reinforce
365 the social bond and maternal attachment with the calf. In a short-range communication context,
366 why yelling when talking is sufficient? Antipredator strategy and male escort avoidance may
367 also be hypothesized to explain such low-amplitude calls (Videsen et al., 2017).

Conclusions

369 Our study provides a first assessment of the vocal repertoire of humpback whale mother-calf
370 groups off Sainte Marie island, Madagascar, South Western Indian Ocean. We found that social
371 calls recorded in these mother-calf groups are highly diversified and may be as diverse as those
372 of the other social groups. A low acoustic intensity level characterized these social calls. The
373 results suggest important vocal interactions between mother and calf and between the mother-
374 calf pairs and the escorts. Our study contributes to the global catalog of humpback whale calls
375 and can be a starting point in investigating the role of acoustic communication in humpback
376 whale mother-calf interactions.

Acknowledgements

378 We thank everyone involved in humpback whale research in Madagascar: Cétamada team
379 (François-Xavier Mayer, Henry Bellon, and Didier Cabocel) and all the eco-volunteers who
380 dedicated their time and energy to this project.

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Figure 1

Spectrograms of low-frequency sounds (LF). A: 100 Hz, B: bass, C: boom, D: gru, E: snort, F: burp, G: guttural sound, H: thwop, I: wop, J: bark, K: drum.

Most of LF sounds were harmonic-structure sounds, produced alone, except boom and snort that can be produced in sequences. Drum sounds were always produced in series. Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap. Generated using Seewave.

