



**HAL**  
open science

## Humpback whale suckling behavior: an insight into the mother-offspring strategy in mysticetes

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

### ► To cite this version:

Maevatiana Nokoloina Ratsimbazafindranahaka, Chloé Huetz, Joy Reidenberg, Anjara Saloma, Aristide Andrianarimisa, et al.. Humpback whale suckling behavior: an insight into the mother-offspring strategy in mysticetes. *Behavioral Ecology and Sociobiology*, 2023, 77 (8), pp.96. 10.1007/s00265-023-03369-9. hal-04207554

**HAL Id: hal-04207554**

**<https://hal.science/hal-04207554>**

Submitted on 10 Nov 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

[Click here to view linked References](#)

# 1 **Humpback whale suckling behavior: an insight into the mother-** 2 **offspring strategy in mysticetes**

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

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

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

7 <sup>3</sup> Association Cétamada, Barachois Sainte Marie, Madagascar

8 <sup>4</sup> Center for Anatomy and Functional Morphology, Icahn School of Medicine at Mount Sinai, New York, United  
9 States of America

10 <sup>5</sup> Institut Jean Le Rond d'Alembert, Sorbonne Université, Paris, France

## 11 **Corresponding Author**

12 Maevatiana Nokoloina Ratsimbazafindranahaka

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

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

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

16 ORCID: 0000-0001-8916-237X

## 17 **Abstract**

18 Despite its biological importance, the nursing behavior in baleen whales has been poorly documented mainly  
19 because of the challenges in tracking whales in their natural environment. We investigated the suckling behavior  
20 (nursing from the calf's perspective) in < 3 months old humpback whale calves off Sainte Marie Island,  
21 Madagascar, South Western Indian Ocean (breeding/calving area). We investigated the temporal pattern of the  
22 suckling behavior, its spatial and behavioral context, and the ontogeny of these characteristics. We exploited  
23 data from both camera-equipped and non-camera-equipped animal-borne multi-sensor tags (Acousonde and  
24 CATS cam) collected from 2013 to 2022 (37 calves). Our dataset constitutes the largest sample assembled so far  
25 to investigate the suckling behavior in free-ranging whales. We found that the suckling events' duration does not  
26 vary much with the calves' relative age. The proportion of time spent suckling was about 1.5%. The suckling  
27 events mainly occurred during the descent and bottom phases of dives and rarely during the ascent phase of  
28 dives or surface activities. Strong evidence of humpback whale suckling at night is presented for the first time.

29 We found that suckling events were performed in series occurring less than 10 min apart, and bouts of suckling  
30 events were separated by about 2 hours of non-suckling periods. In other words, humpback whale calves  
31 suckled several times throughout the day in short sessions similar to terrestrial 'followers.' Our results add to the  
32 evidence that humpback whales, and potentially most baleen whales, are behaviorally and functionally similar to  
33 terrestrial 'followers' regarding maternal strategy.

#### 34 **Keywords**

35 anti-predation strategy, cetaceans, marine habitat, maternal care, mother-young interactions

#### 36 **Statements and Declarations**

##### 37 *Competing Interests*

38 The authors have no competing interests to declare that are relevant to the content of this article.

##### 39 *Data availability*

40 The dataset generated and analyzed during the current study are available in the Supplemental Data S1.

#### 41 **Significance Statement**

42 Young mammals rely on the milk provided by their mother to survive during their early life stage. The suckling  
43 behavior, i.e., the procurement of milk from the mother, has been widely studied for terrestrial mammals but not  
44 for fully aquatic mammals like the baleen whales due to the challenges in tracking them. By placing sensors and  
45 cameras on calves, we described the suckling pattern in humpback whales, the most common baleen whale  
46 species. We found that the temporal pattern of suckling in humpback whales is similar to those of terrestrial  
47 precocial mammals experiencing comparable environments (open habitat with predators): the young suckle  
48 frequently but in short sessions. Our results offer a new insight supporting the hypothesis that the rearing  
49 strategy used by baleen whales is an aquatic version of the 'following' behavior found in these precocial  
50 terrestrial species.

#### 51 **Author contributions**

52 Maevatiana N. Ratsimbazafindranahaka, Chloé Huetz, Isabelle Charrier, Olivier Adam and Anjara Saloma  
53 conceived the ideas and designed methodology; Maevatiana N. Ratsimbazafindranahaka, Chloé Huetz, Isabelle  
54 Charrier, Olivier Adam and Anjara Saloma collected the data; Maevatiana N. Ratsimbazafindranahaka led the  
55 writing of the manuscript. All authors interpreted the data, contributed critically to the drafts, and gave final  
56 approval for publication.

## 57 Introduction

58 Young mammals must obtain care from their mother early in life to survive (Clutton-Brock 1991). The food  
59 provided by the mother in the form of maternal milk represents one of the most critical and energetically  
60 expensive aspects of this care in mammals (Fisher et al. 2002; Balshine 2012). 'Nursing' and 'suckling' behaviors  
61 (associated with the transfer of milk to the offspring, from the mother's perspective and the offspring's  
62 perspective, respectively) vary among species (Lent 1974; Rosenblatt et al. 1985; Oftedal et al. 1987; Fisher et  
63 al. 2002) and are ultimately influenced by their specific adaptation to the environment and by their life history  
64 (e.g., the growth speed and the precociality). For example, among ungulates species, habitat structure and  
65 predation pressure are the main drivers of the emergence of two general rearing strategies: the 'hiding' strategy  
66 for species living in close habitats and the 'following' strategy for species in open habitats (Lent 1974; Fisher et  
67 al. 2002). The 'hiding' strategy corresponds to a scheme where the young remains hidden from the predators in  
68 the vegetation while the mother spends most of her time away foraging. During those unsupervised intervals, the  
69 young is more vulnerable to predation as the mother cannot guard them. In the hiding strategy, the mother-  
70 offspring contact is limited to infrequent but prolonged visits for nursing (Lent 1974; Rosenblatt et al. 1985;  
71 Gloneková et al. 2017). The mother must return to where she left her offspring, where he is supposed to be  
72 waiting for her. In contrast, the 'following' strategy corresponds to a scheme where the mother and the young  
73 maintain constant contact. The young follows the mother wherever she goes and is thus nursed frequently and  
74 protected by its mother (Lent 1974; Rosenblatt et al. 1985; Fisher et al. 2002; Gloneková et al. 2017). The  
75 'following' strategy allows the mother to go where she wants or needs to go, according to her habits or those of  
76 her group (and not those of her offspring).

77 Baleen whales are similar to most ungulates in the fact they give birth to a unique, highly precocial (locomotory,  
78 sensorially, and thermoregulatory independent) offspring (Chivers 2009; Gingerich et al. 2009; Skok 2022).  
79 Previous studies suggested that the mother-calf behavior in baleen whales is consistent with the 'following'  
80 strategy found in some ungulate species (Taber and Thomas 1982; Thomas and Taber 1984; Szabo and Duffus  
81 2008). These studies proposed that this is due to similarities in the habitat structure (openness of the habitat), the  
82 resources distribution (temporally and spatially scattered resources), and the occurrence of predation pressures  
83 (e.g., by killer whales, *Orcinus orcas*). However, these studies on mother-calf associations in baleen whales  
84 mainly focused on the mother-calf spatial relationship and behavioral synchrony. Whether the nursing behavior

85 in baleen whales falls within the general characteristics of suckling in follower species has yet to be formally  
86 investigated.

87 The challenges in tracking cetaceans (baleen and toothed whales, including dolphins and porpoises) in their  
88 natural environment have limited the study of nursing behavior. Boat and aircraft-based observations only allow  
89 a partial description of their behaviors at the sea surface or at most at subsurface (when the water is clear). Even  
90 observations by breath-holding or scuba divers are limited since divers cannot keep pace with traveling or  
91 diving whales. Furthermore, to the best of our knowledge, there have not yet been any studies based on data  
92 collected by Autonomous Underwater Vehicles (AUVs). As a result, most studies have focused only on the  
93 nursing behavior of captive species (Triossi et al. 1998; toothed whales, e.g., Clark and Odell 1999a, b).  
94 Although valuable for understanding the behavioral adaptations to aquatic life, data from such studies may not  
95 represent the natural behavior of cetaceans as the environmental constraints are very different in the wild.  
96 Unlike captive animals, free-ranging cetaceans naturally engage in a lot of horizontal (traveling) and vertical  
97 (diving) movements in search of food or to move to a more favorable location (predator or boat avoidance,  
98 finding a place to rest, etc.).

99 Several studies have attempted to address the nursing behavior in free-ranging baleen whales from surface and  
100 subsurface observations of their behaviors (Glockner and Venus 1983; Thomas and Taber 1984; Glockner-  
101 Ferrari and Ferrari 1985; Würsig et al. 1985; Clapham and Mayo 1987; Morete et al. 2003; Hain et al. 2013;  
102 Videsen et al. 2017). These studies are significant because they provided the first insights into the nursing  
103 modalities, but more in-depth underwater observations could supplement them, especially for a more  
104 comprehensive interpretation. Indeed, the surface and sub-surface observations are incomplete because  
105 behaviors at depth cannot be seen from the surface. Moreover, there needs to be more standardization of how  
106 nursing is observed, recorded, and reported, because the mother-calf pairs may display configurations easily  
107 mistaken for nursing when observed from above (Tackaberry et al. 2020; Ratsimbazafindranahaka et al. 2022).  
108 Finally, the data resolution and the duration of observations are sometimes insufficient for capturing the  
109 temporal pattern of suckling. Recent works by Ratsimbazafindranahaka et al. (2022) and Tackaberry et al.  
110 (2020) based on camera-equipped animal-borne multi-sensor tags allowed an accurate description of the nursing  
111 behavior but were still limited by the sample size since such data acquisition is challenging.

112 In the present study, we describe the suckling/nursing behavior in < 3 months old humpback whale (*Megaptera*  
113 *novaeangliae*) calves. Data were collected using camera-equipped and non-camera-equipped animal-borne

114 multi-sensor tags. We describe the temporal pattern of the suckling behavior, its spatial and behavioral context,  
115 and the ontogeny of these characteristics.

