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Time budget and behavioral synchrony of humpback whale mother-calf pairs on a breeding ground in the southwestern Indian Ocean

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Abstract

Understanding the activity budget of mother-young pairs can inform how energy is allocated and its relation to the development of young. Using suction cup tag data collected off Sainte Marie, Madagascar, during the calving season, we compared the time budgets of mothers and their calves in capital-breeding humpback whales, investigated the changes with age, and assessed mother-calf behavioral synchrony based on their swimming speed. We found that mothers and calves allocated much of their time to low-level activities (i.e., static/quasi-static or swimming at low speed). Young calves engaged more in slow swimming than older calves and mothers. Mothers with younger calves tended to stay static or quasi-static less than mothers with older ones. Calves displayed some degree of independence in activities but were also observed synchronizing their activities with their mothers. Depending on the nature of the activity, the initiation of it was driven by either the calf or the mother. Our study provides additional knowledge for understanding the behavioral dynamics and interactions within humpback whale mother-calf pairs. It provides data that can support the implementation of conservation measures.

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KEYWORDS

breeding area, cetacean, multisensor tags, ontogeny, parent-offspring interactions

1 | INTRODUCTION

Mammals are known for their highly elaborate forms of parental care. Most often provided by the mother, it takes various forms, such as providing the nutrients required for embryo development, protecting, feeding, teaching, etc. (Balshine, 2012; Clutton-Brock, 1991). The purpose of parental care is to improve the fitness of the offspring to favor the preservation of parental genes. It is a costly investment that can reduce the survival chances of the parents themselves or limit their future reproduction (Balshine, 2012; Clutton-Brock, 1991; Trivers, 1974). For female mammals, food provisioning in the form of maternal milk represents one of the most critical and costly aspects of this care (Braithwaite et al., 2015; Gittleman & Thompson, 1988; Oftedal, 2000). In addition to providing food to their offspring, female mammals can provide warmth (thermal assistance), protect the offspring from predators, assist locomotion, etc. (Gubernick & Klopfer, 1981).

In the context of maternal care, efficient resource use is crucial for the well-being and survival of both the mother and the offspring. The mother must allocate energy to meet her offspring's needs while sustaining herself. Simultaneously, the offspring must efficiently utilize the resources provided by the mother to support its high-energy-cost growth and development (Brody, 1945). In some species, the females depend on easily accessible food resources to produce and care for offspring (income breeders). Other species build up energy reserves beforehand (capital breeders; Houston et al., 2007; Jönsson, 1997). Depending on the strategy used by the female, the impact of acute or chronic disturbances in the environment during the breeding period on the quality of care provided, and therefore on the chance of offspring survival, may differ. For example, pure capital breeders may be less flexible to disturbances that force females to spend more energy, as the energy available is already determined in advance (Jönsson, 1997). As a result, mothers may struggle to compensate for the costs of disturbance to meet their needs while maintaining optimal care for the survival of the offspring. For the offspring, whether the mother is a capital or income breeder, disruption of maternal investment as a result of the changes in her energy allocation due to disturbances may affect the milk production of the mother, thus affecting the energy intake of the offspring and implicitly the energy allocated for growth and development (Pirota et al., 2018). More direct effects of disturbances on offspring include increasing disturbance-related extra activity (e.g., avoidance behavior) that diverts energy meant for growth or other vital activities (Braithwaite et al., 2015).

Among marine mammals, mysticetes (baleen whales) generally fall into the capital breeder category, with accentuated spatial and temporal separation of feeding and reproduction. They build up a reserve of energy in mid- to high-latitude feeding areas during the summer and use it to reproduce later in low-latitude breeding areas during the winter (Bannister, 2018). They take advantage of abundant food resources in the feeding areas and the warm temperature and reduced predation pressure (by killer whales, *Orcinus orca*) for calves in the breeding areas (Bannister, 2018; Corkeron & Connor, 1999; Lockyer, 1984; Pérez-Jorge et al., 2020; Steiger et al., 2008). The maternal strategy of mysticetes has been described as equivalent to the “follower” strategy observed in terrestrial ungulates, a strategy used to cope with predation pressure in open habitats (Fisher et al., 2002; Lent, 1974). Indeed, similar to terrestrial followers, young baleen whales are locomotory, sensorially, and thermoregulatory independent relatively soon after birth (precocial species), follow their mother wherever she goes, and are nursed frequently but in short sessions (Huetz et al., 2022; RatsimbazafindranaHaka et al., 2023; Szabo & Duffus, 2008; Tyson et al., 2012).

Baleen whale mothers have a limited energy reserve to care for their precocial calf (born in the breeding/calving ground) during at least the first few months of its life. Thus, they must minimize energy consumption and save energy for the upcoming migration while allocating energy to their calf (Bejder et al., 2019; Braithwaite et al., 2015;

Clapham, 2018; Ejrnæs & Sprogis, 2021). As for the calf, it must optimize the energy taken in from its mother to achieve growth and carry out various activities essential for its cognitive and social development, especially in preparation for the upcoming migration alongside its mother to the feeding area (Braithwaite et al., 2015; Corkeron & Connor, 1999; Ejrnæs & Sprogis, 2021).