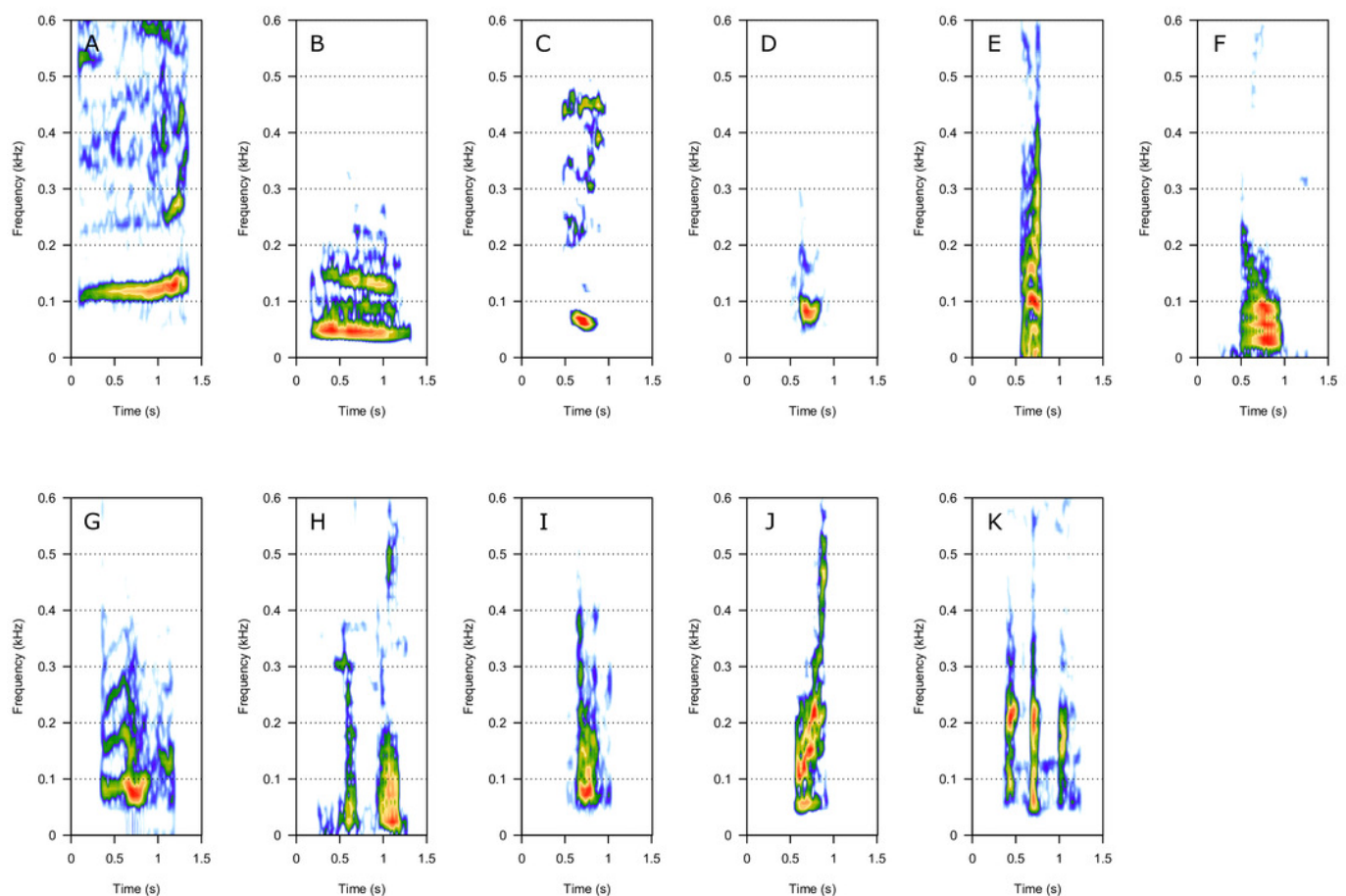



Figure 2

Spectrograms of mid-frequency harmonic sounds (MF). A: groan, B: downsweep, C: woohoo, D: trumpet, E: heek, F: whoop, G: wiper, H: creak.

Downsweep, woohoo and trumpet call were also found in humpback whale songs recorded around the study site. Heek was produced in association with Gru (LF) in some instances. Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap. Generated using Seewave.