116 Humpback whales are migratory baleen whales that move between a feeding area close to the poles in summer  
117 and a breeding/calving area close to the equator in winter (Braithwaite et al. 2015; Clapham 2018). Prolonged  
118 fasting for all individuals except the calves characterizes their stay in the breeding/calving area. The calves feed  
119 on maternal milk during their first six months of life, including during their first migration to the feeding area.  
120 After that period, the calves start to feed on prey but also continue to suckle from the mother until weaning at 10  
121 to 12 months old (Clapham 2018). The main natural predator of humpback whales are killer whales, and the  
122 calves are the primary victims (Pitman et al. 2015). Humpback whales are a good starting point for studying the  
123 suckling behaviors in baleen whales. Compared to other baleen whales, they are abundant and present in all  
124 oceans, easy to spot as mostly close to the coastlines, and one of the most studied in the world (Clapham 2018),  
125 thus facilitating data acquisition and contextualization of the observations.

## 126 **Materials and methods**

### 127 **Field site**

128 We conducted our field works off Sainte Marie Island, Madagascar, South Western Indian Ocean (between  
129 latitudes 17° 19' and 16° 42' South, and longitudes 49° 48' and 50° 01' East) during the southern winter (July-  
130 September) of 2013-2019 and 2021-2022. The area around Sainte Marie Island is an important breeding and  
131 calving zone of the South Western Indian Ocean humpback whale population (Trudelle et al. 2018). The calm  
132 and shallow waters of the area attract several calving females yearly. Our study was conducted under the  
133 national research permits #44/13-MPRH/SG/DGPRH, #43/14-MRHP/SG/DGRHP, #46/15-MRHP/SG/DGRHP,  
134 #28/16-MRHP/SG/DGRHP, #26/17-MRHP/SG/DGRHP and #28/18-MRHP/SG/DGRHP, #36/19-  
135 MAEP/SG/DGPA, #30/21-MAEP/SG/DGPA, and #54/22-MPEB/SG/DGPA and complies with the European  
136 Union Directive on the Protection of Animals Used for Scientific Purposes (EU Directive 2010/63/EU). A part  
137 of the data used in the present study (data in 2018-2019) have been published in a previous study by  
138 Ratsimbazafindranahaka et al. (2022).

### 139 **Tag specifications**

140 We used two models of multi-sensor tags for our study: Acousonde 3B (until 2018) and CATS cam (2018 and  
141 afterward). Both models are small and lightweight (not more than 500 g) and are attached to animals via four

142 suction cups (the tags stick for about four hours on the animals on average but can stick for more than 20 hours).  
143 They share five main common auxiliary sensors (3-axis accelerometer, 3-axis magnetometer, pressure/depth  
144 sensor, temperature sensor, and light sensor), and both have an integrated hydrophone. In addition, the CATS  
145 cam has an HD video camera covering up to 100° field of view. A VHF transmitter attached to the tags allows  
146 tracking for tag retrieval.

147 We used two units of Acousonde and two units of CATS cam. For the Acousonde units, the sampling frequency  
148 was set at 10 Hz or 20 Hz for the auxiliary sensors. Their accelerometer sampling rate was set either at 10 Hz  
149 (when the auxiliary sensors were set to 10 Hz) or at 400 Hz (when the auxiliary sensors were set to 20 Hz). For  
150 the CATS cam units, the sampling frequency of the auxiliary sensors was set to 10 Hz. The accelerometer  
151 sampling rate was set at 400 Hz in 2018 and 800 Hz in 2019 and afterward. For the Acousonde units, the  
152 hydrophone recorded sounds at a 24.453 kHz sampling rate (16-bit resolution). The CATS cam units'  
153 hydrophone recorded sounds at a 48 kHz sampling rate in 2018 and a 24 kHz sampling rate in 2019 and  
154 afterward (also 16-bit resolution). The CATS cam units' camera recorded videos with a 1,280 × 720-pixel  
155 resolution at 30 frames per second in 2018 and a 1,920 × 1,072-pixel resolution at 30 frames per second in 2019  
156 and afterward.

### 157 **Tagging procedures**

158 We deployed the tag(s) on calves or mothers (single deployments), or both (simultaneous deployments),  
159 depending on the opportunity, in calmly behaving humpback whale mother-calf pairs. The deployments were  
160 completed from a 6.40 m rigid motorboat using a 5-m rigid, handheld carbon fiber pole. The approaches are  
161 detailed in Huetz et al. (2022) and Saloma et al. (2022). Tags were placed on the back (CATS cam), in the  
162 dorsal fin area, or slightly on the flank of the animals (Acousonde).

163 For each pair, we estimated the calf's relative age using coloration, skinfolds, and the angle of unfurling of its  
164 dorsal fin (Cartwright and Sullivan 2009; Faria et al. 2013; Huetz et al. 2022; Saloma et al. 2022): C1  
165 (neonate)–calf presenting some folds, scars (assumed to be caused at birth by the barnacles located on the  
166 genital slit of the mother), and skin color that tends to be light grey dorsally and white ventrally and with less  
167 than ~45° dorsal fin furl; C2—very young but non-neonate calves having more than ~45° but less than about 70°  
168 dorsal fin furl; and C3—older calves (but < 3 months old) that have unfurled dorsal fin (approximately >70°).

169 Tagged animals were not followed after the tagging to prevent exacerbating any disturbance of their behavior.  
170 After tag deployment or an aborted attempt, we slowly moved away in the opposite direction of the mother-calf  
171 pair. We retrieved the tags a few hours or a day after the tagging after they detached from the animals (usually  
172 due to the tagged animal rubbing against another individual, surface active behavior, etc.).

### 173 **Sensor data processing**

174 Data from all sensors were downloaded as MT files for the Acousonde units and as CSV files for the CATS cam  
175 units, imported into MATLAB (Mathworks), and calibrated using dedicated scripts (CATS Matlab toolkit,  
176 <https://github.com/wgough/CATS-Methods-Materials>, Cade et al. 2021). We performed a preliminary  
177 inspection for each deployment to check if all auxiliary sensors recorded data correctly and if the tag recorded at  
178 least one dive (essential for data calibration). Deployments not meeting these criteria were considered  
179 unsuccessful and irrelevant to the present study, and were thus discarded. Single deployments on mothers were  
180 also omitted as they are out of the scope of the present study. For successful deployments, all data were  
181 downsampled to obtain a common sampling rate of 10 Hz across all sensors, and depth data (in meters) were  
182 smoothed with a 0.5 s running median filter. The output sampling frequency was set to 10 Hz in all  
183 computations described hereafter. Sensor readings were rotated to match the animal's orientation frame using  
184 established methods (Johnson and Tyack 2003; Cade et al. 2021) and then used to document the whale's  
185 orientation (pitch, roll, and heading, in degree) (Johnson and Tyack 2003; Cade et al. 2021). We low-pass  
186 filtered the pitch and roll data to obtain body posture without fluke stroke signal (0.2 Hz low-pass filter, Simon  
187 et al. 2012). As a proxy for the whale's forward speed for all deployments, we used the flow noise extracted  
188 from the sound recorded by the tags' hydrophone (66-94 Hz frequency band, Cade et al. 2017). Indeed, flow  
189 noise is known to be related to speed (Finger et al. 1979; Izadi et al. 2018). We applied a z-score scaling for  
190 each whale to obtain a speed relative to the mean (relative speed hereafter). We did not use the 'tag jiggle'  
191 recorded in the original high-frequency accelerometer data, as Cade et al. (2017) proposed, because high-  
192 frequency data were unavailable for some of our deployments (The accelerometer sampled at only 10 Hz in  
193 some deployments). We also did not attempt to calculate the absolute speed from the flow noise (Cade et al.  
194 2017) because the available data in the deployments were not always sufficient for a good absolute speed  
195 estimation (insufficient data points for a robust regression of the orientation corrected depth rate against flow  
196 noise). Additionally, we calculated the Overall Dynamic Body Acceleration (ODBA, in G-force) as per Wilson  
197 et al. (2006), the roll rate (in degree /second), and the depth rate (in meter/second) using scripts from the Animal  
198 Tag toolbox (<http://www.animaltags.org>). ODBA values for each whale were divided by the whale's median



199 ODBA to normalize the deployment effects on ODBA (Isojunno et al. 2016), such as those due to variable tag  
200 position and tag model. We will refer to these values as the nODBA (normalized ODBA).

201 Depth data were used to determine various diving phases and to identify surface activity. We defined 'diving' as  
202 any submergence to a depth of >10 m (Stimpert et al. 2012; Huetz et al. 2022; Ratsimbazafindranahaka et al.  
203 2022). Dives were divided into three phases: 'descent,' 'bottom,' and 'ascent.' The bottom phase was defined as  
204 the segment at >85% of the maximal dive depth for a dive (Stimpert et al. 2012). The descent phase was defined  
205 as the segment starting at the surface immediately preceding the bottom phase. Inversely, the ascent phase was  
206 defined as the segment directly following the bottom phase and ending at the surface.

### 207 **CATS cam data labelling**

208 Suckling events in the CATS cam data from calves were identified in the recorded video footages following  
209 Ratsimbazafindranahaka et al. (2022) and Tackaberry et al. (2020). A suckling 'event' was defined as a period  
210 during which the tip of the calf's snout continuously touched (> 2 s) one mammary teat of the mother, and a milk  
211 cloud, even in low density, was observed in the water during the event or upon release of contact. For each  
212 suckling event (referred to as visually confirmed suckling events), we computed its corresponding activity phase  
213 (descent, bottom, ascent, or surface), along with the average depth, depth rate, relative speed, nODBA, pitch,  
214 roll, and roll rate (summarized in Fig. S2, supporting information).

### 215 **Machine learning model for automatically detecting suckling 'blocks'**

#### 216 **Model training**

217 Ratsimbazafindranahaka et al. (2022) have shown that the suckling behavior in humpback whales has very  
218 distinctive kinematic signatures. When data are divided into non-overlapping 2 s 'blocks', blocks corresponding  
219 to suckling events can be automatically detected with high precision and low False Positive Rate (FPR) based on  
220 the depth-derived and accelerometer-derived data alone using supervised machine learning (AdaBoostM1  
221 model). We thus considered such an approach as a basis to detect suckling events in our calf data lacking of  
222 exploitable videos (i.e., CATS cam data corresponding to camera not working, not directed forward, nighttime –  
223 and Acousonde data, all referred to as data 'without video' hereafter) using calf data with exploitable videos (i.e.,  
224 CATS cam data corresponding to camera directed forward and with enough visibility, referred to as data 'with  
225 video' hereafter).

