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# **Behavioural context of call production in humpback whale calves: identification of potential begging calls in a mysticetes species**

Maevatiana Nokoloina Ratsimbazafindranahaka, Chloé Huetz, Anjara Saloma, Aristide Andrianarimisa, Olivier Adam, Isabelle Charrier

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# 1 **Behavioural context of call production in humpback**

## 2 **whale calves: Identification of potential begging calls in a**

### 3 **Mysticete species**

4 Maevatiana Nokoloina Ratsimbazafindranahaka<sup>1,2,3</sup>, Chloé Huetz<sup>1</sup>, Anjara Saloma<sup>3</sup>, Aristide Andrianarimisa<sup>2</sup>,  
5 Olivier Adam<sup>1,4</sup>, Isabelle Charrier<sup>1</sup>

6 <sup>1</sup> Institut des Neurosciences Paris-Saclay, Université Paris-Saclay, CNRS, Saclay, France

7 <sup>2</sup> Département de Zoologie et Biodiversité Animale, Université d'Antananarivo, Antananarivo, Madagascar

8 <sup>3</sup> Association Cétamada, Ambodiforaha Sainte Marie, Madagascar

9 <sup>4</sup> Institut Jean Le Rond d'Alembert, Sorbonne Université, Paris, France

#### 10 **Corresponding Author**

11 Maevatiana Nokoloina Ratsimbazafindranahaka

12 Institut des Neurosciences Paris-Saclay (NeuroPSI), UMR 9197 CNRS

13 Campus CEA Saclay, 151 route de la Rotonde, 91400 Saclay, FRANCE

14 Email address: maevatiana.ratsimbazafindranahaka@universite-paris-saclay.fr

15 ORCID: 0000-0001-8916-237X

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## 24 **Abstract**

25 Baleen whale calves vocalize, but the behavioural context and role of their social calls in mother-calf interactions are  
26 yet to be documented further. We investigated the context of call production in humpback whale (*Megaptera*  
27 *novaeangliae*) calves using camera-equipped animal-borne multi-sensor tags. Behavioural states, including suckling  
28 sessions, were identified using accelerometer, depth, and video data. Call types were categorized through clustering  
29 techniques. We found that call types and rates predict the occurrence of a given state. Milling, resting, and traveling  
30 were associated with a median call rate of 0 calls min<sup>-1</sup>, while surface play, tagging responses, and suckling were  
31 associated with higher call rates, averaging up to a median of 0.5 calls min<sup>-1</sup> for suckling. Suckling sessions were  
32 associated with three sets of low-frequency calls corresponding to previously described burping, barking, and  
33 snorting sounds. Surface play sessions featured mid-frequency calls with whoop-like sounds and other call types.  
34 These results address the significance of vocal signalling in mother-calf communication and the calf's development,  
35 including the first identification of potential begging calls. Overall, this study offers new insights into baleen whale  
36 behaviour, underscores the importance of social calls in mother-calf interactions, and enhances our understanding of  
37 communication systems in aquatic mammalian mother-young pairs.

38 **KEYWORDS:** begging, classification, marine mammals, mother-offspring, vocalizations

## 39 **Background**

40 Mammals mainly rely on their mother during their early life stage to survive. Their mother provides critical care such  
41 as food provisioning, protection from predators, warmth, teaching, etc. [1,2]. For such care to be optimal, the mother  
42 and offspring must communicate with each other. For instance, the offspring must communicate its needs to its  
43 mother [3–5]. In mammals that use the ‘following’ anti-predation strategy, the mother must encourage following  
44 when necessary to ensure that the offspring stays in proximity so she can protect it [4]. More generally, the mother  
45 and the offspring need to communicate their identity to each other so that the mother avoids spending resources on  
46 non-filial young (targeted investment) and the offspring avoids going towards potentially aggressive conspecifics  
47 [3,4,6]. Various modalities can be used, such as olfactory, visual, tactile, and acoustic cues [3,4,6].

48 In aquatic environments, the use of acoustic signalling is one of the best strategies to communicate, as acoustic  
49 signals are efficient at both short and long ranges and are possible to detect and localize given an adequate auditory

50 system [7], in contrast to visual and chemical cues that do not provide such advantages. As such, cetaceans or  
51 whales, a group of fully aquatic mammals, evolved a communication system mainly based on sounds, vocally  
52 produced or not [8]. In baleen whales (mysticetes), non-vocal sounds include percussive sounds from surface  
53 activities such as tail slaps, pectoral slaps, breaching, etc., and vocal sounds encompass songs [8–12] and social calls  
54 [8,12–14] thought to be produced by circulating air from the lungs to the laryngeal sac or vice versa to vibrate the U-  
55 fold [15–17]. Songs are vocalizations organized in a repeated manner and typically in long bouts, primarily  
56 associated with reproduction and only produced by males. In contrast, social calls are vocalizations produced by all  
57 individual categories (males, females, juveniles, calves) in various contexts, variable through time, interrupted by  
58 silent periods, apparently unpredictable, and not showing a stereotyped rhythmic, consistent, and continuous  
59 temporal pattern of the same level as songs [14,18].