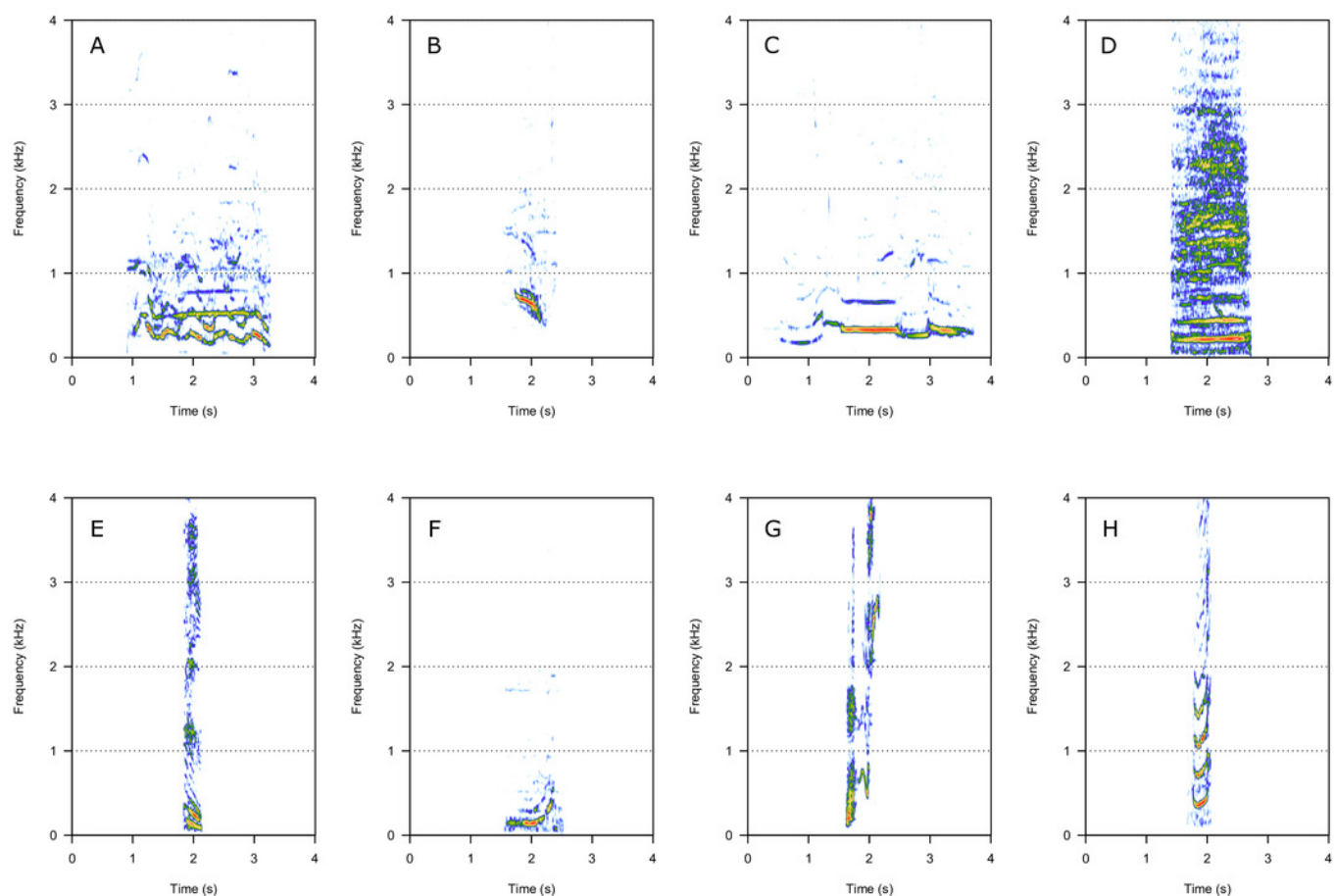



Figure 3

Spectrograms of high-frequency sounds (HF). A: squeak, B: ascending shriek.

Squeak was a very short call with frequencies above 1 kHz and ascending shriek was one of the longest social call types with the highest frequencies among all call types. Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap. Generated using Seewave.