226 For the model training, the data processing chain was as follow: first, the learning set was defined as the labelled  
227 calves' CATS cam data with video subdivided into non-overlapping blocks of 2s duration (labeled as suckling  
228 vs. non-suckling); second, a set of features (see below) was computed for each block; third, a machine learning  
229 model (AdaBoostM1) was trained on the learning set using a 15-run Bayesian Optimization approach with 5-  
230 fold cross-validation (see details regarding the machine learning workflow in the study by  
231 Ratsimbazafindranahaka et al. 2022). The initial set of features chosen for the machine learning process were  
232 the summary statistics of various kinematic data (the mean, minimum, maximum, kurtosis, skewness, variance  
233 of depth, depth rate, relative speed, nODBA, pitch, roll, and roll rate). However, after analyzing the inter-  
234 individual differences in the features using a Random Forest (RF) analysis following Ratsimbazafindranahaka et  
235 al. (2022), we chose to exclude the maximum, mean, and minimum values for both depth and relative speed.  
236 These six features were identified as contributing the most to the inter-individual difference in suckling (Fig. S1,  
237 supporting information). Excluding them can help improve the general ability of the machine learning model to  
238 detect suckling blocks. The number of runs we used for the optimization of the machine learning model was  
239 chosen to optimize processing speed while still having relatively stable results.

240 As per the 'data segmentation' described by Ratsimbazafindranahaka et al. (2022), blocks that were *a priori*  
241 considered as unlikely to corresponds to suckling events were directly excluded from all of our machine  
242 learning process (from learning to validation and application described below). These blocks were those too  
243 close to the surface (depth < 1.5 m, as periods corresponding to suckling events were never seen at less than 1.5  
244 m depth), or of high-speed activities (relative speed < 1.5, as suckling behavior was never seen being performed  
245 at high speed, Fig. S2, supporting information). Such blocks were therefore attributed by default to non-  
246 suckling.

#### 247 Validation of the suckling block detection

248 To estimate the ability of our machine learning procedure to correctly detect suckling blocks, we used a Leave-  
249 One-Out design (LOO). The procedure described above was replicated but using the data with videos from  $N-1$   
250 calves as learning set. The machine learning model trained with this learning set was then tested on the  
251 remaining calf (test deployment). In other words, the trained model was used to detect the suckling blocks in the  
252 test deployment. Three main evaluation metrics were calculated by comparing the predicted labels with the true  
253 labels: the sensitivity, the precision, and the FPR. The analysis was repeated  $N$  times, leaving out a different calf  
254 each time (i.e., using a different test deployment each time,  $N=11$  calves). The LOO is a good approach to

255 determine the performance of the machine learning procedure as it simulates the present situation where a set of  
256 labelled data is used to label new, unlabeled data usually coming from a new individual. Our method is expected  
257 to reach similar performance regardless of the tag's model (Acousonde or CATS cam) since both tag models  
258 contain similar sensors.

## 259 **Suckling events detection in data without videos**

### 260 **Extension of the suckling block detection to event detection**

261 The detection of suckling events when no visual cues were available (i.e., for data without video) was performed  
262 in two steps. In step 1, the trained machine learning model was applied on the data without video to detect  
263 suckling blocks. Similar to the learning set, the data without video were subdivided into non-overlapping 2 s  
264 blocks and segmented beforehand. In step 2, the block detection results were combined with the known  
265 characteristics of suckling events in order to go from suckling blocks to suckling events. Each suckling event  
266 has been shown by Ratsimbazafindranahaka et al. (2022) to correspond to a positive or negative deviation of the  
267 roll from zero as the calf rolls to the right or left to reach one mammary teat. The transition from detected  
268 suckling blocks to suckling events was thus performed automatically in the step 2 by locating the roll deviation  
269 corresponding to each block or each block group and then by applying some exclusion rules to retain the most  
270 probable suckling events. We considered that a deviation period starts when the absolute roll exceeds  $20^\circ$  and  
271 ends when it reaches back  $20^\circ$ . This threshold was determined based on the typical characteristics of the  
272 suckling events confirmed by video (see Fig. S2, supporting information). For a deviation period to be  
273 considered as a suckling event, (1) the number of blocks falling in it must exceed one (a criterion that was based  
274 on the probability of detecting a suckling block, see Results), (2) it must not contain parts corresponding to  
275 blocks too close to the surface (depth  $< 1.5$  m) or with high speed (relative speed  $> 1.5$  – same thresholds as in  
276 the segmentation process), (3) its duration must be less than 100 s (about twice the maximum duration of the  
277 visually confirmed suckling events, see Results).

### 278 **Validation of the suckling events detection**

279 To validate the ability of our method for detecting suckling events, as a first evaluation, we extended the LOO  
280 presented previously to the event detection level described above. The suckling events in each test deployment  
281 were identified based on the detected blocks (i.e., the blocks detected by the model that learned from the data  
282 with good videos of N-1 calves). The sensitivity and the precision of the event detection for each test were then  
283 calculated by confronting the predicted suckling events with the true suckling events. Additionally, the False

284 Event Rate (FER, count hour<sup>-1</sup>) was calculated for each test deployment by dividing the number of false  
285 suckling events (false positive) with the data duration (in hours).

286 As a second evaluation, we checked if the characteristics of the suckling events detected in the data without  
287 videos were similar to those of the visually confirmed suckling events. We compared the duration, the average  
288 depth, relative speed, normalized ODBA, pitch, roll, and roll rate used a linear mixed-effects model (LMMs)  
289 estimated in R software (R core team, <https://www.r-project.org/>) using REML (Restricted Maximum  
290 Likelihood, lme4 package, Bates et al. 2015). We included event type as a fixed effect (automatically detected  
291 vs. visually confirmed events) and individuals as random effects.

292 In addition to the performance evaluations above, we checked the detection results on simultaneous  
293 deployments (mothers and calves tagged simultaneously). We calculated the vertical distance between the  
294 mother and the calf (strictly speaking, the vertical distance between the tags) and checked if it complied with  
295 plausible nursing configuration during the detected suckling events (Fig. S3, supporting information). We  
296 expected the vertical distances during nursing to range between (1) the minimum distance case where the  
297 mother is almost vertical, and the calf is almost horizontal in the water column (calf's tag level about 1-2 m  
298 above the mother's tag level), and (2) the maximum distance case where the mother is almost horizontal, and the  
299 calf is almost vertical (calf's tag level about 5-6 m below the mother's tag level). The average is expected to  
300 correspond to the calf's tag level being 2-3 m below the mother's tag level. These expectations are based on the  
301 known nursing configuration reported in the literature (Glockner-Ferrari and Ferrari 1985; Zoidis and Lomac-  
302 MacNair 2017; Ratsimbazafindranahaka et al. 2022), the tag placements, and the reported average dimensions  
303 and body proportions of mothers and calves found in the area (Ratsimbazafindranahaka et al. 2021).

## 304 **Data analysis**

305 To compare the suckling events' duration between age classes, we used a LMM that included the calf's age class  
306 as a fixed effect and individuals as a random effect. To compare time spent suckling per age class, we separately  
307 calculated the percentage of time spent suckling for each age class. Only deployments longer than two hours  
308 were included in the calculation of the percentage of time spent suckling.

309 The roll deviation during a suckling event is known to be associated with the suckled teat  
310 (Ratsimbazafindranahaka et al., 2022). When the calf suckles on the right teat, it rolls to the right, and a positive  
311 average roll is recorded. Inversely, when the calf suckles on the left teat, it rolls to the left, and a negative

312 average roll is recorded. To check whether the calves show a side preference when suckling, we counted the  
313 events with a positive average roll and those with a negative roll. Where applicable, the suckling side was also  
314 visually checked on the video. We compared the occurrence of suckling on the right and the left using a chi-  
315 squared test. We also counted the number of times the calf changed sides between two successive suckling  
316 events. In addition, we compared the duration of the suckling events on the right and the left using a LMM that  
317 included the side as a fixed effect and individuals as a random effect.

318 Regarding the activity context, the number of suckling events corresponding to each activity phase per age class  
319 was counted. These data provide an overview of the distribution of suckling events among the different activity  
320 phases. To compare suckling depth between the different age classes, we used a LMM that included the calf's  
321 age class as a fixed effect and individuals as a random effect.

322 To investigate whether suckling happened during the night, we calculated the total number of suckling events  
323 between sunset and sunrise. Between July and September, the sunset and sunrise in Sainte Marie, Madagascar,  
324 are around 1730 and 0530 local time, respectively. We thus used 1800 and 0500 local time as conservative  
325 values for defining the beginning and end of the night.

326 When applicable, Standard Deviations (SDs) are presented along with the mean in the format mean $\pm$ SD.  
327 Statistical model assumptions were checked graphically (homoscedasticity, independence, and normality of the  
328 residuals). The LMMs were followed by Tukey's post-hoc multiple comparisons tests using the R package  
329 emmeans (Lenth et al. 2018) when more than two groups were compared and a statistical difference was  
330 detected. The statistical significance level was set to  $\alpha = 0.05$ .

## 331 **Results**

332 Over the nine fieldwork seasons, we obtained 18 successful single Acousonde calf deployments, 12 successful  
333 single CATS cam calf deployments, and seven successful simultaneous Acousonde deployments from 37  
334 mother-calf pairs. One CATS cam deployment had the camera directed downward the whole time and thus was  
335 considered like an Acousonde deployment. For the simultaneous deployments, one did not have overlapping  
336 data for the two individuals (i.e., the tag detached from the first individual before the second was tagged). Thus,  
337 the calf deployment was considered like a single deployment, and the deployment on the mother was discarded.  
338 Our dataset consisted of 112.21 hours of Acousonde data, including 29.53 hours of data from the mothers of six  
339 studied calves (simultaneous deployments) and 46.8 hours of CATS cam data, including 39.14 hours of data

340 with exploitable videos in total (Table S1, supporting information). The data from three of the 12 calves CATS  
341 deployments included in the present study correspond the data from three individuals published in the study by  
342 Ratsimbazafindranahaka et al. (2022).