60 The behavioural context of social calls among baleen whales has been studied for years. Studies have notably been  
61 conducted on species such as the blue whale (*Balaenoptera musculus*) [19,20], humpback whale (*Megaptera*  
62 *novaeangliae*) [14,21–26], right whale (*Eubalaena glacialis*) [27], and even the minke whale (*B. bonaerensis*) [28].  
63 However, our knowledge remains somewhat limited regarding the specific case of mother-calf pairs. It is understood  
64 that these pairs produce vocalizations, albeit at a typically lower rate than other social groups [29–33]. Nonetheless,  
65 the significance of their calls in mother-calf interactions and for the calf itself is still not well understood.

66 In humpback whales, given the relatively extensive vocal repertoire of mother-calf pairs [30], it is anticipated that  
67 social calls serve various purposes/correspond to various categories, such as contact calls, alarm calls, distress calls,  
68 and begging calls. For instance, contact calls are vocalizations used to keep in touch and transmit information about  
69 the caller [34]. These calls are especially crucial in mammalian mother-young pairs, where staying close spatially  
70 and socially is essential for the young's survival [35,36]. Alarm and distress calls are vocalizations used to signal  
71 danger or distress, alerting other individuals to potential environmental threats [37–39]. For mother-young pairs,  
72 alarm and distress calls are critical for the young's survival; a mother might use alarm calls to alert her young to the  
73 presence of predators or other dangers, and the young might use distress calls in distressing situations to elicit  
74 responses from the mother. Begging calls are vocalizations typically produced by an individual to express their  
75 nutritional needs to their caregiver, and the caregiver uses them to regulate and adapt their provisioning rate [40–42].  
76 In the case of mammalian mother-young interactions during the first stage of a young's life, begging for milk is the

77 primary form of begging, helping the mother know the calf's need for milk and respond accordingly. This  
78 communication is vital for the young's growth and well-being.

79 The context and function of calls in mother-calf interactions have been particularly studied in humpback whales  
80 among baleen whales due to their relatively accessible nature. For instance, Zoidis et al. [24] noted that certain social  
81 calls seemed to prompt the mother's approach and were interpreted as the calf's isolation or alarm calls to alert or call  
82 the mother. Videsen et al. [25] discovered that nursing initiation was not based on acoustic cues but rather on tactile  
83 signals, which was unexpected. They suggested that social calls serve more of a cohesive function in maintaining  
84 contact during active dives. Indeck et al. [26] found that during resting periods, associated with more frequent  
85 separations, the vocal activity in mother-calf pairs increased, supporting the hypothesis that some calls function as  
86 contact calls. Data from Ratsimbazafindranahaka [43] further suggested that the calf is primarily responsible for  
87 acoustic contact. One limitation of several of these studies in understanding further the role of social calls was the  
88 focus on overall vocal activities (the occurrence of any call) rather than specific call types.

89 Several challenges make it difficult to study the behavioural context of social call production in baleen whale calves.  
90 First, the existence of graded calls makes it challenging to objectively fully separate social calls into distinct call  
91 labels (types) with sufficient reproducibility to associate them with behaviours [30,44]. Nevertheless, unsupervised  
92 learning or clustering [45], i.e., automatically finding clusters from unlabelled data, can be a starting point to identify  
93 call categories if a set of closely related calls is explicitly used in a given context.

94 Another challenge concerns the data acquisition itself. Animal-borne multi-sensor tags are now routinely used to  
95 study whales' behaviour and vocalizations [20,25,26,28,46] as they allow to accurately track and describe the  
96 underwater activities of whales and focus on an individual. Unfortunately, when the studied individual is a mother or a  
97 calf, the identification of the caller is problematic as a tag placed on a mother may also record calls from the calf  
98 and vice-versa. As a result, tag-based studies attempting to associate vocalizations to behaviours in mother-calf  
99 groups thus often did not distinguish between the calls from the mother and the calf and assumed that the studied  
100 calls represent the total vocal output of the mother-calf pair [25]. Recent results based on data from simultaneous  
101 deployments on mother and calf, however, suggest that most calls (90%) recorded by a tag placed on a calf are more  
102 likely from the calf than from the mother, at least for low-frequency calls (which represent the majority of calls  
103 produced in mother-calf pairs) [43]. This conclusion was supported by a comparison of the acoustic features of calls

104 recorded simultaneously on both the calf and mother's tags with calls recorded exclusively on the calf's tag versus  
105 those recorded only on the mother's tag.

106 In the present study, we investigated the behavioural context of social calls recorded by tags equipped with a video  
107 camera placed on humpback whale calves off Sainte Marie Island, Madagascar, South Western Indian Ocean, with  
108 the assumption that calls recorded by a tag placed on a calf mainly record the calls from the calf as suggested by the  
109 data from Ratsimbazafindranahaka [43]. We aimed to gain insights into the relationship between activities and calf  
110 vocalizations in baleen whales and understand the potential roles of the various call types they produce.

## 111 **Methods**

### 112 **Dataset**

113 We used data from CATS cam tags, sets of sensors including a depth sensor, a 3-axis accelerometer, a hydrophone,  
114 and a video camera, placed on the back of eight young humpback whale calves (< 3-month-old given the season –  
115 see below – and their relatively small size, i.e., not more than half the size of their mother), for which the amplitude  
116 of the sound recorded by the hydrophone was not saturated (usually due to very high flow noise, which is related to  
117 tag placement and orientation). The average data duration per calf was  $4.1 \pm 2.5$  hours (range = 1–8.2 hours), and the  
118 total was 32.6 hours. The data were collected off Sainte Marie Island, Madagascar, South Western Indian Ocean,  
119 during the winter (breeding/calving season) of 2022 under the Malagasy national research permit #54/22-  
120 MPEB/SG/DGPA delivered by Ministry of Fisheries Resources, Madagascar, and are part of the data presented by  
121 Ratsimbazafindranahaka et al. [47,48]. The data collection complies with the European Union Directive on the  
122 Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU). Detailed tagging procedures and tag  
123 specifications have been presented elsewhere [30,47,49,50].