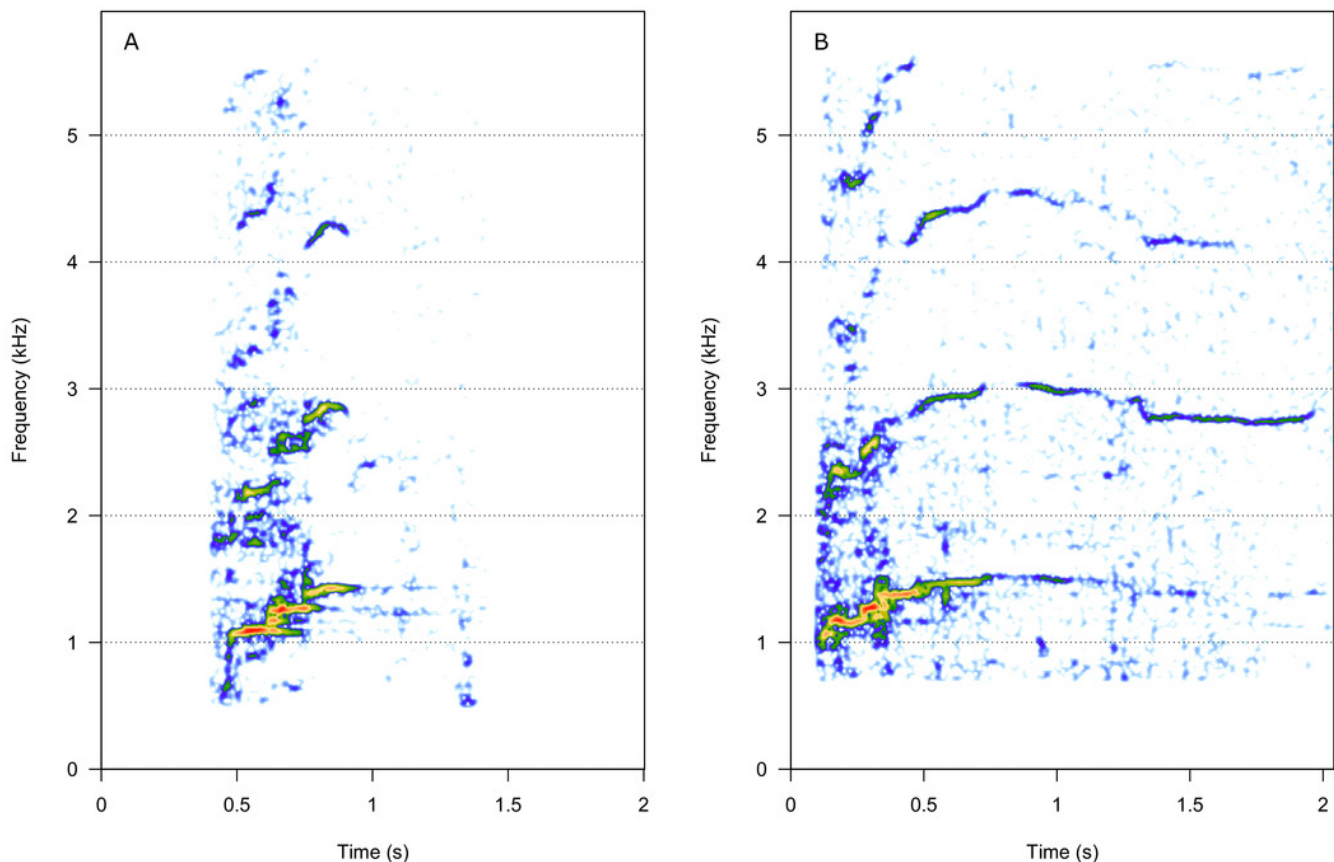



Figure 4

Spectrograms of amplitude-modulated sound (AM). A: door, B: whine, C: trill, D: bug sound, E: AM grunt.

AM sounds are long calls except for AM grunt, and ranged from 1 to 5 seconds with a peak frequency between 100 and 400 Hz, produced in bouts of random durations. Whine, trill, and bug sound were also found in humpback whale songs recorded around the study site. Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap. Generated using Seewave.