Humpback whales (*Megaptera novaeangliae*) are among the most common and well-studied baleen whale species. Female humpback whales care for their calves for about 1 year (Clapham, 2018). Calves spend their first 3 months on the breeding ground, relying exclusively on maternal milk (RatsimbazafindranaHaka et al., 2022, 2023; Videsen et al., 2017). They begin feeding on prey when they reach about 7 months old (Clapham, 2018). During their stay in the breeding area, humpback whale calves undergo remarkable growth and development. They gain about 3 cm in length per day (Christiansen et al., 2016), for a daily weight gain estimated to be about 30 kg (Ofstedal, 1997). Their diving and swimming abilities also improve rapidly (Cartwright & Sullivan, 2009; Ejrnæs & Sprogis, 2021; Huetz et al., 2022). The cost associated with sustaining such rapid growth and development of the calf in the breeding ground is considerable for the mother, as indicated by Christiansen et al. (2016), who observed an elevated rate of body condition decline in lactating females compared to nonlactating adults. In these contexts, and with the alarming increase in human coastal activities that impact whales, how the mother and calf organize their activities in the breeding ground is of particular interest to gain insight into energy allocation, the calf's needs, and the level of dependence of the calf on its mother, and to understand the potential impact of disturbances from anthropic activities during the critical phase of calf's development. Such insights are essential for fine tuning conservation initiatives.

Several past studies have examined the activity budgets, energy allocation, and ontogenetic behavioral changes in humpback whale mother-calf pairs (Bejder et al., 2019; Cartwright & Sullivan, 2009; Ejrnæs & Sprogis, 2021). However, our current knowledge could benefit from studies based on high-resolution data from multisensor tags deployed on mothers and calves that can capture their activities even during dives. Indeed, the studies by Cartwright and Sullivan (2009) and by Ejrnæs and Sprogis (2021), for example, have been limited to surface and subsurface behaviors because of the method employed (vessel-based or aerial vehicle-based observations) and even to a specific context (activities while the mother is logging, Ejrnæs & Sprogis, 2021). The study by Bejder et al. (2019) used multisensor tags but classified calf's and mother's behaviors as binary—suckling versus other and resting versus other, respectively.

Because the humpback whale is considered a follower species, it is expected that the activities of the mother and her calf are highly synchronized, as observed in terrestrial followers (e.g., sheep, Gluesing et al., 1980; American bison, Green, 1993). However, because the mother and calf are two individuals with different physiological needs and different physical performances (e.g., the need to breathe more frequently in whale calves, Huetz et al., 2022), they may also present periods of asynchrony (still optimized to limit the risks of separation) where each individual of the pair engages in activities adapted to its own needs. The differences and similarities, but also how the activities of the individuals are tied, should be investigated as part of the study of the time budget of closely associated individuals such as mother-calf pairs as they are keys for ensuring mitigation measures that consider impact of disturbances, both at the group and individual levels. For instance, overlooking potential behavioral independence of the calf may lead to inadequate inferences and policies that focus only on the mother's behavior.

Most studies that have addressed behavioral synchrony in humpback whales focused on dive synchrony and distance maintenance (Huetz et al., 2022; Tyson et al., 2012). Because dive data mainly capture spatial relationships between the mother and her calf, details on how the mother's and calf's activities coincide are yet to be investigated. For instance, the mother and the calf may both be staying at the same depth but with differing activities (e.g., one resting and one wandering around the other) or at different depths but engaging in the same activity (e.g., one resting at depth and one resting at the surface).

In the present study, we focused on the activities of humpback whale mother-calf pairs off Sainte Marie, Madagascar, where no study has been conducted on mother-calf pairs' time budget. The study site is a blooming

location for whale watching, with boat traffic mainly related to this activity during the peak calving period (Saisho, 2022; Trudelle et al., 2018). Monumental efforts and initiatives are undertaken in the area to ensure the sustainability of such activity, serving as a model in the Southwestern Indian Ocean (Saisho, 2022). In line with such efforts and initiatives, it is essential to continue building a body of knowledge that would help raise awareness of the potential disturbances to the most sensitive groups like mother-calf pairs and reinforce existing whale-watching guidelines and regulations if needed.

We investigated the time budget of humpback whale mother-calf pairs and evaluated their behavioral synchrony by focusing on their swimming speed. We used multisensor tag data sets, including one of the most extensive multisensor tag samples on calves yet published. Because of the need for the mother to save her limited energy reserve and the need for the calf to maximize energy allocated to its growth and development, both the mother and the calf are expected to display a low activity level (Bejder et al., 2019; Ejrnæs & Sprogis, 2021). It is, however, also expected that the mother and the offspring's activities change with the evolving offspring's independence and energetic needs (Cartwright & Sullivan, 2009; Ejrnæs & Sprogis, 2021; Huetz et al., 2022; Trivers, 1974). Here, by categorizing their activities into four levels, from the lowest (static/quasi-static) to the highest (fast swimming) during the breeding season, we assessed whether time budgets change as calves age, whether those of the mothers and their calves are similar, and how they are linked.