### 124 **Call analysis**

125 We analysed the acoustic recording using Avisoft SASLab Pro version 5.3.01 (Avisoft Bioacoustics, Nordbahn,  
126 Germany). We produced spectrograms of the acoustic recordings using a 1024-point Fast Fourier Transform, 75%  
127 overlap, and Hamming window. We inspected the audio files aurally and visually to isolate clearly distinguishable  
128 social 'calls', i.e., sounds vocally produced and excluding non-vocally produced social sounds such as surface  
129 percussive sounds – breaches, slaps –, apparent bubble sounds, rubbing sounds, etc. [24,30]. We distinguished the  
130 social calls from the male songs in the background based on the temporal pattern and overlaps [30]. For each

131 distinguishable social call, we measured seven acoustic features: the duration (Dur, in s), the peak frequency (Fmax,  
132 in Hz), the first, second and third energy quartile frequency (Q25, Q50, Q75 respectively, in Hz), the frequency  
133 bandwidth within which the total energy fell within 12 dB of Fmax (Bdw, in Hz), and the fundamental frequency  
134 (F0, in Hz). The duration of the call was measured on the oscillogram. The spectral characteristics were measured on  
135 the averaged spectrum (frequency ranges: 30-1000 Hz for low-frequency calls with peak frequency < 160 Hz, and  
136 100-6000 Hz for mid- and high-frequency calls with peak frequency from 160 to 700 Hz and > 700 Hz,  
137 respectively). All measurements of spectral characteristics were performed automatically except for the F0, which  
138 was measured manually using the harmonic cursor available in Avisoft SASLab Pro to find harmonic structures on  
139 the averaged spectrum.

#### 140 Behavioural state definition

141 The data from each calf were broken down into sequences constituted by six possible behavioural states: suckling  
142 session (*Suckl.*), surface play session (*Play*), traveling (*Travel*), milling (*Mil.*), response to tag deployment (*Tg. res.*),  
143 and resting (*Rest*). These states were defined by a classification algorithm using a combination of depth, 3D  
144 accelerometer, sound, and video data. First, the data were globally broken down into four base states based on the  
145 calf's relative speed (obtained by z-scoring the flow noise recorded by the hydrophone within the 66-94 Hz  
146 frequency band [51]), using a first-order Hidden Markov Model trained on multi-sensor tag data collected since 2013  
147 in the study site: Lv0, Lv1, Lv2, Lv3, from the one with the lowest speed to the one with the highest, respectively  
148 (see [48]). Concurrently, suckling events were visually identified on the video data [47], except during periods of  
149 uncertainty due to tag movement (camera not directed forward). During those exceptions (12% of the data), the  
150 suckling events were identified automatically based on the 3D accelerometry data and depth data using a supervised  
151 automatic detection method (see [47]). Subsequently, (1) any state during which a suckling event occurred plus the  
152 state directly before was considered as a suckling session (*Suckl.*), (2) any Lv2 and Lv3 states during which the calf  
153 was observed displaying surface active behaviours (breaches, head slaps, pectoral slaps, etc.) was considered as  
154 surface active playing session (*Play*), (3) any Lv2 and Lv3 states, except those occurring immediately after the  
155 tagging, were considered as traveling (*Travel*) if the mother was swimming alongside the calf at approximately the  
156 same pace, (4) any Lv2 and Lv3 states during which the mother was resting or was not swimming alongside the calf  
157 was considered as milling (*Mil.*), and (5) any state directly immediately after the tag deployment was considered as

158 response to tagging (*Tg. res.*). Finally, the remaining Lv0 and Lv1 states were associated with Resting (*Rest*) and  
159 Milling (*Mil.*), respectively.

## 160 Statistical analyses

### 161 *Cluster analysis of the social calls*

162 We used cluster analysis to objectively identify relatively homogeneous groups of calls, referred to as call types in  
163 the present study. The relevant number of clusters was determined using the *NbClust* package [52] in R (R core team,  
164 <https://www.r-project.org/>). The Calinsky and Harabasz (CH) index was used as it is among the indexes with the best  
165 performance in determining the number of clusters [53]. We set the minimum cluster number to 6 to avoid capturing  
166 just the main categories of calls (Low-frequency, Mid-frequency, High-frequency, Pulsed, and Amplitude-modulated  
167 [24,30,44,54,55]). Once the relevant number of clusters was determined, we used a Hierarchical Clustering on  
168 Principal Components (HCPC) to group the social calls using the *FactoMineR* R package [56]. The principal  
169 components (i.e., PC scores) were computed using the seven measured acoustic features as input variables in a  
170 Principal Component Analysis (PCA).

### 171 *Analysis of the behavioural context of call production*

172 For each continuous period corresponding to one state (referred to as a ‘segment’), we calculated the call rate  
173 (count/minute) and noted the presence/absence of each identified call type. To investigate how the produced calls  
174 and behavioural states related to each other, we tested whether the information on the rate of calls and the type of  
175 calls produced allowed the prediction of the behavioural state using a balanced random forest classification. We used  
176 the R package *rfPermute* [57], which allows the estimation of the statistical significance of the variable importance  
177 metrics (here, the importance of the call rate and the presence/absence of each call type) in the prediction by  
178 permuting the response variable (here the behavioural state). In our model, the number of variables randomly  
179 selected at each split was set at 3, and the number of trees grown was set at 1000.