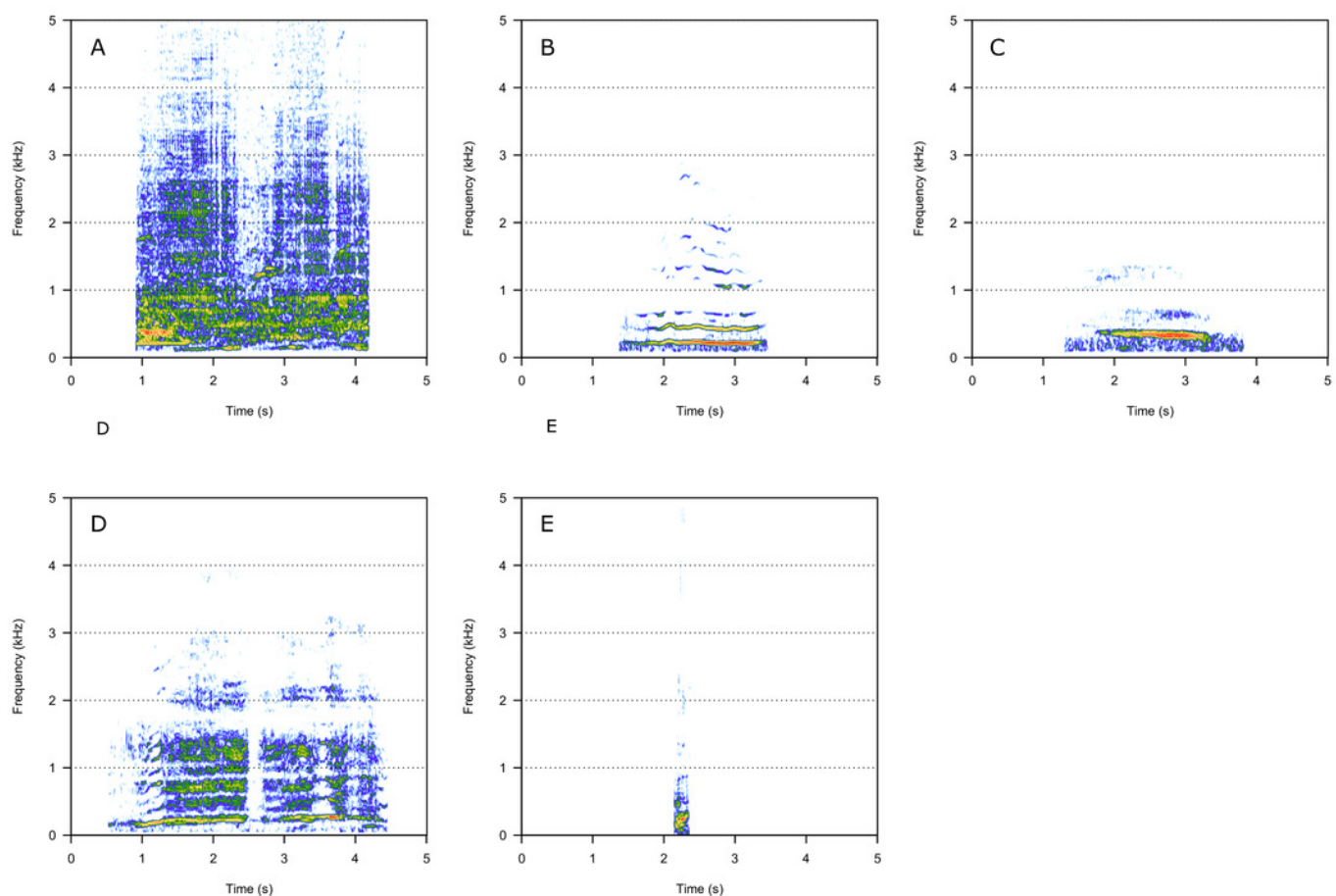
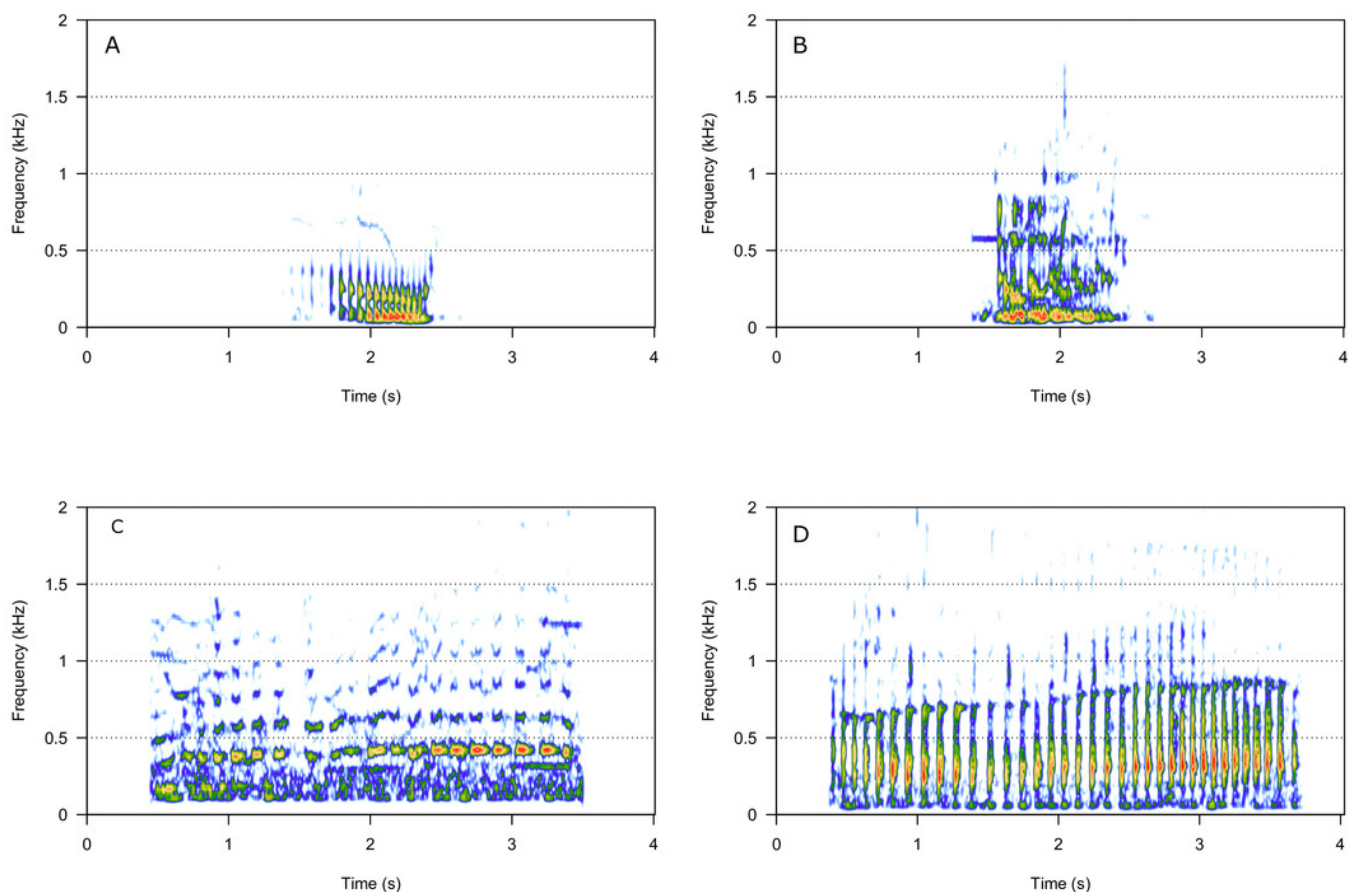