2 | MATERIALS AND METHODS

2.1 | Data sets

We used animal-borne multisensor tag data sets from 47 mother-calf pairs off Sainte Marie Island, Madagascar, southwestern Indian Ocean (Figure 1), during the winter (July–September) of 2013–2019 and 2021–2022, tagged

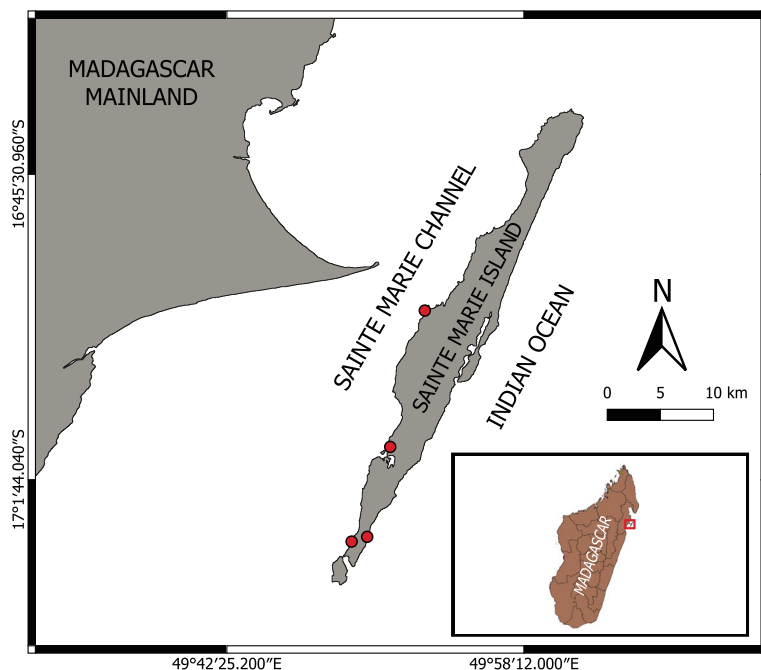


FIGURE 1 Map of the study site. Red points indicate the various boat departure locations between 2013 and 2022.

either with Acousonde 3B (<https://www.acousonde.com>) or CATS cam tags (deployed only on calves; <https://cats.is>). The data sets were obtained from 31 single tag deployments on calves, 10 single deployments on mothers, and six simultaneous deployments (i.e., the mother and the calf were both tagged, and their data overlapped in time). They included pressure data sampled at 10 Hz (sampled initially at 20 Hz for some individuals but then downsampled for consistency) and sound data sampled at 12 kHz (sampled initially at 24 kHz, 24.453 kHz, or 48 kHz but then downsampled for consistency and because 12 kHz sampling is sufficient for capturing flow noise and humpback whale vocalizations). Detailed tagging procedures and specifications have been presented elsewhere (Huetz et al., 2022; Ratsimbazafindranahaka et al., 2022, 2023; Saloma et al., 2022).

For each individual, we computed the depth (in meters) and the whale's relative forward speed (relative speed hereafter) with a sampling frequency of 10 Hz. The depth was obtained from the pressure data. It was smoothed with a 0.5 s running median filter. The relative speed was calculated as the z-scored flow noise (per individual) extracted from the sound data (66–94 Hz frequency band, Cade et al., 2017). We associated each deployment (each individual) to an age class (C1, C2, or C3 for the calves, see below, or A, Adult, for the mothers). Mothers were further categorized into A-C1, A-C2, or A-C3, depending on the age of their calf.

The relative age of the calves was estimated visually based on skin coloration, skinfolds, and the angle of unfurling of their dorsal fin (Cartwright & Sullivan, 2009; Faria et al., 2013; Huetz et al., 2022; Ratsimbazafindranahaka et al., 2023; Saloma et al., 2022) during the pretagging observation of the pair (Saloma et al., 2022): C1 (neonate) for calf presenting some folds, scars, and skin color that tends to be light gray dorsally and white ventrally and with less than $\sim 45^\circ$ dorsal fin furl; C2 for very young but nonneonate calves having more than $\sim 45^\circ$ but less than about 70° dorsal fin furl; and C3 for older calves (but <3 months old) that have unfurled dorsal fin (approximately $>70^\circ$).

2.2 | Behavioral states modeling

We used the hidden Markov model (HMM) to model the time organization of the activities of the mothers and the calves. For this purpose, we computed the average relative speed of each whale on a nonoverlapping 20 s sliding windows basis as the input time series data (i.e., the sampling unit for the modeling corresponded to one 20 s window). HMMs are commonly used for modeling and analyzing behavioral time series in cetaceans because they consider the nonrandom temporal sequence and switching patterns of behaviors (here, the state related to the activity level) based on an observable behavioral parameter (DeRuiter et al., 2017; Tennessen et al., 2019). We modeled the activities as a first-order four-state Markov chain that gives rise to the observed swimming speed. In the model, we assumed that all state transitions were possible. We constructed the HMM using the “depmixS4” package (Visser & Speekenbrink, 2010) in R. We included the relative speed (assumed to have a Gaussian distribution) as the response. The model was fitted by maximum likelihood estimation using the expectation–maximization (EM) algorithm in the “depmixS4” package following the framework described by Tennessen et al. (2019). Finally, the Viterbi algorithm was applied to find the most likely state sequence that best translates to the observed behavior (the relative speed). From the behavioral state with the lowest speed to the highest, we will refer to them as Lv0, Lv1, Lv2, and Lv3 states hereafter. We chose to use a model in its simplest possible form, with only the speed considered, as the goal was to capture the general activity pattern of the individuals in mother-calf pairs. The averaging time of 20 s was selected as a trade-off between avoiding capturing very short-term speed changes and keeping enough time resolution (about three windows per min, the average dive duration in young calves, Huetz et al., 2022) to capture activity change within a dive.