## 180 Results

181 A total of 508 social calls were detected and labelled in the data from eight deployments on calves. Each deployment  
182 has been subdivided into  $88 \pm 66$  segments on average (range: 18–212 segments, total: 700 segments) based on  
183 automatic classification of the behavioural state. The average duration of the segments was  $2.8 \pm 3.9$  min (range =

184 0.3–36). Most of the segments corresponded to milling (*Mil.*, 60%), followed by resting (*Rest*, 27%), traveling  
185 (*Travel*, 7%), surface playing (*Play*, 2%), suckling session (*Suckl.*, 2%), and finally tagging response (*Tg. res.*, 1%).

## 186 Main call types recorded

187 The Calinsky and Harabasz (CH) index suggested the occurrence of 13 main call types that were then successfully  
188 identified using a Hierarchical Clustering on Principal Components (HCPC) (Type #1 to #13, figure 1). Examples of  
189 calls from each type are presented in Media S1 (supplemental information). The first two principal components  
190 (PC1–PC2) explained 76% of the sample variance (figure S1, supplemental information). PC1 was primarily  
191 positively correlated to the spectral characteristics, whereas PC2 was positively correlated to the call duration (Dur).  
192 The Type #1–3 calls were constituted by low-frequency sounds. Type #1 calls were long grunting sounds – about  
193  $2\pm 0.6$  s on average; Type #3 were relatively short barking/snorting sounds – about  $0.3\pm 0.1$  s on average, and Type #2  
194 calls were in between these two (figure 1, table S1, supplemental information). Type #4 and #5 calls showed similar  
195 spectral characteristics and time duration (overlapped on the PC1 and PC2) but were of higher frequencies than Type  
196 #1–3 calls (figure 1, table S1, supplemental information) with generally a characteristic whooping sound. They  
197 mainly differed in their bandwidth (Bdw) and fundamental frequency (F0) (The average F0 values of Type #4 calls  
198 was more than twice those of F0 of the Type #5 calls while the average Bdw of Type #4 was less than 1/3 of the Bdw  
199 of Type #5 calls) (table S1, supplemental information). Type #6–9 calls overlapped along the PC1 but spread more  
200 on PC2. They were mainly whooping, whining, squeaking, or bubbling-like sounds. Among these four call types,  
201 Type #7 appeared to have the narrowest bandwidth, the highest F0 ( $434\pm 41$  Hz on average), and the longest duration  
202 ( $1\pm 0.6$  s on average, figure 1, table S1, supplemental information). Type #8 had the lowest F0 ( $65\pm 53$  Hz on average,  
203 table S1, supplemental information). Type #6 and #9 had similar F0 values, but Type #9 clearly had a broader  
204 bandwidth (about four times the Bdw of Type #6) and had, in fact, the broadest bandwidth among Type #6–9 (figure  
205 1, table S1, supplemental information). Type #10 and #13, both heek-like sounds, had more energy in high  
206 frequencies (average  $F_{\max} > 1300$  Hz) than all other main call types. Type #10 and #11 (also heek-like sound) had  
207 broader bandwidth and were shorter compared to Type #12 (squeaking sound) and #13 (also a heek-like sound)  
208 (average Bdw almost five times or more than Type #12's and #13's average Bdw and average Dur not more than  
209 two-thirds of Type #12's and #13's Dur), but #10 had higher  $F_{\max}$  (about four times) and with narrower bandwidth  
210 (about the half) than Type #11 (figure 1, table S1, supplemental information). Type #12 and #13 were represented by  
211 only a single call each and were high-frequency calls with narrow bandwidth. The Type #12 call had much higher F0

212 values (eight times) compared to Type #13 (figure 1). Type #3 was the most abundant main type (59%) and was  
213 common to all calves, followed by Type #2, which was also relatively abundant (16%) and found in all calves except  
214 one. Each remaining call type only constituted < 1% to 9% of all calls detected and was at most common to only half  
215 of the studied calves (figure S2, supplemental information).

#### 216 Behavioural state and call production

217 Milling (*Mil.*), Resting (*Rest*), and Travelling (*Travel*) states were mostly associated with silence (median call rate =  
218 0 call min<sup>-1</sup>), although on rare occasions, they were associated with a high level of vocal production (call rate > 1 call  
219 min<sup>-1</sup> in 21/423 *Mil.*, in 3/192 *Rest*, and in 2/50 *Travel*; range, *Mil.*: 0–11 calls min<sup>-1</sup>; *Rest*: 0–2 calls min<sup>-1</sup>; *Travel*: 0–  
220 3 calls min<sup>-1</sup>, Figure 2A). In contrast, Surface play session (*Play*), response to tagging (*Tg. res.*), and Suckling  
221 session (*Suckl.*) states tended to be associated with a call production at an average rate (median) of 0.1 calls min<sup>-1</sup>  
222 (range = 0–8 calls min<sup>-1</sup>), 0.1 calls min<sup>-1</sup> (range = 0–2 calls min<sup>-1</sup>), and 0.5 calls min<sup>-1</sup> (range = 0–2 calls min<sup>-1</sup>),  
223 respectively.