343 From the 11 CATS deployments with videos, we labeled 79 visually confirmed suckling events. The average  
344 visually confirmed suckling events duration was  $18.5 \pm 8.3$  s (range = 4.8–51.2 s). The general characteristics of  
345 these events are shown in Fig. S2 (supporting information), along with the characteristics of 20 s non-suckling  
346 segments selected randomly for comparison ( $N = 214$ ). Our suckling event detection method found 165 suckling  
347 events in the CATS dataset without videos and Acousonde data. The average duration of the automatically  
348 detected suckling events was  $31.4 \pm 17$  s (range = 8.9–91.7 s).

### 349 **Ability of the machine learning method to detect suckling blocks**

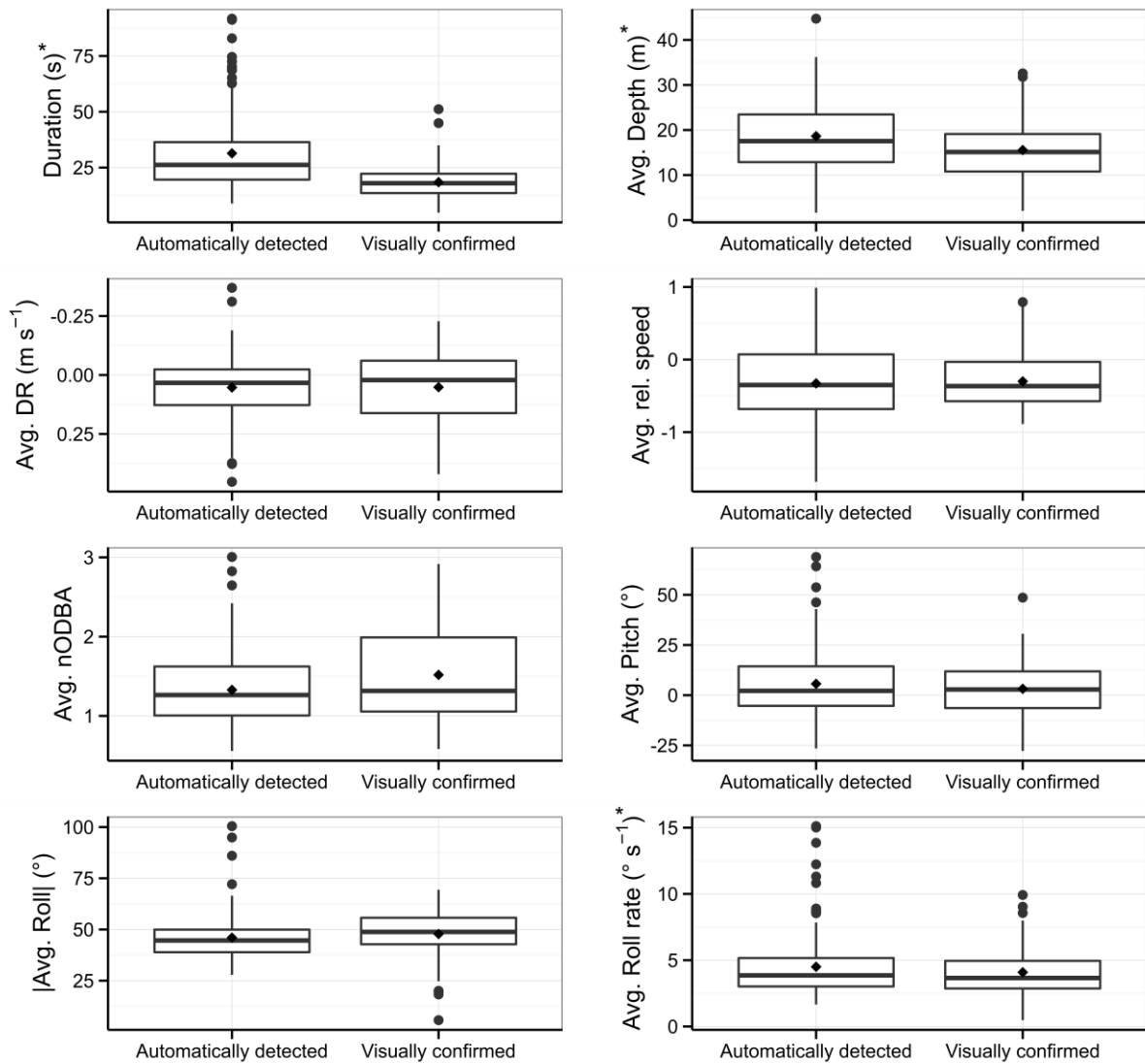
350 With the 11 CATS cam deployments, there were 11 splitting combinations for the LOO tests to assess the block  
351 detection performance. Two deployments did not have any suckling events. For these deployments, the only  
352 performance metric we calculated was the False Positive Rate (FPR). With the supervised machine learning, the  
353 mean sensitivity in detecting suckling blocks was 0.43 (range = 0.15–0.84,  $N = 9$ ). On average, the precision  
354 was 0.79 (range = 0.63–0.93,  $N = 9$ ). The average FPR was 0.34% (range = 0.06–0.88%,  $N = 11$ ).

### 355 **Validity of the suckling events detection**

356 Using the detected suckling blocks to identify suckling events in the tests, the average precision was 0.82 (range  
357 = 0.5–1,  $N = 9$ ), and the average sensitivity was 0.75 (range = 0.2–1,  $N = 9$ ). The False Events Rate (FER) was  
358 0.36 event per hour on average (range = 0.36–0.94 event per hour), i.e., the equivalent of about one false  
359 suckling event per 3 hours of data on average.

360 The mean duration of the automatically detected suckling events was higher than the mean duration of visually  
361 confirmed suckling events (Fig. 1). The difference, although moderate, was statistically significant (LMM,  $\beta = -$   
362  $8.73$ ,  $P = 0.002$ ). The mean average depth and mean average roll rate of the automatically detected suckling  
363 events were also higher compared to visually confirmed suckling events (Fig. 1). These differences were  
364 statistically significant but yet relatively small (LMM, average depth:  $\beta = -3.6$ ,  $P = 0.045$ ; average depth:  $\beta = -$   
365  $0.87$ ,  $P = 0.034$ ). The remaining characteristics were relatively close and not statistically different for both  
366 visually confirmed suckling events and automatically detected suckling events (LMMs, average depth rate:  $\beta =$

367 0.01,  $P = 0.685$ ; average relative speed:  $\beta = 0.13$ ,  $P = 0.303$ ; average normalized ODBA:  $\beta = 0$ ,  $P = 0.971$ ;  
 368 average pitch:  $\beta = -6.31$ ,  $P = 0.061$ ; average absolute roll:  $\beta = 2.02$ ,  $P = 0.363$ ; Fig. 1)



369

370 **Fig. 1** Characteristics of the automatically detected and visually confirmed suckling events. Avg.: average, DR:  
 371 depth rate, rel.: relative, nODBA: normalized Overall Dynamic Body Acceleration. The mean and median are  
 372 indicated by diamond marks and bold horizontal lines, respectively. (\*) indicate a statistically significant  
 373 difference ( $P < 0.05$ , Linear mixed-effects model)

374 Thirty-two suckling events were detected in five simultaneous Acousonde deployments (no suckling events in  
 375 one simultaneous deployment). We found that the average depth difference between the calf and the mother was  
 376  $2.5 \pm 2.1$  m. The minimum depth difference was -1.2 m and the maximum was 6.5 m (i.e., the calf's tag was at 1.2  
 377 above and 6.5 m below the mother's tag, respectively).

378 Time spent suckling and laterality

379 Due to the slight difference between the visually confirmed suckling events and the automatically detected  
 380 suckling events regarding the duration, we separated the two in all analyses involving the suckling duration.

381 Regarding the time spent suckling, we also separated the analyses for deployments in which all suckling events  
 382 were identified automatically (thus Acousonde deployments and CATS cam deployment without video during  
 383 the whole deployment) and for deployments with visually confirmed suckling events (for which part without  
 384 video were not considered).

385 The duration of the suckling events was similar for C1, C2, and C3 calves (Table 1). In our LMMs, for the  
 386 visually confirmed suckling events, the effect of C3 class on the duration of suckling events was positive but  
 387 statistically non-significant (C3:  $\beta = 1.93$ ,  $P = 0.542$ , Reference: C2, no C1 data available). For the  
 388 automatically detected suckling events, both the effect of C2 and C3 classes on the duration of suckling events  
 389 were positive but statistically non-significant (C2:  $\beta = 0.04$ ,  $P = 0.995$ , C3:  $\beta = -1.39$ ,  $P = 0.845$ , Reference: C1).  
 390 In addition, the difference in duration of suckling events for C2 and C3 calves was small and statistically non-  
 391 significant (Tukey's post-hoc test, C2 vs. C3,  $\beta = 1.44$ ,  $P = 0.954$ ).

392 Eleven deployments with video were longer than 2 hours (part without video not considered). In these data, the  
 393 percentage of time spent suckling was higher in C3 calves than in C2 calves (Table 1). Besides, 15 deployments  
 394 in which suckling events were all automatically detected had data longer than 2 hours (14 Acousonde  
 395 deployments and one CATS cam deployment without video). The percentage of time spent suckling in these  
 396 data was similar for the C2 and C3 calves; although it was slightly higher in C3 (Table 1). No sufficiently long  
 397 deployment was available for C1 for calculating the proportion of time spent suckling.