The model choice was motivated by the observations in the field and from animal-borne camera tags (Ratsimbazafindranahaka, unpublished data) of four distinct behavioral states associated with a typical swimming speed (activity level) for both the mother and the calf. The first state, Lv0, is when the whale is at minimal speed, i.e., static or quasi-static (speed less than one knot), as it rests. The second state, Lv1, is when the whale swims at a

slow speed corresponding to their global average speed, thus less than their average traveling speed, which is around 2–4 knots (Chittleborough, 1953; Indeck et al., 2022; Kavanagh, 2014), namely when it wanders/is lolling around or milling (e.g., a calf circling its mother). The third and fourth states, Lv2 and Lv3, correspond to a swimming speed higher than the global average speed: one to the average traveling speed, and the other to a more hastened traveling that is above the usual traveling speed (fast swimming, e.g., flight behavior).

2.3 | Data analysis

2.3.1 | Time budget and ontogeny

With the state sequences from the HMM, we established the time budget for each individual. In other words, we calculated the proportion (in percentage) of time spent in each behavioral state for each whale. Then we tested whether the proportion of time spent in a given state varies with age class using linear models in R (linear regression), followed by Tukey's post-hoc multiple comparisons test with adjusted p values using the “emmeans” package (Lenth et al., 2018) when a statistically significant effect was detected. We also tested whether the proportions vary depending on the category of the mothers. For the analysis, we transformed each proportion of interest into a log-ratio of proportion using one of the states as a reference, i.e., $\log\text{-ratio}_{\text{state of interest}} = \log(\text{proportion}_{\text{state of interest}} / \text{proportion}_{\text{reference}})$.

Such transformation is required in compositional data analysis for the standard statistical approaches to be valid (Aitchison, 1986). The choice of the reference for the transformation is arbitrary because of the permutation invariability property of the log-ratio approach (Aitchison, 1986). In our analyses, we used the proportion of time spent in Lv2-3 (i.e., Lv2 + Lv3) as a reference. The grouping of Lv2 and Lv3 into one broad class was because the Lv3 state contained zero proportion, preventing us from calculating a log-ratio with it either as a reference or as a state of interest. All proportions of time spent in each state per whale were assumed to be independent of the deployment length. Exploratory analyses supported this assumption.

Due to the low number of C1 calves (see results), we pooled them with the C2 calves for the statistical tests (C1-C2 calves). Similarly, because only one A-C1 was tagged, we pooled her with the A-C2 for the statistical tests (A-C1/C2). While such grouping dilutes the classes, it still allows us to capture ontogenetic changes as the C1-C2 represents younger calves while C3 represents more mature calves, analogous to the class 1 versus class 2 calf classification in Cartwright and Sullivan (2009).

2.3.2 | Behavioral synchrony

We analyzed the behavioral synchrony between the mother and the calf using the data from simultaneous deployments ($n = 6$). We aligned the calf's predicted state sequence with the mother's predicted state sequence (only overlapping periods were considered). As the internal clock of the tag units sometimes had seconds of delay (time drift), simultaneous mother-calf data had to be manually aligned. For the process, we used sound cues detected in both units to align the mothers' and calves' data (crew voices recorded between the tagging time and the moment the tags were turned on, impact noises recorded prior to tagging, or even distant male songs; Huetz et al., 2022).

We calculated the proportion of synchronized behavior for each aligned pair, the behavioral independence scores (calculated for each state), and the Hinde's association index (Hinde & Atkinson, 1970). The proportion of synchronized behavior was calculated as the time corresponding to the mother and calf being in the same state relative to the total simultaneous data length. The behavioral independence score for each state was calculated as the ratio of the total time spent in the state to the time spent in that state at the same time as the other individual of the pair. The Hinde's index was obtained with the following formula that takes as argument the number of times the mother

and the calf initiated or terminated a bout of synchronized state (respectively, M_I and M_T for the mother and C_I and C_T for the calf):

$$\text{Hinde's index} = [M_I / (M_I + C_I)] - [M_T / (M_T + C_T)]$$

The Hinde's index varies between -1 and $+1$, which corresponds to the calf or the mother being exclusively responsible for the synchrony, respectively. For the calculation, an individual was considered as having initiated a bout of synchronized state when it changed its behavioral state to synchronize with the other individual. Conversely, it was considered as having terminated the synchronized bout when it changed its behavior state and broke the synchrony (Fellner et al., 2013). It is worth noting that in our framework, synchrony does not necessarily assume spatial proximity and spatial synchrony (i.e., individuals being close to each other). As already introduced above, it must be distinguished from dive and spatial synchrony (Huertz et al., 2022; Tyson et al., 2012) as the calf may for example engage in a different activity than its mother while still staying close to her as much as possible or engage in the same activity as its mother while being vertically or horizontally separated from her.