Figure 5

Spectrograms of pulsed sound (PS). A: fry, B: bubble sound, C: moped, D: gloop.

PS are repetitive short and low frequency sounds. Spectrogram parameters: Hamming window, FFT window size: 1024 pts, 90% overlap. Generated using Seewave.

Details of the tagging sampling effort. MC: lone mother-calf pair. MCE: mother-calf pair accompanied by one or several escorts.

C1 (neonate) – calf presenting some folds, scars, and skin color that tends to be light grey dorsally and white ventrally and with less than 44° dorsal fin furl. C2: very young but non-neonate calves having more than 45° but less than 72° dorsal fin furl. C3: older calves that have unfurled dorsal fins (> 72°).

Date	Tagged individual	Group type	Calf relative age	Analyzed recording duration
07/08/2013	Mother	MCE	C3	04:05
16/08/2013	Mother	MCE	C1	01:22
05/09/2013	Mother	MC	C3	01:26
09/09/2013	Mother	MCE	C3	00:39
12/09/2013	Calf	MC	C3	03:14
15/09/2013	Calf	MCE	C3	01:06
05/08/2013	Mother	MC	C3	05:15
24/08/2014	Mother	MC	C3	02:00
26/08/2014	Mother	MCE	C2	14:23
29/08/2014	Calf	MC	C3	00:27
08/09/2014	Calf	MCE	C3	03:27
09/09/2014	Calf	MC	C3	05:00
10/09/2014	Calf	MC	C1	02:15
11/09/2014	Calf	MCE	C2	00:35
17/09/2014	Calf	MC	C3	00:28
11/08/2016	Calf	MCE	C2	05:38
17/08/2016	Calf	MCE	C3	07:14
18/08/2016	Calf	MC	C1	10:14
05/09/2016	Calf	MC	C3	07:46
28/08/2017	Calf	MC	C3	05:32
01/09/2017	Calf	MC	C3	02:30

Random Forest classification matrix for mother-calf social call categories.