398 **Table 1** Duration of suckling events and proportion of time spent suckling according to the relative age in  
 399 young humpback whale calves (< 3 months old). The analyzes were separated in such a way so that the  
 400 duration-related parameters were comparable

Calf's relative age	C1	C2	C3
Suckling event durations	No data	17.5±8.6 s	19.1±8.1 s
(s):		(5.9–51.2 s; $N = 31$ )	(4.8–44.9 s; $N = 48$ )



visually confirmed

mean±SD (range, *N*)

---

Suckling event durations	29.7±10.7 s	30.3±11 s	31.9±19.1
(s):	(12.5–45.8; <i>N</i> = 10)	(14.3–65.2, <i>N</i> = 39)	(8.9–91.7, <i>N</i> = 116)

automatically detected

mean±SD (range, *N*)

---

% of time spent suckling	No data	0.73 <sup>a</sup>	1.36 <sup>b</sup>
		1.5 <sup>c</sup>	1.58 <sup>d</sup>

---

401 <sup>a</sup> Proportion calculated using five deployments with video (> 2 hours' duration each, part without video  
402 excluded)

403 <sup>b</sup> Proportion calculated using three deployments with video (> 2 hours' duration each, part without video  
404 excluded)

405 <sup>c</sup> Proportion calculated using four deployments without video (> 2 hours' duration each)

406 <sup>d</sup> Proportion calculated using 11 deployments without video (> 2 hours' duration each)

407 We did not find any side bias in the context of suckling behavior. The calves suckled to the right teat almost as  
408 often as to the left teat ( $\chi^2 = 0.803$ ,  $df = 1$ ,  $P = 0.37$ , Table S2, supporting information). The calves tended to  
409 alternate between the right and left teats between successive suckling events. A change in the suckling side was  
410 observed in 68% of successive suckling events. In addition, the duration of suckling to the right (mean =  
411 29.3±16.2 s, range = 8.9–91.7 s, *N* = 86) and to the left (mean = 33.7±17.7 s, range = 12.6–74.6 s, *N* = 79) did  
412 not show statistically significant differences (LMs, right vs. Left:  $\beta = -3.79$ ,  $P = 0.121$ ). When we considered  
413 the suckling events as clustered in series spaced less than a minute apart in several cases (see Suckling rhythm  
414 and occurrence at night) and looked at the first suckling side (the suckling side of the sole event in the case of  
415 isolated suckling event), we also did not find any striking side bias except for one individual (Table S3,  
416 supporting information).

417 **Activity and spatial context of suckling**

418 The suckling events mainly occurred during descent and bottom phases of dives for all age classes. Suckling  
 419 events at the surface and during ascent phases were not common (Table 2).

420 **Table 2** Number of suckling events found in each activity phase for C1, C2, and C3 humpback whale calves (<  
 421 3 months old). The data included both visually confirmed and automatically detected suckling events. The total  
 422 number suckling events recorded per age class is shown alongside each count

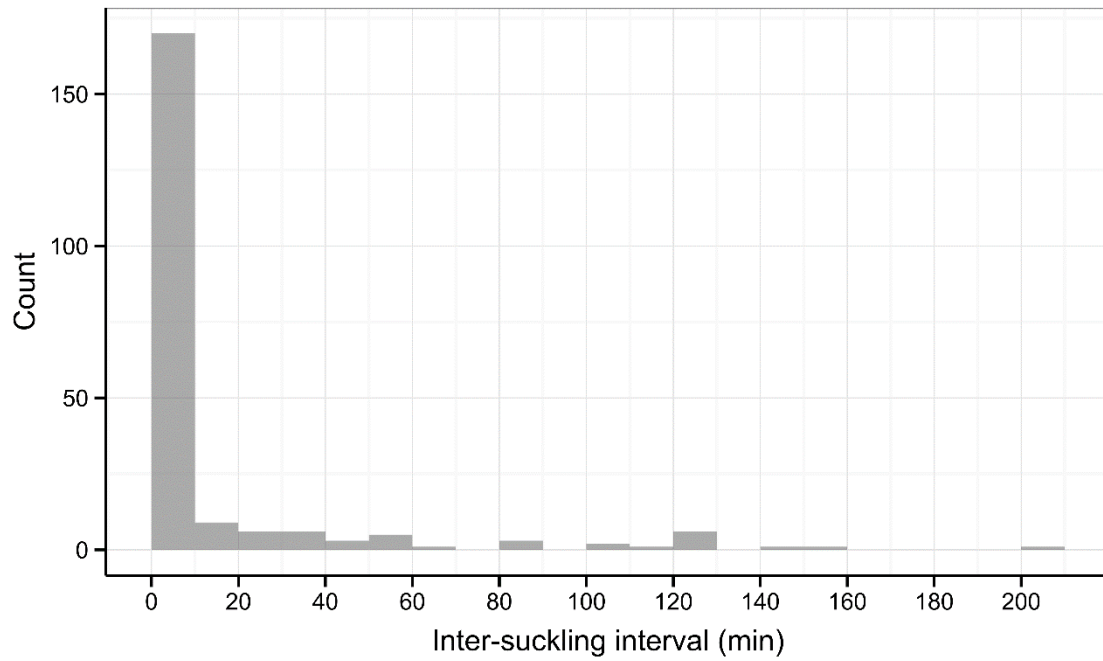
Age classes	Phases			
	Surface	Descent	Bottom	Ascent
C1	0/10	3/10	6/10	1/10
C2	4/70	14/70	50/70	2/70
C3	17/164	27/164	111/164	9/164

423

424 Suckling events occurred at a mean average depth of  $14.5 \pm 3.7$  m (10.2–19.6 m,  $N = 10$ ) in C1 calves, at  
 425  $16.7 \pm 5.5$  m (5–34.1 m,  $N = 70$ ) in C2 calves, and at  $18.2 \pm 8.1$  m (1.6–44.7 m,  $N = 164$ ) in C3 calves. The effect  
 426 of age class on the average suckling depth was positive but weak and statistically non-significant (LMM, C2:  $\beta$   
 427 = 3.04,  $P = 0.521$ ; C3:  $\beta = 4.56$ ,  $P = 0.310$ ; Reference: C1). In addition, the difference in average suckling depth  
 428 in C2 and C3 calves was small and statistically non-significant (Tukey’s post-hoc test, C2 vs. C3,  $\beta = -1.52$ ,  $P =$   
 429 0.819).

430 **Suckling rhythm and occurrence at night**

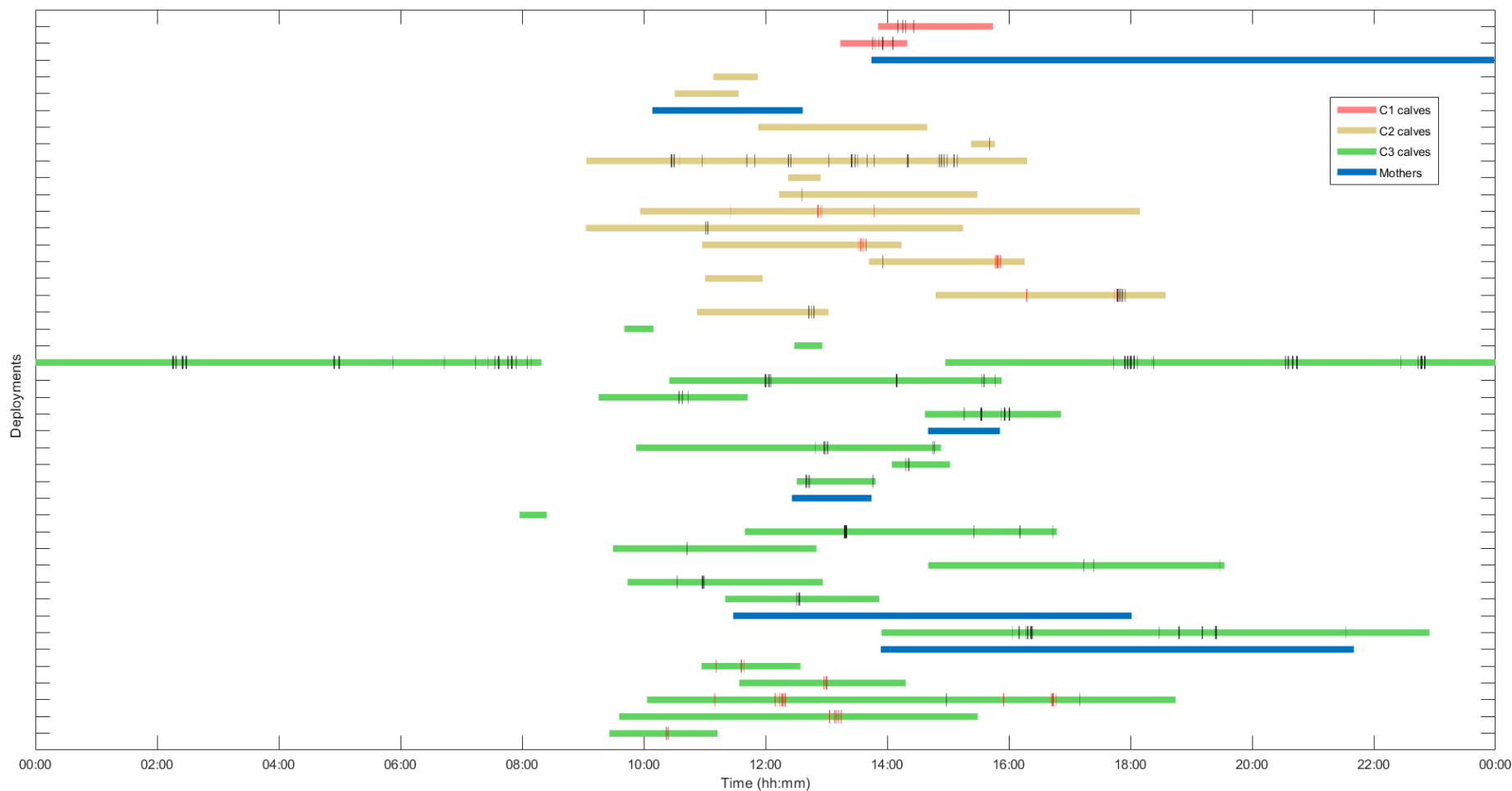
431 Inter-suckling intervals appeared to be bimodal (Fig. 2). The major mode was between 0 and 10 min, and the  
 432 minor mode was around 120 and 130 min. In other words, suckling events are highly grouped (often in  
 433 occurring less than 10 min apart), and sessions of suckling events are separated by about 2 hours. Such a pattern  
 434 is particularly evident in long deployments (Fig. 3). On a smaller timescale, the suckling events appeared to be  
 435 either isolated (102/244 events) or in series or bouts of 2-6 successive events occurring less than a minute apart  
 436 (142/244 events grouped in 52 bouts).



437

438 **Fig. 2** Frequency distribution of the inter-suckling intervals observed in 29 young humpback whale calves (< 3  
 439 months old)

440 Only six deployments recorded data during the night and thus provided nighttime data. The deployments  
 441 covered nighttime between 1800 and 0500 local time (about 15% of the whole calf dataset, Fig. 3). All  
 442 deployments with long nighttime data (> 1 hour) were on C3 calves. Twenty-nine suckling events at night were  
 443 found in these data (12% of the whole suckling events found).