3 | RESULTS

A total of 202.63 hr of data were analyzed from all 53 individual deployments (41 single deployments plus 6 simultaneous deployments). The analyzed time per deployment was 3.82 hr on average (range = 0.39–17.36 hr). For the behavioral synchrony study, 13.65 hr of simultaneous mother-calf data from the six simultaneous deployments were used. The analyzed time per simultaneous deployment was 2.28 hr on average (range = 0.48–7.77 hr). Among the 37 calves, two were C1 calves, 14 were C2 calves, and 21 were C3 calves. Among the 16 mothers, one was with C1 calf (A-C1), three were with C2 calf (A-C2), and 12 were with C3 calf (A-C2).

Our HMM model successfully captured the general activity pattern of the whales. The corresponding transition probabilities are presented in Figure S1. The HMM captured (1) a state with a mean average speed of about one standard deviation below the global average swimming speed (Lv0: mean average relative speed = -1.1 ± 0.5 , range = -3.8 – 0.3 , $n = 8,594$), (2) a state with a mean average speed coinciding with the global average swimming speed (Lv1: mean average relative speed = -0.1 ± 0.3 , range = -1.1 – 1.3 , $n = 13,254$), (3) a state with a mean average speed of about half a standard deviation above the global average swimming speed (Lv2: mean average relative speed = 0.6 ± 0.3 , range = -0.3 – 1.5 , $n = 10,747$), and (4) a state with a mean average speed of more than one standard deviation above the global average swimming speed (Lv3: mean average relative speed = 1.3 ± 0.4 , range = -0.2 – 3.6 , $n = 3,733$). On average, the C1-C2 calves, the C3 calves, and the mothers (A) switched from one state to another 22 ± 9 , 20 ± 7 and 17 ± 8 times per hour, respectively (range, C1-C2: 9–41 switches per hour, C3: 7–36 switches per hour, A: 9–38 switches per hour).

We found no statistically significant effect of age on the proportion of time spent in Lv0 state (linear model with log-ratio transformed response: $F_{2,50} = 1.29$, $p = .283$; Table 1, Figure S2). However, we detected a statistically significant effect of age (C1-C2, C3, and A classes) on the proportion of time in Lv1 state (linear model with a log-ratio transformed response: $F_{2,50} = 3.76$, $p = .03$; Table 1, Figure S2). The linear model revealed a gradual decrease in the proportion of time in Lv1 state from C1-C2 to A (mothers). The proportion of Lv1 state for mothers was statistically different compared to C1-C2 calves (Tukey's post-hoc test, A vs. C1-C2, $\beta = -0.58$, $p = .023$) but not statistically different compared to C3 calves (Tukey's post-hoc test, A vs. C3, $\beta = -0.332$, $p = .227$). In addition, the difference between C1-C2 and the C3 calves was not statistically significant (Tukey's post-hoc test, A vs. C3, $\beta = 0.246$, $p = .435$). Regarding the variation of the mothers' time budget according to their calf's age, in A-C1/C2, the time spent in Lv0 state was lower and the time spent in Lv1 state was higher compared to A-C3 (Table 1, Figure S2). However, the differences were not statistically significant (linear model with log-ratio transformed response, A-C1/C2 vs. A-C3, Lv0: $F_{1,14} = 2$, $p = .179$; Lv1: $F_{1,14} = 2.07$, $p = .172$).

TABLE 1 Behavioral time budget of humpback whale calves and mothers in the breeding area off Sainte Marie, Madagascar. Behaviors were modeled using a hidden Markov model (HMM) based on the relative swimming speed. Lv0, Lv1, Lv2, Lv3: behavioral states, from the one with the lowest swimming speed, Lv0, to the highest, Lv3. C1, C2, and C3 represent the relative age of the calves estimated based on skin coloration, skinfolds, and the angle of unfurling of their dorsal fin. A corresponds to Adults (mothers), further categorized according to the age of their dependent calf. Values are presented as mean (min–max). Note that no mean was calculated when $n = 2$.

| Category | Lv0 (%) | Lv1 (%) | Lv2 (%) | Lv3 (%) |
|---------------------|------------|------------|------------|-----------|
| C1-C2 ($n = 16$) | 22 (9–31) | 43 (23–77) | 25 (11–51) | 10 (0–20) |
| C1 ($n = 2$) | (24–30) | (40–47) | (11–20) | (10–20) |
| C2 ($n = 14$) | 22 (9–31) | 43 (23–77) | 27 (12–51) | 10 (0–16) |
| C3 ($n = 21$) | 22 (13–38) | 39 (14–62) | 31 (12–51) | 9 (3–16) |
| A ($n = 16$) | 26 (15–41) | 31 (14–57) | 29 (10–43) | 14 (3–25) |
| A-C1/C2 ($n = 4$) | 20 (16–26) | 40 (37–43) | 27 (17–33) | 13 (8–20) |
| A-C3 ($n = 12$) | 28 (15–41) | 28 (37–43) | 30 (10–43) | 14 (3–25) |