224 The random forest analysis correctly predicted 29% of the behavioural state based solely on the presence/absence of  
225 each of the 13 main call types and the call rate (table 1). This percentage of correct prediction was statistically  
226 significantly greater than the result expected by chance, which was about 16.7% ( $P < 0.001$ ). The random forest  
227 analysis was able to predict the states corresponding to *Rest* and *Suckl.* at rates that were statistically significantly  
228 greater than the values expected by chance (table 1). However, it failed to predict the states corresponding to *Play*  
229 and *Tg. res.* at rates statistically significantly greater than the values expected by chance but close to the significance  
230 level for *Play* (table 1). The correct prediction rate was zero for *Mil.* and *Travel*. *Mil.* was primarily confused with  
231 *Rest*, but sometimes with *Tg. res.*, *Play*, and *Suckl.* *Travel* was also primarily confused with *Rest*.

232 The variables contributing the most (statistically significant contribution) to the prediction of *Suckl.* were, by  
233 decreasing order of importance, the presence of Type #3 and #2 calls (barking/snorting sounds with slightly different  
234 duration), the high call rate, and, to a lesser extent, the presence of Type #8, #5, and #6 calls (whining, whooping,  
235 and bubbling-like sounds). For *Play*, the variables contributing the most to its prediction were the presence of Type  
236 #4 and #6 calls (whooping and bubbling-like sounds). Regarding *Rest*, the information on the presence/absence of  
237 several call types and the call rate were important in its prediction as it was mainly associated with silence (thus the  
238 absence of calls in general) (figure 2).

## 239 Discussion

240 Our initial objective was to identify the behavioural context of call production by young calves in a baleen whale  
241 species, the humpback whale, using data from animal-borne tags. We assumed that the calls recorded by the tags  
242 placed on calves were from the calves. Indeed, this is supported by the findings in Ratsimbazafindranahaka [43],  
243 showing that most calls recorded by a tag placed on the calf were likely from the calf than from the mother (about  
244 90% of the calls). The study compared calls recorded from simultaneous tag deployments on both the mother and  
245 calf and found that the acoustic characteristics of calls detected only on the calf's tag (i.e., not detected on the  
246 mother's tag at the corresponding time) were distinct from those detected only on the mother's tag (i.e., not detected  
247 on the calf's tag at the corresponding time), and that four-fifths of the remaining calls – for instance those heard  
248 simultaneously on both tags – shared acoustic characteristics with those detected solely on the calf's tag and not the  
249 mother's tag. Due to the potential existence of graded calls in humpback whales and especially in calves [30,44], we  
250 used an unsupervised approach to group social calls with similar acoustic characteristics. Our result suggested that  
251 the call rate and the production (or non-production) of one or several specific call types are related to the calf's  
252 behaviour. Indeed, we found that these parameters can be sufficient to predict the occurrence of a specific  
253 behavioural state in a given data segment. It is especially true for two main behaviours – the suckling behaviour and  
254 the resting behaviour – and likely the play behaviour.

255 Suckling sessions, on average, were associated with a higher call rate than any other behavioural state and were  
256 mainly associated with Type #3 and Type #2 calls. Qualitatively speaking, these calls corresponded mainly to low-  
257 frequency calls such as burps, barks, wops, thwops, snorts, basses, and grunts presented in the literature  
258 [23,24,30,31,44,45,54,58,59]. Most of these calls have been identified as very common in humpback whale vocal  
259 repertoire and were suggested to be calls with important social functions [30]. Given that their occurrence predicts  
260 the occurrence of suckling sessions, we suggest that one biological function is related to the calf's feeding behaviour.  
261 More specifically, evidence suggests they serve as begging calls in mother-calf pairs to initiate nursing, given that  
262 they occurred before or during suckling sessions. They are unlikely a by-product of the act of suckling itself as  
263 calves are not known to produce sound while locked on a teat [47,50,60]. Previous studies on the potential stimuli  
264 calves use to initiate nursing suggested, however, that mechanical stimuli rather than acoustic signals are involved  
265 [25]. These modalities are not necessarily exclusive, considering that calves may use various sensory modalities to  
266 communicate with their mothers in a given context (interchangeably or in combination). For nursing, while

267 mechanical stimuli can also be used [25], the use of acoustic signals may prevail given that they are of more  
268 extended range compared to tactile or even visual signals in a low light condition. Acoustic signals may allow calves  
269 to communicate to their mother their nutritional needs (or that they intend to suckle) even when they are not near  
270 their mother, particularly during vertical separation as the calf surfaces to breathe while the mother stays at depth  
271 [47,49,61].

272 Nevertheless, it is important to consider the methodologies used to investigate the signals involved in nursing.  
273 Videsen et al. [25] defined nursing primarily based on activity levels measured with the minimum specific  
274 acceleration (MSA), using a threshold based on apparent nursing events observed from the surface. This approach  
275 can potentially capture periods of rest for the calf, which also exhibit low MSA, and not necessarily nursing sessions.  
276 In contrast, our study used direct calf point-of-view visual identifications (i.e., video from tags deployed on calves),  
277 providing a different perspective.

278 Surface active playing sessions and periods directly following tagging were associated with either a high call rate or  
279 with silence. Various call types were associated with the playing state, but only the presence of Type #4 and Type #6  
280 had a statistically significant importance in its prediction. In particular, Type #4 qualitatively corresponded mainly to  
281 the whoops presented in the literature [30], and they may be the expression of a positive and high arousal state  
282 expressed during a playful state. Indeed, humpback whale's social calls have the potential to encode motivational  
283 information [62].