444

445 **Fig. 3** Summary of the deployments used for studying the suckling behavior and the occurrence of suckling events in each calf deployment. Each deployment (each tick in the  
 446 vertical axis) corresponds to one distinct individual. Each horizontal line represents the time period when the tag was on the target animal. When available, successful  
 447 deployments on mothers is shown below their respective calves. Suckling events are represented with red vertical dashes for visually confirmed suckling events (by video)  
 448 and black vertical dashes for automatically identified suckling events

## 449 **Discussion**

450 Our study investigated the suckling/nursing behavior of humpback whales, by exploiting data from camera-  
451 equipped and non-camera-equipped animal-borne multi-sensor tags (Acousonde and CATS cam). We described  
452 the temporal pattern of the suckling behavior, its spatial and behavioral context, and the ontogeny of these  
453 characteristics. We based our study on combining kinematic data with visual cues (CATS cam data with video)  
454 and kinematic data lacking visual cues (Acousonde data, nighttime CATS cam data, and CATS cam data  
455 without exploitable video).

456 In addition to the data from three calves published by Ratsimbazafindranahaka et al. (2022), our base dataset  
457 (CATS cam data) for detecting suckling events in the absence of video included data with visually confirmed  
458 labels from eight new calves. With the new data, the average duration of the visually confirmed suckling events  
459 matched the result of the study by Ratsimbazafindranahaka et al. (2022) (mean =  $19 \pm 9$  s,  $N = 32$ ) and was  
460 similar to the result of the study by Tackaberry et al. (2020) for older calves in the feeding grounds (> 6 months  
461 old calves,  $23 \pm 7$  s,  $N = 11$ ). The kinematic characteristics of the suckling events (Tackaberry et al. 2020;  
462 Ratsimbazafindranahaka et al. 2022) were also confirmed by the additional data. Specifically, the suckling  
463 events were primarily characterized by a sharp increase in average absolute roll, an increase in swimming effort,  
464 and sometimes a decrease in swimming speed. We found no behavior similar to suckling but without a visible  
465 milk cloud within our data with videos. Our data thus suggest that some milk was always available for the calf  
466 every time the calf suckled or, in other words, that most suckling events in young calves are nutritive. Such  
467 observation suggest a behavioral and biological adaptations that maximize nutritive suckling. In terrestrial  
468 mammals, the young does not likely need to spend more energy related to locomotory effort to keep the suckling  
469 configuration. They thus can afford to use the suckling behavior as mother-calf relationship reinforcement and  
470 for comfort in addition to the nutritive function (Wolff 1968; Lent 1974; Hall and Williams 1983). For whales,  
471 since the calf generally needs to put effort into sustaining grips on the mammary gland (Tackaberry et al. 2020;  
472 Ratsimbazafindranahaka et al. 2022), suckling without any nutritive value may be disadvantageous due to  
473 energetic cost.

474 Our method for detecting suckling events in data lacking visual cues using visually labeled data had high  
475 robustness. Indeed, our tests showed that the method allowed the detection of most suckling events in a  
476 deployment (high sensitivity) with high confidence (high precision) and with a very low amount of false  
477 positives. Furthermore, the tests on simultaneous Acousonde data (simultaneous Acousonde deployment on the

478 mother and the calf) showed that the automatically detected suckling events (i.e., in calves) followed the known  
479 nursing configuration (of the mother-calf pair) presented in the literature (Glockner-Ferrari and Ferrari 1985;  
480 Zoidis and Lomac-MacNair 2017; Ratsimbazafindranahaka et al. 2022). Indeed, the depth recorded by the calf's  
481 tag was at most 1.2 m higher or 6.5 m lower than the depth recorded by its mother's tag and on average the  
482 calf's tag was at 2.4 m below the mother's tag.

483 Our automatic detection method overestimated the duration of individual suckling events, which was expected.  
484 Indeed, when a video is available, we can exactly see when the calf starts touching the mother's teat. However,  
485 in data lacking video, the detection of the start and end of a suckling event is only based on the roll deviation, so  
486 a few seconds before and after the actual suckling event may be included in the event. It may correspond to the  
487 calf still positioning itself to suckle or when it goes away from the teat. The slight difference induced by such a  
488 situation is unlikely to affect the conclusions of the present study. In fact, to facilitate interpretations, the  
489 analyses of the visually and automatically identified/detected suckling events in the present study were  
490 separated to take into account these differences. The other characteristics of the automatically detected suckling  
491 events were similar to the characteristics of the visually confirmed events. Thus, the method appears to be very  
492 robust in detecting suckling events.

493 In this study, the proportion of time spent suckling, which can be associated to the suckling effort, was several  
494 times superior to the proportion reported in the feeding ground (0.3 %, Tackaberry et al. 2020). The  
495 developmental stage of the calves can partly explain this difference. Calves on breeding grounds are very young  
496 calves (< 3 months old) still relying entirely on maternal milk. In comparison, calves on feeding grounds are  
497 older (> 6 months old) and already feeding on prey (Clapham 2018), thus potentially having decreased benefits  
498 and interest in getting maternal milk. The higher proportion of time spent suckling in the breeding ground  
499 compared to the feeding grounds may also be related to a reduction of the nursing opportunity given by the  
500 mother to the calf in the feeding grounds due to an increased mother-offspring conflict as the calf grows (Trivers  
501 1974).

502 Age-related trend regarding the time spent suckling was less clear. Both data with and without video indicated  
503 an increasing trend (time spent suckling tend to be higher for C3 compared to C2 age classes). However, the  
504 trend observed in data without video was less obvious. As only C2 and C3 age classes were well represented, we  
505 could not tell if the time spent suckling in C1 calves, i.e., freshly born/very young calves, differed from the older  
506 classes. In several mammals, including ungulates, the suckling rate decreases slowly during the mid-stage period

507 of dependence on the mother and differences primarily exist during the very early stage and towards the  
508 weaning time (Oftedal et al. 1987; Triossi et al. 1998; Clark and Odell 1999a, b; Skok 2022). An increasing  
509 trend may exist for species with offspring constrained to rapidly grow, as in phocids (Oftedal et al., 1987), to  
510 optimize the growth speed as the young's nutritional needs increase. This may explain the increasing trend we  
511 observed in young humpback whales. In migrating baleen whales, it is believed that the rapid growth of the calf  
512 is crucial, especially in preparation for the long migration to the feeding ground (Lockyer 1984; Corkeron and  
513 Connor 1999; Braithwaite et al. 2015).

514 We did not find any evidence regarding the suckling side preference. The results did not support the previous  
515 research conducted on a smaller sample (Zoidis and Lomac-MacNair 2017). In monotocous mammals (i.e.,  
516 mammals having only one offspring at a time), while there should not be a preference since the teats are equally  
517 available for the sole young, there may be a suckling preference associated with asymmetry in brain processing  
518 ability (Skok 2022). Several studies suggested the existence of lateral preferences in mother-infant pairs in  
519 cetaceans due to brain lateralization (Karenina and Giljov 2018). However, as Karenina & Giljov (2018)  
520 suggested, such preference may not manifest in the final positioning of suckling. Indeed, the confirmation of the  
521 identity of the mother for suckling by the calf, the only step that may require the use of the dominant  
522 hemisphere for social processing in the context of suckling (Karenina and Giljov 2018), is only needed before  
523 initiating the suckling. It is not relevant when the calf is already locked on a teat (confirmed to be the teat its  
524 mother beforehand). The absence of side preference, even in terms of duration, also likely excludes milk  
525 availability asymmetry between teats (Karenina and Giljov 2018). As in Ratsimbazafindranahaka et al. (2022),  
526 we found a typical pattern of alternation between successive suckling events from one side to the other. It has  
527 been suggested that it may be related to whales' milk production/storage/ejection system  
528 (Ratsimbazafindranahaka et al. 2022). Alternating the suckled teat would allow one breast to refill in preparation  
529 for the subsequent ejection. It is also important to note that studies on lateral preferences in mother-calf pairs in  
530 cetaceans were mostly conducted in toothed whales (Karenina and Giljov 2018). Toothed whales' head are  
531 anatomically asymmetrical, unlike baleen whales' head (Coombs et al. 2020). This anatomical difference  
532 between the two groups may induce differences in the level of behavioral laterality found in each of them.

533 Our results regarding the activity and spatial context suggest that suckling events occurred mostly at depth, so  
534 during dives and rarely during surface activities. These results match those mentioned in earlier studies (Videsen  
535 et al. 2017; Tackaberry et al. 2020; Ratsimbazafindranahaka et al. 2022) and may be associated with calf's

536 buoyancy control and diving performance (Videsen et al. 2017; Ratsimbazafindranahaka et al. 2022). Videsen et  
537 al. (2017) also suggested that suckling at depth may be a strategy for coping with the noise associated with the  
538 surface. More noises are near the surface due to the waves and wind, and the sound does not propagate well. The  
539 mother may prefer to be at depth to have better acoustic vigilance during potential vulnerability periods, such as  
540 while nursing.

541 Our nighttime data strongly supports that suckling events occur also at night and may even be as frequent as  
542 during the day. Our results are the first strong evidence of baleen whale suckling at night. In giraffes, suckling is  
543 less frequent during the night, but it is because the mother is often in a recumbent posture as she rests during this  
544 time, making it difficult for the young to access the nipples (Saito et al. 2020). This situation, however, does not  
545 apply to whales as they do not have any known resting posture that would limit access to the nipples. Moreover,  
546 humpback whales likely do not specifically use the nighttime for resting. Indeed, males are, for example, known  
547 to show more intense singing activity at night (Au et al. 2000; Kobayashi et al. 2021). In addition, a study on  
548 their feeding ground showed that they can be very active at night and that resting occurs throughout the day and  
549 night (Friedlaender et al. 2013). The occurrence of suckling during the night demonstrates baleen whales'  
550 remarkable ability to navigate and locate a specific target (here the teats) in very low light conditions. While  
551 baleen whales probably have vision adapted to low light levels, it has been suggested that their vision is not as  
552 efficient during the night (Goldbogen et al. 2011; Izadi et al. 2018). As in the prey detection context (Goldbogen  
553 et al. 2011; Izadi et al. 2018), suckling calves likely use a combination of different sensory modalities  
554 (chemoreception, touch, vision, and hearing) to locate and grasp mammary teats during the night successfully.