Complete results on the behavioral synchrony in six mother-calf pairs are presented in Table 2. An example of paired mother-calf data (pair G28) showing the behavioral synchrony between the mother and the calf is presented in Figure 2. The proportion of synchronized behavior per pair, relative to the total simultaneous data, ranged from 34% to 79% (median = 50%). The behavioral independence scores were relatively variable from one individual to another for all the behavioral states. Still, on average, they were closer to 1 (expected value if an individual always engages in the same behavior as the other individual) for calves compared to mothers for Lv0 state (calves: median = 1.11, range = 1.04–6.6; mothers: median = 1.55, range = 1.11–2.16; Table 2) and Lv3 state (calves: median = 1.01, range = 1.01–1.68; mothers: median = 1.78, range = 1.01–7.45; Table 2). For Lv1 and Lv2 states, the behavioral independence scores were, on average, higher than 1 for both the calves (Lv1: median = 3.39, range = 1.33–5.32; Lv2: median = 1.53, range = 1.29–2.08; Table 2) and the mothers (Lv1: median = 1.66, range = 1.03–4.05; Lv2: median = 1.9, range = 1–5.12; Table 2). The Hinde's index of association was relatively variable. It ranged from -0.3 , i.e., the calf being more responsible for the synchrony, to 0.7 , i.e., the mother being more responsible for the synchrony (median = 0.12; Table 2).

4 | DISCUSSION

Our objective was to assess the time allocation patterns of humpback whale mother-calf pairs' activities and to estimate the level of synchrony in their activities by comparing their swimming speeds. We compared the time budgets of the mothers and calves, investigated changes in the quantified time budget as the calves age, quantified the degree of synchronization between their activities, and determined which individual within the pair was the leader. Although we based our study on the use of suction cup multisensor tags, which only inform partially on the daily life of mothers and their calves due to limited deployment time (which averaged just over 3 hr), our study allowed us to gain additional knowledge on the behavioral dynamics and interactions within humpback whale mother-calf pairs thanks to the ability of such devices to provide continuous data with minimum disturbance including during dives (not just life at the surface or subsurface). We found that both mothers and calves allocated a substantial portion of their time to low activity levels (Lv0 or Lv1), i.e., they spent most of their time resting (static or quasi-static, Lv0) or swimming at a slow speed (Lv1), likely corresponding to milling (*sensu* Weilgart & Whitehead, 1990). Additionally, we found that the time spent in Lv1 state was the highest in young calves (C1–C2) and the lowest in adults. Although the calves displayed some degree of independence in their behaviors, they also frequently engaged in activities

TABLE 2 Synchronized behaviors of six humpback whale mother-calf pairs in the breeding area off Sainte Marie, Madagascar. Lv0, Lv1, Lv2, Lv3: behavioral states, from the one with the lowest swimming speed, Lv0, to the highest, Lv3. Async.: no period of synchrony has been observed.

| Pair ID | Calf's age | Total synchronized state (%) | State | Behavioral independence scores | | Initiation | | Termination | | Hinde's index |
|---------|------------|------------------------------|-------|--------------------------------|--------|------------|--------|-------------|--------|---------------|
| | | | | Calf | Mother | Calf | Mother | Calf | Mother | |
| G2 | C1 | 34 | Lv3 | async. | async. | 7 | 6 | 6 | 6 | 0 |
| | | | Lv2 | 1.62 | 5.12 | | | | | |
| | | | Lv1 | 4.96 | 2.81 | | | | | |
| | | | Lv0 | 2.3 | 2.01 | | | | | |
| G10 | C2 | 46 | Lv3 | 1.01 | 1.55 | 1 | 6 | 6 | 1 | 0.71 |
| | | | Lv2 | 1.31 | 2.36 | | | | | |
| | | | Lv1 | 5.32 | 4.05 | | | | | |
| | | | Lv0 | 6.6 | 1.11 | | | | | |
| G28 | C3 | 79 | Lv3 | 1.01 | 1.01 | 6 | 4 | 3 | 6 | -0.3 |
| | | | Lv2 | 1.44 | 1 | | | | | |
| | | | Lv1 | 1.33 | 1.51 | | | | | |
| | | | Lv0 | 1.1 | 1.63 | | | | | |
| G30 | C3 | 46 | Lv3 | 1.68 | 7.45 | 11 | 19 | 18 | 12 | 0.25 |
| | | | Lv2 | 2.08 | 1.02 | | | | | |
| | | | Lv1 | 3.39 | 1.64 | | | | | |
| | | | Lv0 | 1.06 | 2.16 | | | | | |
| G36 | C3 | 54 | Lv3 | 1.01 | 2.08 | 11 | 16 | 12 | 15 | 0.04 |
| | | | Lv2 | 2.03 | 3.86 | | | | | |
| | | | Lv1 | 2.73 | 1.03 | | | | | |
| | | | Lv0 | 1.04 | 1.39 | | | | | |
| G37 | C3 | 66 | Lv3 | 1.37 | 1.78 | 41 | 53 | 60 | 35 | 0.2 |
| | | | Lv2 | 1.29 | 1.44 | | | | | |
| | | | Lv1 | 3.39 | 1.67 | | | | | |
| | | | Lv0 | 1.12 | 1.47 | | | | | |

similar to their mothers (50% of the time on average). Interestingly, our result suggested that the initiation of specific activities within the pair could be driven by either the calf or the mother, depending on the nature of the activity.