284 Additionally, the production of diverse call types during play with no clear association pattern for the majority may  
285 indicate the calf is also playing with its voice (vocalizing without immediate practical goal or benefit) and thus  
286 emitting calls randomly, or it might be a by-product of high physical activity. For instance, in rats (Long Evans rats),  
287 the production of some call types is, for example, closely tied to breathing [63]. In mysticetes, surface active play  
288 involves rapid vertical swimming and breaching, which could cause involuntary air circulation within the respiratory  
289 system that also serves for sound production (air circulation from the lungs to the laryngeal sac or vice versa) or air  
290 release in response to changing ambient pressure and the calf's attempts to play with its buoyancy by actively  
291 changing its internal pressure [15,16]. This may result in sounds being produced involuntarily. On a side note, low-  
292 frequency calls produced by the calf during surface playing sessions were associated with bubble production  
293 (personal observations) and Type #6 calls usually featured bubbling sound, supporting that some calls may be tied to

294 air movements within the respiratory system while playing at the surface. In summary, the observed call patterns  
295 during play sessions could be influenced by a combination of intentional vocalization, physical exertion, and  
296 respiratory mechanics.

297 Resting was mostly associated with silence, which is expected since resting corresponds to periods of low activity  
298 during which both the mother and calf are usually in the same behavioural state [48,49,61]. The absence of a clear  
299 pattern in the calls associated with traveling suggests that the calf does not need to vocalize to synchronize travelling  
300 movements with its mother. The side-by-side swimming configuration may be sustained based mainly on vision and  
301 touch (direct physical contact or by sensing surrounding water displacement), and the mother may adjust her pace  
302 voluntarily without the need for the calf to signal her acoustically. In ungulate species using the ‘following’ strategy,  
303 such maternal behaviour has been referred to as ‘pacing’, a behaviour proposed to induce a maximal following  
304 response by the offspring [4]. In these species, it is known that the young instinctively follow a nearby moving object  
305 of an appropriate size [4].

306 Our study provides an advanced assessment of the behavioural context of call production in humpback whale calves.  
307 It proposes potential biological functions of some call types, ultimately shedding light on their communication  
308 patterns and behaviour. Notably, the potential begging calls of humpback whale calves have been identified for the  
309 first time. Such results help us understand the underlying mechanism of mother-young acoustic communication in  
310 baleen whales and the significance of acoustic signalling for calves’ development and survival. Begging calls have  
311 been described in many vertebrate species, such as songbirds [41,64], seabirds [65,66], and mammals [67,68]. In  
312 cetaceans, begging calls have not been clearly evidenced but suggested in bottlenose dolphins (*Tursiops truncatus*)  
313 [69] and Araguaian river dolphin (*Inia araguaiaensis*) [70].

314 Our results provide new data helping in interpreting baleen whales' behaviours, highlight the importance of social  
315 calls in mother-calf interactions, and is thus decisive for regulating noise-inducing human activities that may perturb  
316 vital behaviour such as nursing. The existence of context-dependent vocal behaviour suggests an adaptive strategy to  
317 balance the need to communicate acoustically and the cost of communication in mother-young pairs, especially in an  
318 environment where eavesdropping by predators or unsolicited conspecifics may occur [33,71]. Further investigations  
319 are encouraged, and playback experiments on mothers/females could be carried out to assess the biological function  
320 of some calves' calls identified in the present study in a controlled setup now that we have more information on their

321 behavioural context and hypotheses regarding their usage and importance. They must, of course, be designed  
322 carefully and have to be done by experts to minimize negative impacts on the whales, and all relevant regulations  
323 about approach and respect of cetaceans should be strictly followed. While playback experiments have already been  
324 conducted on humpback whales in breeding and calving grounds, including mother-calf pairs [72,73], particular  
325 attention should be paid to the potential impacts on mother-calf pairs. Avoidance behavior, for example, may occur  
326 in response to playback stimuli [73]. It is essential to assess how these potential responses could affect the calf,  
327 disrupt the mother-calf bond, or compromise their overall welfare. Any decision regarding playback experiments  
328 should carefully consider these factors and any exposition, especially for the calf, should be kept to the strict  
329 minimum.

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499 species [Dataset]. (doi:10.5061/dryad.kh18932hb)

500

501

502 **Data accessibility**

503 The code and data used for this study are publicly available on Dryad

504 (<https://doi.org/10.5061/dryad.kh18932hb>)[74].