555 The analyses regarding the intervals of inter-suckling events suggest that suckling events are highly clustered in  
556 time in humpback whales, and the sessions are separated by around two hours of non-suckling periods. Cyclic  
557 suckling sessions throughout the day may be an inevitable mother-young strategy that mitigates the need for the  
558 mother to feed the calf for rapid growth intensely and to engage in other crucial activities in the breeding season  
559 and during migration. (e.g., traveling). The mothers need to travel a lot (up to 100 km per day) to move to calm  
560 resting areas with their calves (Trudelle et al. 2016, 2018; Dulau et al. 2017) or to reach the feeding area (Szabo  
561 and Duffus 2008; Tyson et al. 2012; Clapham 2018). The observed temporal pattern of suckling would give the  
562 mother time to move with her calf to a zone with less disturbance and less predation risk while they stay in the  
563 breeding/calving area. Ultimately, these time windows would also give the mother-calf pair the time to travel to  
564 reach the feeding area during the peak season. Indeed, even if suckling may be performed while moving as



565 suggested by our current data and by previous studies (Tackaberry et al. 2020; Ratsimbazafindranahaka et al.  
566 2022), it still requires the pair to slow down to facilitate the calf's attachment to the nipple (Tackaberry et al.  
567 2020; Ratsimbazafindranahaka et al. 2022). The two hour intervals between suckling sessions may also  
568 correspond to the optimal time needed for the calf to digest the milk before the subsequent sessions (next suite  
569 of suckling events or bouts). Similar inter-session intervals have been reported in American bison, a terrestrial  
570 mammal that uses the 'following' strategy (Green 1986). In contrast to what we found in humpback whales,  
571 however, the suckling sessions found in American bison were mainly composed of just one continuous suckling  
572 bout with suckling events spaced by less than 10 s pauses. The difference may be related to whale calves  
573 holding their breath while suckling, which limits the time for long continuous suckling bout. Young humpback  
574 whale calves go up to the surface to breathe after about 2 min under water on average (Huetz et al. 2022).  
575 Sessions must thus be divided into a few bouts to allow the calf to breathe. Despite the difference, the suckling  
576 pattern in humpback whales falls into the common characteristics of species using the following strategies  
577 where the young are nursed several times a day in short sessions, unlike in species that use the hiding strategies  
578 (Lent 1974; Rosenblatt et al. 1985; Fisher et al. 2002; Gloneková et al. 2017). In terrestrial followers, the  
579 following strategy has been described as a way to reduce predation on young in open habitats while allowing the  
580 mother not to interrupt various vital activities for a prolonged time to nurse (Lent 1974; Rosenblatt et al. 1985;  
581 Fisher et al. 2002; Gloneková et al. 2017). This hypothesis is consistent with the ecology of baleen whales.  
582 Indeed, whales live in habitats that can be qualified as open, which do not provide cover to the young against  
583 predators (killer whales, Pitman et al. 2015) and they exploit temporally and spatially scattered resources.

584 We were constrained regarding comparing our results with other studies on other species. Due to variability and  
585 sometimes ambiguity regarding how suckling duration and inter-suckling intervals are defined in the available  
586 literature, direct comparison among studies of suckling regarding the duration and temporal pattern is  
587 challenging (Lent 1974; Oftedal et al. 1987). Most of the time, the reported durations correspond to both on-teat  
588 (referred to as suckling events in the present study) and off-teat intervals between successive on-teat periods. An  
589 arbitrarily chosen off-teat time limit was usually set to group successive on-teat periods into bouts or sessions of  
590 suckling on which duration is calculated. The demarcation usually has no biological foundation (Blank and  
591 Yang 2015). Different values regarding the duration and inter-suckling intervals may be obtained depending on  
592 the chosen limit. A more appropriate approach to describe and compare the duration and temporal pattern of  
593 suckling would be to systematically report on-teat durations (suckling events) along with the frequency  
594 distribution of inter-on-teat intervals (inter-suckling events intervals). This approach would allow seeing

595 whether the young grab the teat (suckle) for a prolonged period or not, whether the on-teat periods are regularly  
596 dispersed (unimodal distribution) or clustered in time (multimodal distribution), and whether among species the  
597 clustering or periodicity is different or not. That being said, our results globally agree with the general suckling  
598 characteristics attributed to the following strategy found in ungulates experiencing predation in an open  
599 environment. Our study thus reinforces the status of the humpback whale, and potentially most baleen whales,  
600 as being both behaviorally and functionally similar to terrestrial 'followers' in terms of mother-young strategy  
601 (Szabo and Duffus 2008; Tyson et al. 2012).

## 602 **Acknowledgements**

603 We warmly thank the Cetamada team members who contributed to the data collection. This study was supported  
604 and funded by the Centre National de la Recherche Scientifique, the Cétamada association, the Western Indian  
605 Ocean Marine Science Association (MARG Program), the Association for Tropical Biology and Conservation  
606 (ATBC seed grant), the CeSigma company, and anonymous donors who supported the study via the  
607 KissKissBankBank crowdfunding platform for MNR. MNR received a cotutelle Ph.D. scholarship from the  
608 ADI2020 project funded by the IDEX Paris-Saclay, ANR-11-IDEX-0003-02.

## 609 **References**

- 610 Au WWL, Mobley J, Burgess WC, et al (2000) Seasonal and diurnal trends of chorusing humpback whales  
611 wintering in waters off western Maui. *Marine mammal science* 16:530–544. [https://doi.org/10.1111/j.1748-](https://doi.org/10.1111/j.1748-7692.2000.tb00949.x)  
612 [7692.2000.tb00949.x](https://doi.org/10.1111/j.1748-7692.2000.tb00949.x)
- 613 Balshine S (2012) *Patterns of parental care in vertebrates*. Oxford University Press Oxford
- 614 Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of*  
615 *Statistical Software* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- 616 Blank DA, Yang W (2015) Strategy of goitered gazelle suckling behavior. *Mammal Research* 60:393–401.  
617 <https://doi.org/10.1007/s13364-015-0239-8>
- 618 Braithwaite JE, Meeuwig JJ, Hipsey MR (2015) Optimal migration energetics of humpback whales and the  
619 implications of disturbance. *Conservation Physiology* 3:cov001. <https://doi.org/10.1093/conphys/cov001>

620 Cade DE, Barr KR, Calambokidis J, et al (2017) Determining forward speed from accelerometer jiggle in  
621 aquatic environments. *Journal of Experimental Biology* 221:jeb170449. <https://doi.org/10.1242/jeb.170449>

622 Cade DE, Gough WT, Czapanskiy MF, et al (2021) Tools for integrating inertial sensor data with video bio-  
623 loggers, including estimation of animal orientation, motion, and position. *Animal Biotelemetry* 9:1–21.  
624 <https://doi.org/10.1186/s40317-021-00256-w>

625 Cartwright R, Sullivan M (2009) Behavioral ontogeny in humpback whale ( *Megaptera novaeangliae* ) calves  
626 during their residence in Hawaiian waters. *Marine Mammal Science* 25:659–680. <https://doi.org/10.1111/j.1748->  
627 [7692.2009.00286.x](https://doi.org/10.1111/j.1748-7692.2009.00286.x)

628 Chivers SJ (2009) Cetacean life history. In: *Encyclopedia of marine mammals*. Elsevier, pp 215–220

629 Clapham PJ (2018) Humpback Whale. In: *Encyclopedia of Marine Mammals*. Academic Press, pp 489–492

630 Clapham PJ, Mayo CA (1987) Reproduction and recruitment of individually identified humpback whales,  
631 *Megaptera novaeangliae* , observed in Massachusetts Bay, 1979–1985. *Canadian Journal of Zoology* 65:2853–  
632 2863. <https://doi.org/10.1139/z87-434>

633 Clark ST, Odell DK (1999a) Nursing behaviour in captive false killer whales (*Pseudorca crassidens*). *Aquatic*  
634 *Mammals* 25:183–191

635 Clark ST, Odell DK (1999b) Nursing parameters in captive killer whales (*Orcinus orca*). *Zoo Biology*:  
636 Published in affiliation with the American Zoo and Aquarium Association 18:373–384.  
637 [https://doi.org/10.1002/\(sici\)1098-2361\(1999\)18:5<373::aid-zoo2>3.0.co;2-d](https://doi.org/10.1002/(sici)1098-2361(1999)18:5<373::aid-zoo2>3.0.co;2-d)

638 Clutton-Brock TH (1991) *The evolution of parental care*. Princeton University Press

639 Coombs EJ, Clavel J, Park T, et al (2020) Wonky whales: the evolution of cranial asymmetry in cetaceans.  
640 *BMC biology* 18:1–24. <https://doi.org/10.1186/s12915-020-00805-4>

641 Corkeron PJ, Connor RC (1999) Why do baleen whales migrate? 1. *Marine Mammal Science* 15:1228–1245.  
642 <https://doi.org/10.1111/j.1748-7692.1999.tb00887.x>

643 Dulau V, Pinet P, Geyer Y, et al (2017) Continuous movement behavior of humpback whales during the  
644 breeding season in the southwest Indian Ocean: on the road again! *Movement ecology* 5:1–17.  
645 <https://doi.org/10.1186/s40462-017-0101-5>

646 Faria M-A, DeWeerd J, Pace F, Mayer F-X (2013) Observation of a humpback whale (*Megaptera*  
647 *novaeangliae*) birth in the coastal waters of Sainte Marie Island, Madagascar. *Aquatic Mammals* 39:296.  
648 <https://doi.org/10.1578/AM.39.3.2013.296>

649 Finger RA, Abbagnaro LA, Bauer BB (1979) Measurements of low-velocity flow noise on pressure and  
650 pressure gradient hydrophones. *The Journal of the Acoustical Society of America* 65:1407–1412.  
651 <https://doi.org/10.1121/1.382927>

652 Fisher DO, Blomberg SP, Owens IPF (2002) Convergent maternal care strategies in ungulates and macropods.  
653 *Evolution* 56:167–176. <https://doi.org/10.1111/j.0014-3820.2002.tb00858.x>

654 Friedlaender AS, Tyson RB, Stimpert AK, et al (2013) Extreme diel variation in the feeding behavior of  
655 humpback whales along the western Antarctic Peninsula during autumn. *Marine Ecology Progress Series*  
656 494:281–289. <https://doi.org/10.3354/meps10541>

657 Gingerich PD, Ul-Haq M, von Koenigswald W, et al (2009) New protocetid whale from the middle Eocene of  
658 Pakistan: birth on land, precocial development, and sexual dimorphism. *PLoS one* 4:e4366.  
659 <https://doi.org/10.1371/journal.pone.0004366>

660 Glockner-Ferrari DA, Ferrari MJ (1985) Individual identification, behavior, reproduction, and distribution of  
661 humpback whales, *Megaptera novaeangliae*, in Hawaii.