4.1 | Time budget

Our result on the time spent at a low activity level is in accordance with previous results suggesting that mothers and calves minimize their energy consumption (Bejder et al., 2019; Ejrnæs & Sprogis, 2021). For mothers, energy saving is crucial as they do not feed for a prolonged period while producing milk for their calf (Braithwaite et al., 2015; Clapham, 2018). Optimizing the time spent at a low activity level minimizes the decline in body condition. It thus ensures sufficient milk production to nurse their calf and secure enough energy reserve left to migrate back to the feeding ground (Bejder et al., 2019; Christiansen et al., 2016). A low activity level for the calves helps maximize energy allocation into growth (Braithwaite et al., 2015; Ejrnæs & Sprogis, 2021).

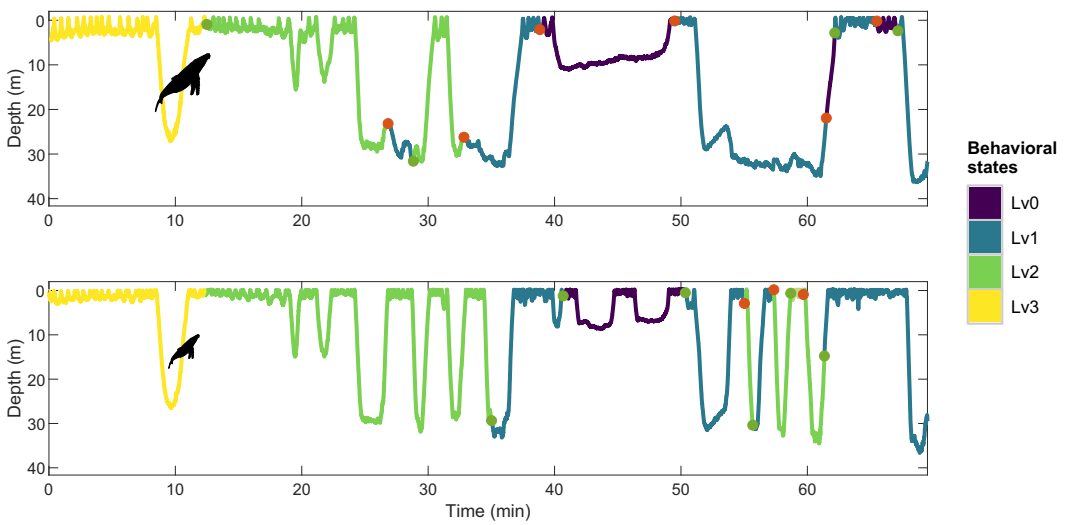


FIGURE 2 Dive profile of a simultaneously tagged humpback whale mother (top) and calf (bottom) showing the behavioral synchrony between the two (G28 pair). Lv0, Lv1, Lv2, Lv3: behavioral states, from the one with the lowest swimming speed, Lv0, to the highest, Lv3. Green and red dots represent each time the individual initiated and terminated a bout of synchronized state, respectively.

The ontogeny of the Lv0 activity appears to diverge from the surface observations made by Cartwright and Sullivan (2009), who noted that older calves exhibit increased resting activity. It is conceivable that, contrary to surface-level observations, the overall percentage of time spent resting remains constant across different age groups. The discrepancy in the findings may be attributed to a shift in resting behavior as calves mature. It is plausible that older calves, being more independent, no longer rest below their mother, pressed against her – a stationary behavior reported by Ratsimbazafindranahaka (2023) – as much as young calves do, giving the impression of increased resting at the surface.

Concerning the time spent in Lv1 state, i.e., slow swimming, in calves, the decreasing trend is consistent with results from past studies suggesting that young cetaceans tend to swim continuously for locomotor practice and muscle development (Cartwright & Sullivan, 2009; Thomas & Taber, 1984). Calves spending much time swimming at slow speed, likely wandering around the mother, may also be a display of a more playful nature of young individuals. Play behavior by young animals is crucial for their cognitive and social development (Bekoff, 1972; Burghardt, 2005).

A change in the time budget with the increasing age of calves was expected for the mother. Indeed, depending on the age of the calf, a mother may adjust her activity to accommodate the specific needs of her calf at various developmental stages (Huetz et al., 2022; Szabo & Duffus, 2008; Von Keyserlingk & Weary, 2007). Our data suggest that mothers with younger calves spend less time in Lv0 state and more time in Lv1 state than mothers with older calves, but further data are needed as our test with a small sample failed to detect statistically significant differences. Nonetheless, these results suggest that the mother increasingly enters deeper states of low activity level as her calf grows, potentially because the calf becomes more and more independent, allowing the mother to maximize her rest. For example, as the calf grows, its awareness of the potential hazards in its natural environment improves (learning hypothesis, Pangle & Holekamp, 2010), and it also becomes more mobile and has an improved locomotory autonomy (Cartwright & Sullivan, 2009; Huetz et al., 2022; Taber & Thomas, 1982; Tyson et al., 2012). As a result, the mother has less and less need to assist and (or) follow the calf in its movements. Additionally, as the calf grows, its milk consumption potentially increases (Ratsimbazafindranahaka et al., 2023), resulting in higher energy demands for the mother (Trivers, 1974). Consequently, mothers with an older calf may require more deep state of low activity periods to save energy and meet the needs of their growing offspring and for the upcoming migration. Further studies are

needed, especially with respect to the social behavior and postpartum maternal investment, to clarify what influence the switch in resting behavior of the mother. Finally, it must be noted that besides changes with respect to calf age, further investigations on the potential difference in the time budget of the mothers in relation to their maternal experience should be undertaken as we may expect changes in the maternal care pattern with maternal experience (primiparous vs. multiparous females) or age (Lang et al., 2011) and thus potential differences in time budget. However, it is important to highlight the inherent challenges of such research, particularly the challenge of resighting the same mothers over multiple years.