505 **Tables**

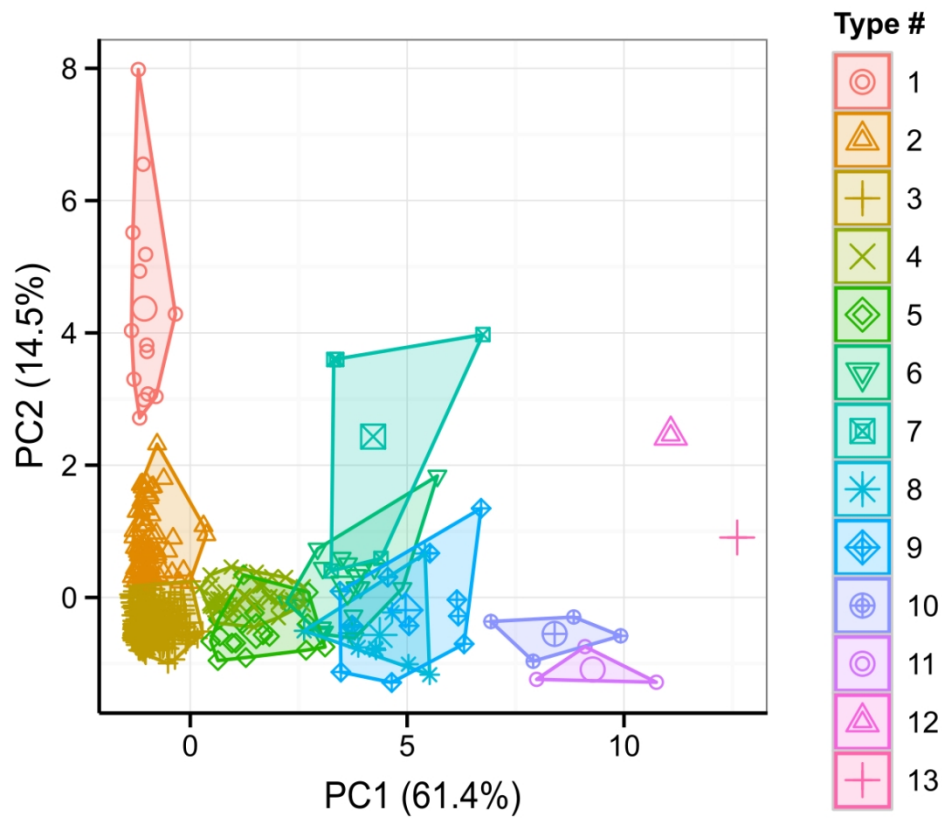
506 **Table 1.** Result of a random forest (confusion matrix) analysis in predicting the behavioural state corresponding to each data segment based on the  
 507 presence/absence of the 13 main call types identified and the call rate. The numbers in the table's true class vs. predicted class section indicate the count of  
 508 segments. *Mil.*: milling, *Play*: surface active playing session, *Tg. res.*: response to tagging, *Rest*: resting, *Suckl.*: suckling session, *Travel*: traveling. Grey cells  
 509 along the primary diagonal indicate agreement between the true class (behavioural state) and the predicted class (predicted behavioural state). Bold *P*-values  
 510 indicate statistically significant differences between the correct prediction rate and the rate expected by chance.

		Predicted class						% correct	% chance	<i>P</i>
		<i>Mil.</i>	<i>Play</i>	<i>Tg. res.</i>	<i>Rest</i>	<i>Suckl.</i>	<i>Travel</i>			
True class	<i>Mil.</i>	0	8	21	371	23	0	0	17	1
	<i>Play</i>	0	4	2	7	2	0	27	17	0.09
	<i>Tg. res.</i>	0	0	2	4	2	0	25	17	0.135
	<i>Rest</i>	0	1	2	187	2	0	97	17	<b>0</b>
	<i>Suckl.</i>	0	0	4	3	5	0	42	17	<b>0.008</b>
	<i>Travel</i>	0	1	3	42	4	0	0	17	1
Overall								28	17	<b>0</b>

## 512 **Figure captions**

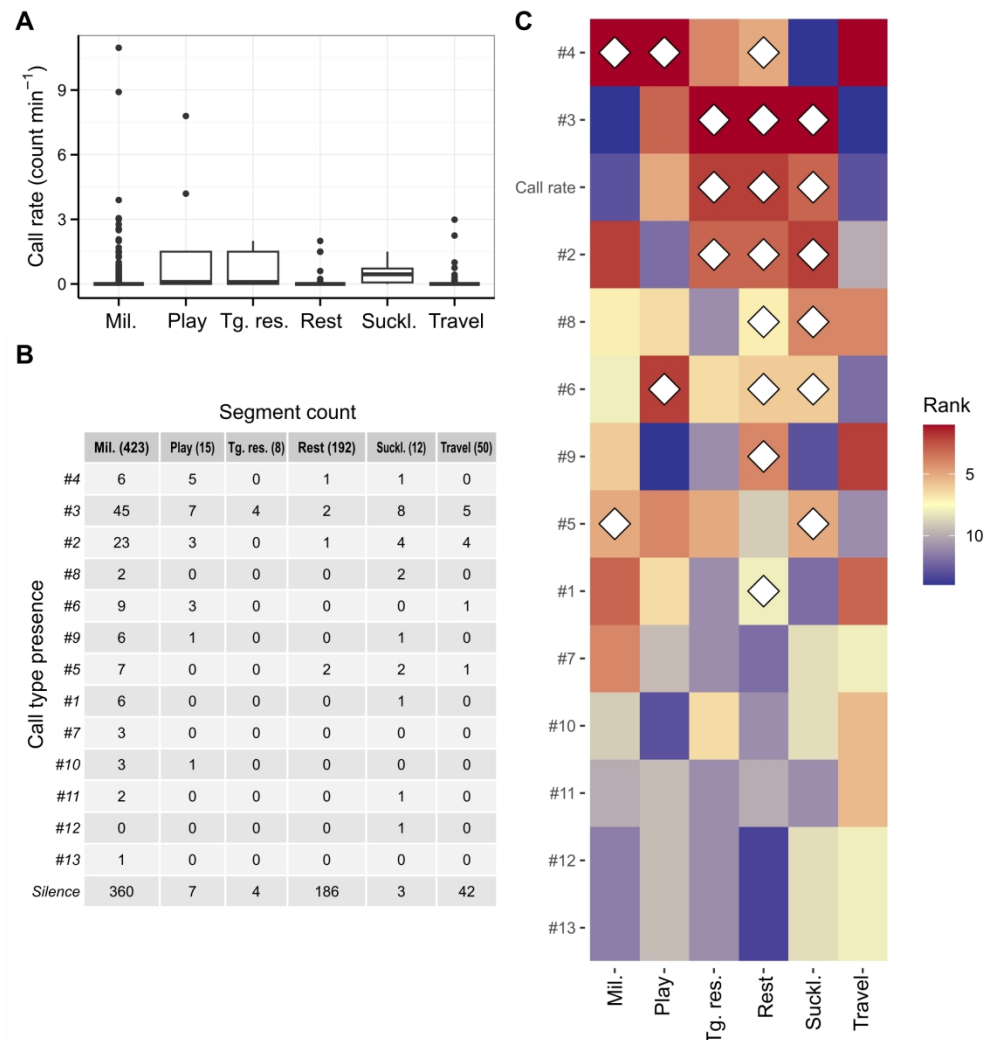
513 **Figure 1.** Hierarchical clustering on principal components analysis (HCPC) showing the identified main call types  
514 (delimited by polygons) and calls within each of them (small symbols). Cluster centres are indicated by bigger  
515 symbols. Thirteen call types were identified. The calls are dispersed along the PC1 axis, which is positively  
516 correlated to spectral characteristics (F0, Fmax, Q25, Q50, and Q75 and Bdw), and dispersed along PC2, which is  
517 highly correlated to duration (Dur).