662 Glockner DA, Venus SC (1983) Identification, growth rate, and behaviour of humpback whale (*Megaptera*  
663 *novaeangliae*) cows and calves in the waters off Maui, Hawaii, 1977--79: 223--258 in Payne, R.(ed),  
664 *Communication and behavior of whales*

665 Gloneková M, Vymyslická PJ, Žáčková M, Brandlová K (2017) Giraffe nursing behaviour reflects  
666 environmental conditions. *Behaviour* 154:115–129. <https://doi.org/10.1163/1568539x-00003413>

667 Goldbogen JA, Calambokidis J, Oleson E, et al (2011) Mechanics , hydrodynamics and energetics of blue whale  
668 lunge feeding : efficiency dependence on krill density. <https://doi.org/10.1242/jeb.048157>

669 Green WCH (1986) Age-related differences in nursing behavior among American bison cows (*Bison bison*).  
670 *Journal of Mammalogy* 739–741. <https://doi.org/10.2307/1381136>

671 Hain JHW, Hampp JD, McKenney SA, et al (2013) Swim speed, behavior, and movement of North Atlantic  
672 right whales (*Eubalaena glacialis*) in coastal waters of northeastern Florida, USA. *PloS one* 8:e54340.  
673 <https://doi.org/10.1371/journal.pone.0054340>

674 Hall WG, Williams CL (1983) Suckling isn't feeding, or is it? A search for developmental continuities. In:  
675 *Advances in the Study of Behavior*. Elsevier, pp 219–254

676 Huetz C, Saloma A, Adam O, et al (2022) Ontogeny and synchrony of diving behavior in Humpback whale  
677 mothers and calves on their breeding ground. *Journal of Mammalogy* gyac010.  
678 <https://doi.org/10.1093/jmammal/gyac010>

679 Isojunno S, Curé C, Kvadsheim PH, et al (2016) Sperm whales reduce foraging effort during exposure to 1--2  
680 kHz sonar and killer whale sounds. *Ecological Applications* 26:77–93. <https://doi.org/10.1890/15-0040>

681 Izadi S, Johnson M, de Soto NA, Constantine R (2018) Night-life of Bryde's whales: ecological implications of  
682 resting in a baleen whale. *Behavioral Ecology and Sociobiology* 72:1–12. <https://doi.org/10.1007/s00265-018->  
683 2492-8

684 Johnson MP, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine  
685 mammals to sound. *IEEE journal of oceanic engineering* 28:3–12. <https://doi.org/10.1109/JOE.2002.808212>

686 Karenina K, Giljov A (2018) Mother and offspring lateralized social behavior across mammalian species.  
687 *Progress in Brain Research* 238:115–141. <https://doi.org/10.1016/bs.pbr.2018.06.003>

688 Kobayashi N, Okabe H, Higashi N, et al (2021) Diel patterns in singing activity of humpback whales in a winter  
689 breeding area in Okinawan (Ryukyuan) waters. *Marine Mammal Science* 37:982–992.  
690 <https://doi.org/10.1111/mms.12790>

691 Lent PC (1974) Mother-infant relationships in ungulates. The behaviour of ungulates and its relation to  
692 management 1:14–55

693 Lenth R, Singmann H, Love J, et al (2018) Emmeans: Estimated marginal means, aka least-squares means. R  
694 package version 113

695 Lockyer C (1984) Review of baleen whale (Mysticeti) reproduction and implications for management. Rep int  
696 Whal Commn 6:27–50

697 Morete ME, Freitas A, Engel MH, et al (2003) A novel behavior observed in humpback whales on wintering  
698 grounds at Abrolhos Bank (Brazil). *Marine Mammal Science* 19:694–707

699 Oftedal OT, Boness DJ, Tedman RA (1987) The behavior, physiology, and anatomy of lactation in the  
700 pinnipedia. In: *Current mammalogy*. Springer, pp 175–245

701 Pitman RL, Totterdell JA, Fearnbach H, et al (2015) Whale killers: prevalence and ecological implications of  
702 killer whale predation on humpback whale calves off Western Australia. *Marine Mammal Science* 31:629–657.  
703 <https://doi.org/10.1111/mms.12182>

704 Ratsimbazafindranahaka MN, Huetz C, Andrianarimisa A, et al (2022) Characterizing the suckling behavior by  
705 video and 3D-accelerometry in humpback whale calves on a breeding ground. *PeerJ* 10:e12945.  
706 <https://doi.org/10.7717/peerj.12945>

707 Ratsimbazafindranahaka MN, Razafimahatratra E, Mathevet R, et al (2021) Morphometric study of humpback  
708 whale mother-calf pairs in the Sainte Marie channel, Madagascar, using a simple drone-based photogrammetric  
709 method. *Western Indian Ocean Journal of Marine Science* 20:95–107. <https://doi.org/10.4314/wiojms.v20i2.8>

710 Rosenblatt JS, Mayer AD, Siegel HI (1985) Maternal behavior among the nonprimate mammals. In:  
711 *Reproduction*. Springer, pp 229–298

712 Saito M, Takagi N, Tanaka M, Yamanashi Y (2020) Nighttime suckling behavior in captive giraffe (*Giraffa*  
713 *camelopardalis reticulata*). *Zoological science* 37:1–6. <https://doi.org/10.2108/zs190094>

714 Saloma A, Ratsimbazafindranahaka MN, Martin M, et al (2022) Social calls in humpback whale mother-calf  
715 groups off Sainte Marie breeding ground (Madagascar, Indian Ocean). *PeerJ* 10:e13785.  
716 <https://doi.org/10.7717/peerj.13785>

717 Simon M, Johnson M, Madsen PT (2012) Keeping momentum with a mouthful of water: behavior and  
718 kinematics of humpback whale lunge feeding. *Journal of Experimental Biology* 215:3786–3798.  
719 <https://doi.org/10.1242/jeb.071092>

720 Skok J (2022) Suckling strategies in terrestrial ungulates (Artiodactyla, Perissodactyla) and the factors  
721 influencing them: The offspring perspective. *CABI Reviews*. <https://doi.org/10.1079/cabireviews20221701>

722 Stimpert AK, Mattila D, Nosal E-M, Au WWL (2012) Tagging young humpback whale calves: methodology  
723 and diving behavior. *Endangered Species Research* 19:11–17. <https://doi.org/10.3354/esr00456>

724 Szabo A, Duffus D (2008) Mother--offspring association in the humpback whale, *Megaptera novaeangliae*:  
725 Following behaviour in an aquatic mammal. *Animal Behaviour* 75:1085–1092

726 Taber S, Thomas P (1982) Calf development and mother-calf spatial relationships in southern right whales.  
727 *Animal behaviour* 30:1072–1083. [https://doi.org/10.1016/S0003-3472\(82\)80197-8](https://doi.org/10.1016/S0003-3472(82)80197-8)

728 Tackaberry JE, Cade DE, Goldbogen JA, et al (2020) From a calf's perspective: humpback whale nursing  
729 behavior on two US feeding grounds. *PeerJ* 8:e8538. <https://doi.org/10.7717/peerj.8538>

730 Thomas PO, Taber SM (1984) Mother-infant interaction and behavioral development in southern right whales,  
731 *Eubalaena australis*. *Behaviour* 88:42–60

732 Triossi F, Pace DS, Terranova ML, Renzi P (1998) The development of suckling behavior in two captive-born  
733 calves of bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals* 24:75–84

734 Trivers RL (1974) Parent-offspring conflict. *Integrative and comparative biology* 14:249–264.  
735 <https://doi.org/10.1093/icb/14.1.249>

736 Trudelle L, Cerchio S, Zerbini AN, et al (2016) Influence of environmental parameters on movements and  
737 habitat utilization of humpback whales (*Megaptera novaeangliae*) in the Madagascar breeding ground. *Royal*  
738 *Society open science* 3:160616. <https://doi.org/10.1098/rsos.160616>

739 Trudelle L, Charrassin J-B, Saloma A, et al (2018) First insights on spatial and temporal distribution patterns of  
740 humpback whales in the breeding ground at Sainte Marie Channel, Madagascar. *African Journal of Marine*  
741 *Science* 40:75–86. <https://doi.org/10.2989/1814232X.2018.1445028>

742 Tyson RB, Friedlaender AS, Ware C, et al (2012) Synchronous mother and calf foraging behaviour in  
743 humpback whales *Megaptera novaeangliae*: insights from multi-sensor suction cup tags. *Marine Ecology*  
744 *Progress Series* 457:209–220

745 Videsen SKA, Bejder L, Johnson M, Madsen PT (2017) High suckling rates and acoustic crypsis of humpback  
746 whale neonates maximise potential for mother--calf energy transfer. *Functional Ecology* 31:1561–1573.  
747 <https://doi.org/10.1111/1365-2435.12871>

748 Wilson RP, White CR, Quintana F, et al (2006) Moving towards acceleration for estimates of activity-specific  
749 metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* 75:1081–1090.  
750 <https://doi.org/10.1111/j.1365-2656.2006.01127.x>

751 Wolff PH (1968) Sucking patterns of infant mammals. *Brain, Behavior and Evolution* 1:354–367

752 Würsig B, Dorsey EM, Fraker MA, et al (1985) Behavior of bowhead whales, *Balaena mysticetus*, summering  
753 in the beaufort sea: a description. *Fishery Bulletin* 83:

754 Zoidis AM, Lomac-MacNair KS (2017) A note on suckling behavior and laterality in nursing humpback whale  
755 calves from underwater observations. *Animals* 7:51. <https://doi.org/10.3390/ani7070051>

756