The overall error rate (out-of-bag error rate, OOB) was 7%. The last column indicates the classification error for each main call category. The bottom lines show the used acoustic variables along with the Gini index reflecting their relative importance in the classification.

		Predicted class					
		AM	HF	LF	MF	PS	Error
	AM	21	0	0	2	0	0.09
	HF	0	94	0	0	0	0
True class	LF	0	0	438	16	0	0.04
	MF	17	7	8	143	0	0.18
	PS	0	0	0	0	11	0
Variables		Q25	Fmax	PR	Dur	Q50	Q75
Gini index		10.24	10.18	6.93	6.85	5.1	4.68

Random Forest classification matrix for mother-calf social call types.

The overall error rate (out-of-bag error rate, OOB) was 23%. The last column indicates the classification error for each main call type. The bottom lines show the used acoustic variables along with the Gini index reflecting their relative importance in the classification.

	Predicted class																	
	100 hz	Bass	Boom	Gru	Snort	Burp	Thowp	Wop	Downsweep	Woohoo	Trumpet	Heek	Whoop	Squeak	Ascending shriek	Trill	Fry	Error
100 Hz	132	0	7	0	4	0	0	0	0	0	0	8	0	0	0	0	0	0.13
Bass	0	49	0	4	1	2	0	1	0	0	0	0	0	0	0	0	0	0.14
Boom	18	0	121	0	3	0	0	1	0	0	0	13	0	0	0	0	0	0.22
Gru	0	1	1	6	0	1	3	0	0	0	0	0	0	0	0	0	0	0.5
Snort	4	0	0	2	21	0	8	4	1	0	0	3	0	0	0	0	0	0.51
Burp	0	0	0	1	0	12	0	1	0	0	0	0	0	0	0	0	0	0.14
Thowp	1	0	1	1	5	0	0	1	0	0	0	0	0	0	0	0	0	1
Wop	0	1	0	0	2	1	2	5	0	1	0	0	0	0	0	0	0	0.58
Downsweep (True class)	0	0	0	0	0	0	0	0	27	8	0	0	5	0	1	1	0	0.36
Woohoo	0	0	0	0	0	0	0	0	6	18	0	0	0	0	0	4	0	0.36
Trumpet	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	3	0	0.23
Heek	2	0	0	0	0	0	0	0	0	0	0	11	0	1	2	0	0	0.31
Whoop	0	0	0	0	0	0	0	0	6	4	2	3	61	0	0	0	0	0.2
Squeak	0	0	0	0	0	0	0	0	0	0	0	1	0	68	7	0	0	0.11
Ascending shriek	0	0	0	0	0	0	0	0	0	0	0	0	0	2	16	0	0	0.11
Trill	0	0	0	0	0	0	0	0	2	2	1	0	0	0	0	18	0	0.22
Fry	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0
Variables	Fmax		Q25		Dur		Q50		Q75		PR							
Gini index	32.10		31.78		26.94		24.78		20.74		7.52							

Received level measured for the most common and aurally and visually easily identifiable call types.

Calls	Amplitude Received level (in dB re 1µPa RMS)	N	Tagged individual
100Hz	141 ± 4	10	Mother
bass	154 ± 6	10	Mother
boom	135 ± 3	10	Mother
trill	132 ± 2	10	Mother
heek	145 ± 6	10	Calf