4.2 | Behavioral synchrony

The activities of humpback whale mothers and calves showed a behavioral synchrony level consistent with the expectations for follower species (in opposition to hider species with low behavioral synchrony; Espmark, 1969; Gluesing et al., 1980; Green, 1993; Lickliter, 1987). Mother-young behavioral synchrony may serve as a way to strengthen bonds, establish social relationships, and mediate social interactions (Ham et al., 2023). Given the potential adaptive value of the behavioral synchrony, we may tend to expect a particularly high, not a moderate, level of synchrony. However, it must be considered that there are still instances that would force the mother and her calf to engage in different behaviors because of the differences in their needs (e.g., the need for the calf to develop its muscles and quickly grasp how to move around in its environment by swimming continuously, as mentioned earlier, Cartwright & Sullivan, 2009; Thomas & Taber, 1984) and in their performances (e.g., lower apnea performance in calves, Huetz et al., 2022; Szabo & Duffus, 2008). The moderate level of synchrony observed in humpback whales may be a trade-off between gaining social advantage from behavioral synchrony and allowing each individual of the mother-calf pair to adjust their differential needs and diving skills.

Although the calf might be expected to be responsible for maintaining synchrony (i.e., follow the mother's lead, Huetz et al., 2022; Tyson et al., 2012), the Hinde's index failed to show a consistent pattern that points in this direction regarding activity level. The calf seems to consistently follow its mother's activity level only in the specific case of very low- and very high-level activities (Lv0 and Lv3, respectively), as suggested by the behavioral independence scores. Such results suggest that the mother controls when (and potentially where) to rest and when to move fast, similar to terrestrial ungulate mothers who control the behavior of their young regarding the choice of resting areas and predator avoidance as mothers have a better knowledge of the habitat (Blank, 2017). In contrast, in the case of slow (Lv1) and moderate swimming (Lv2) activities, the mother and the calf do not necessarily synchronize their activities. They behave according to their individual needs such as the need to come back to the surface for air, the need to continuously swim, etc. (Cartwright & Sullivan, 2009; Huetz et al., 2022; Szabo & Duffus, 2008; Thomas & Taber, 1984). It is important to note that the behavioral synchrony in the present study was based on a limited number of mother-calf pairs and limited deployment time. Thus, care must be taken regarding these conclusions. Nevertheless, these results already provide valuable insights into the link between the mother's behavior and the calf's behavior.

4.3 | Conclusion

Our study presents the first fine-scale humpback whale mother-calf activity budget off Sainte Marie, Madagascar, a breeding ground where the whale-watching activity is increasing (Trudelle et al., 2018). The results have several implications for whale conservation and well-being, helping to improve existing regulations for sustainable whale-watching activity (and any other ocean-related human activities) at a local level but also at a regional level (south-western Indian Ocean) and in other comparable breeding grounds. First, our findings suggest that mothers and calves spend considerable time in low-activity levels off Sainte Marie, underscoring the area's importance as a critical

resting zone for lactating females and young calves. Regulations to minimize disturbances of the resting activities of mother-calf pairs and awareness campaigns should thus be reinforced (e.g., more significant consideration of the vital areas for whales, regulation of economic activities at sea, promotion of scientific research, etc.). Second, our study suggests changes in the behaviors of mother-calf pairs with the age of the calf, emphasizing the importance of incorporating the progression of the whale season in decision-making for conservation. Indeed, changes in behaviors with age imply potentially different impacts of human activities on mother-calf pairs as the calf grows, thus as the season progresses since the calf's age is slightly correlated with the season progression (Cartwright & Sullivan, 2009). Finally, our results suggest that calves can engage in activities different from their mothers, highlighting that conservation efforts should not solely focus on maternal behavior or assume that measures addressing the behavior of the pair consider both the needs of the calf and the mother adequately. In other words, our results emphasize the necessity for targeted conservation measures. Considering the mother's potential role in leading resting and fast swimming activities, we propose that her behaviors can serve as an indicator of critical resting areas and areas with disturbances. However, actual conservation measures must account for the calf's high independence in milling and swimming activities, highlighting, for instance, the importance of increased vigilance of boat operators. Seeing a swimming calf does not necessarily mean the mother is not resting, and observing a resting mother does not imply that the calf is immobile beside her.

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AUTHOR CONTRIBUTIONS

Maevatiana N. Ratsimbazafindranahaka: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing – original draft. **Chloé Huetz:** Conceptualization; investigation; methodology; project administration; supervision; validation; writing – review and editing. **Anjara Saloma:** Conceptualization; funding acquisition; investigation; methodology; project administration; writing – review and editing. **Aristide Andrianarimisa:** Conceptualization; investigation; methodology; supervision; validation; writing – review and editing. **Isabelle Charrier:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; validation; writing – review and editing. **Olivier Adam:** Conceptualization; funding acquisition; investigation; methodology; project administration; supervision; validation; writing – review and editing.

CONFLICT OF INTEREST

The authors declare no competing interests.

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SUPPORTING INFORMATION

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