518 **Figure 2.** Relation between the behavioural states *Mil.*, *Play*, *Tg. res.*, *Rest*, *Suckl.*, and *Travel*, and call type  
519 production. *Mil.*: milling, *Play*: surface active playing session, *Tg. res.*: response to tagging, *Rest*: resting, *Suckl.*:  
520 suckling session, *Travel*: traveling. (A) Call rates by behavioural state. *Suckl.*, *Play*, and *Tg. res.* were associated with  
521 higher call rates than *Mil.*, *Rest.*, and *Travel*, which were mainly associated with silence. (B) Relation between the  
522 call type produced, numbered from #1 to #13, and the behavioural states. Each count represents the number of  
523 segments per behavioural state during which the specified call type was detected. The number of segments per  
524 behavioural state during which no call was detected are presented in the bottom row (silence). (C) Ranked  
525 importance of the presence/absence of each call type and the call rate in predicting the behavioural state in a random  
526 forest analysis. The heat map presents importance scores scaled by ranked importance. The diamonds indicate  
527 statistically significant scores. The predictors are sorted by Mean Decrease Accuracy. By descending order of  
528 importance, the most significant variables contributing to the prediction of *Suckl.* were the presence/absence of type  
529 #3 and #2 calls, the call rate, and the presence/absence of Type #8, #5, and #6 calls. In the case of *Play*, the variables  
530 with the greatest contribution to its prediction were the presence/absence of Type #4 and #6 calls. As for *Tg. res.*, the  
531 variables that played a crucial role in its prediction were the presence/absence of Type #3 calls, the call rate, and the  
532 presence/absence of Type #2 calls. In predicting *Rest*, the presence/absence of several call types, along with the call  
533 rate, were important since *Rest* is predominantly associated with the absence of most calls in general.



Hierarchical clustering on principal components analysis (HCPC) showing the identified main call types (delimited by polygons) and calls within each of them (small symbols). Cluster centres are indicated by bigger symbols. Thirteen call types were identified. The calls are dispersed along the PC1 axis, which is positively correlated to spectral characteristics (F0, Fmax, Q25, Q50, and Q75 and Bdw), and dispersed along PC2, which is highly correlated to duration (Dur).

266x228mm (118 x 118 DPI)



Relation between the behavioural states Mil., Play, Tg. res., Rest, Suckl., and Travel, and call type production. Mil.: milling, Play: surface active playing session, Tg. res.: response to tagging, Rest: resting, Suckl.: suckling session, Travel: traveling. (A) Call rates by behavioural state. Suckl., Play, and Tg. res. were associated with higher call rates than Mil., Rest., and Travel, which were mainly associated with silence. (B) Relation between the call type produced, numbered from #1 to #13, and the behavioural states. Each count represents the number of segments per behavioural state during which the specified call type was detected. The number of segments per behavioural state during which no call was detected are presented in the bottom row (silence). (C) Ranked importance of the presence/absence of each call type and the call rate in predicting the behavioural state in a random forest analysis. The heat map presents importance scores scaled by ranked importance. The diamonds indicate statistically significant scores. The predictors are sorted by Mean Decrease Accuracy. By descending order of importance, the most significant variables contributing to the prediction of Suckl. were the presence/absence of type #3 and #2 calls, the call rate, and the presence/absence of Type #8, #5, and #6 calls. In the case of Play, the variables with the greatest contribution to its prediction were the presence/absence of Type #4 and #6 calls. As for Tg. res., the variables that played a crucial role in its prediction were the presence/absence of Type #3 calls, the call rate, and the presence/absence of Type #2 calls. In predicting Rest, the presence/absence of several call types, along with the call rate, were important since Rest is predominantly associated with the absence of most calls in general.