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Further insights into postpartum signature whistle use in bottlenose dolphins (*Tursiops truncatus*)

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Mother-offspring recognition is found across the animal kingdom, and its importance as a means of facilitating exclusive maternal care and investment is well documented (Sèbe *et al.* 2008). Such individual recognition can take a number of forms including visual, olfactory and acoustic recognition (Tibbetts and Dale 2007). Acoustic signatures in particular have been shown to be crucial for facilitating mother-offspring recognition in colonial breeders such as swallows (Medvin *et al.* 1993) and sea lions (Charrier *et al.* 2001), as well as in gregarious species such as bats (Balcombe and McCracken 1992, Jin *et al.* 2015) and sheep (Searby and Jouventin 2003). In species where offspring mobility is restricted vocal recognition may be one sided. For example, playback experiments with the greater sac-winged bat (*Saccopteryx bilineata*) reveal that although mothers can recognize the isolation calls of their pups, the pups are unable to discriminate between the echolocation calls of their mothers and other females (Knörnschild and von Helverson 2008). Whether recognition is one-sided or mutual is likely explained by the selective pressures that govern mother-offspring recognition (Knörnschild and von Helverson 2008). In those species where neonates are precocial immediately following parturition, particularly in highly social species, mother-offspring recognition tends to be mutual. For example, vocal activity in sheep is highest in the first three hours following birth (Sèbe *et al.* 2007). Females can recognize the calls of their young after only 24 h postpartum, and this is reciprocated at 48 h postpartum for the offspring (Sèbe *et al.* 2007, 2010). In colonial breeders, such as the subantarctic fur seal (*Arctocephalus tropicalis*), pups learn to recognize their mother's voice when they are just 2-5 d old, upon which the mother then departs for her first foraging trip (Charrier *et al.* 2001). It is therefore important that mother-offspring recognition develops before this first separation (Charrier *et al.* 2001).

Another taxon that is highly social and gives birth to precocial young is the bottlenose dolphin (*Tursiops* spp.). Individual vocal signatures are known to play an important role in mediating mutual mother-offspring recognition in bottlenose dolphins (Sayigh *et al.* 1990, Smolker *et al.* 1993). Each dolphin uses vocal learning to develop its own signature whistle in the first few months of life (Sayigh *et al.* 1990, Tyack 1997), which it uses to broadcast its identity (Caldwell *et al.* 1990, Sayigh *et al.* 1999, Janik *et al.* 2006). As well as encoding individual identity, signature whistles also function in maintaining group cohesion. When animals become separated from one another they predominately produce their signature whistles to reunite (Janik and Slater 1998). This is particularly true for mother-calf separations (Sayigh *et al.* 1990, Smolker *et al.* 1993, Tyack and Sayigh 1997, King *et al.* 2013).

Earlier studies provided some insight into maternal whistle production of bottlenose dolphins immediately following the birth of a calf in marine mammal facilities (Mello and Amundin 2005,

Fripp and Tyack 2008). Fripp and Tyack (2008) reported that maternal signature whistle production increased 10 fold immediately after calves were born until the third week postpartum. Imprinting remains the most favorable hypothesis for this increase in postpartum signature whistle production (Fripp and Tyack 2008). Mann and Smuts (1998) predicted that vocal imprinting should occur in the first week of the calf's life, corresponding with the observation that wild dolphins are generally intolerant of separations from their calves in the first week postpartum (Mann and Smuts 1998). Given the fission-fusion dynamics of the bottlenose dolphin social system, which can lead to frequent separations and reunions between mothers and calves (Smolker *et al.* 1993), a calf must learn to recognize its mother's highly individualized call before these separations occur. However, other explanations for elevated signature whistle rates postpartum have been discussed. Limited evidence suggests that male dolphins tend to develop signature whistles similar to their mother's whilst female calves do not (Sayigh *et al.* 1995). Fripp and Tyack (2008) discussed the possibility that an increase in maternal signature whistle rate could allow male calves to model their signature whistle on their mother's whistle. If such modeling is the primary reason behind the increase in signature whistles, then one would expect that females only increase their signature whistle rate for male calves and not for females.

Given these alternative hypotheses and that Fripp and Tyack (2008) had a limited sample size with the majority of data coming from one male calf (three of their four calves died within 10 days of being born), which was subjected to an unusual circumstance during data collection (the calf was stolen by another mother for the first six days of his life), we investigate postpartum signature whistle production in greater detail by exploring how maternal signature whistle production changed when two female calves were born. Moreover, because signature whistles are contact calls, another hypothesis to consider is that signature whistle production should increase as the calf gets older and starts becoming more independent and moving further away from its mother. We therefore made recordings over a 12 week study period, including a postpartum recording period of seven weeks, in order to determine how postpartum maternal signature whistle rate changed as the calves became more independent from their mother in the weeks following their birth. Given that dolphins are excellent vocal mimics and can copy the signature whistles of animals that are not in their current social group (King *et al*. 2013), we used an array of hydrophones to locate the source of calls to determine whether an increase in maternal signature whistle was a result of the mother calling more or of other group members copying the new mother's signature whistle.

Recordings were made at the Dolphin Research Center (DRC) in Grassy Key, Florida between January and April 2015. At the time of study DRC housed a total of 26 bottlenose dolphins

(*Tursiops truncatus*) and 1 Atlantic spotted dolphin (*Stenella frontalis*). The subjects were two female Atlantic bottlenose dolphins named Pandora (17 yr old) and Calusa (14 yr old), who were both born at DRC and share the same mother. The animals were housed in natural seawater lagoons (ranging from 344 to 537 m^2) with depth dependent on tide (4.5-5.5 m). They were housed with a third adult female, Molly (approximately 53 yr old and wild caught in 1968, living at DRC since 1996), during weeks 1-3 of the prepartum recordings. In week three Molly was moved to a different lagoon. In the beginning of week four Pandora and Calusa were also separated from one another and housed in individual lagoons in preparation for the births. Each mother gave birth to a female calf in week six, Pandora's calf was named Atocha and Calusa's calf was named Cacica. The mothers were housed separately with their calves until the end of week seven, upon which they were reintroduced and kept together for the remainder of the study. A full description of the group composition for the 12 wk study is provided in Table S1. Two other adult females were used as control females during weeks 4, 5, 6 and 7 of this study period. Merina (30 yr old) and Tursi (41 yr old) were both born at DRC. Merina had a female calf, Windley, who was just over one year old at the time of the recordings. Merina was also the mother of both Pandora and Calusa. Merina and Windley were housed in a pool adjacent to Pandora, and Tursi was housed in a pool adjacent to Calusa. The pools are seawater lagoons separated from one another by underwater fencing and therefore animals in adjacent pools are in acoustic contact. Therefore, during this time the control females were in acoustic contact with the mothers. Unfortunately, prior to week 4 and after week 7, Merina and Tursi were housed in different pools and we were unable to obtain recordings of them.

Signature whistles were identified by recording the most common whistle type produced by each female when isolated (Caldwell *et al.* 1990) either prior to the birth of their calf (Pandora and Calusa) or during medical assessments (Merina and Tursi). Recordings were made in-air and in water with an HTI-96 MIN hydrophone (frequency response: 0.002-30 kHz ± 1 dB) onto a TASCAM DR-680 multitrack recorder at a sampling rate of 96 kHz. The signature whistles of Pandora, Calusa, Merina, and Tursi are provided in Figure 1.
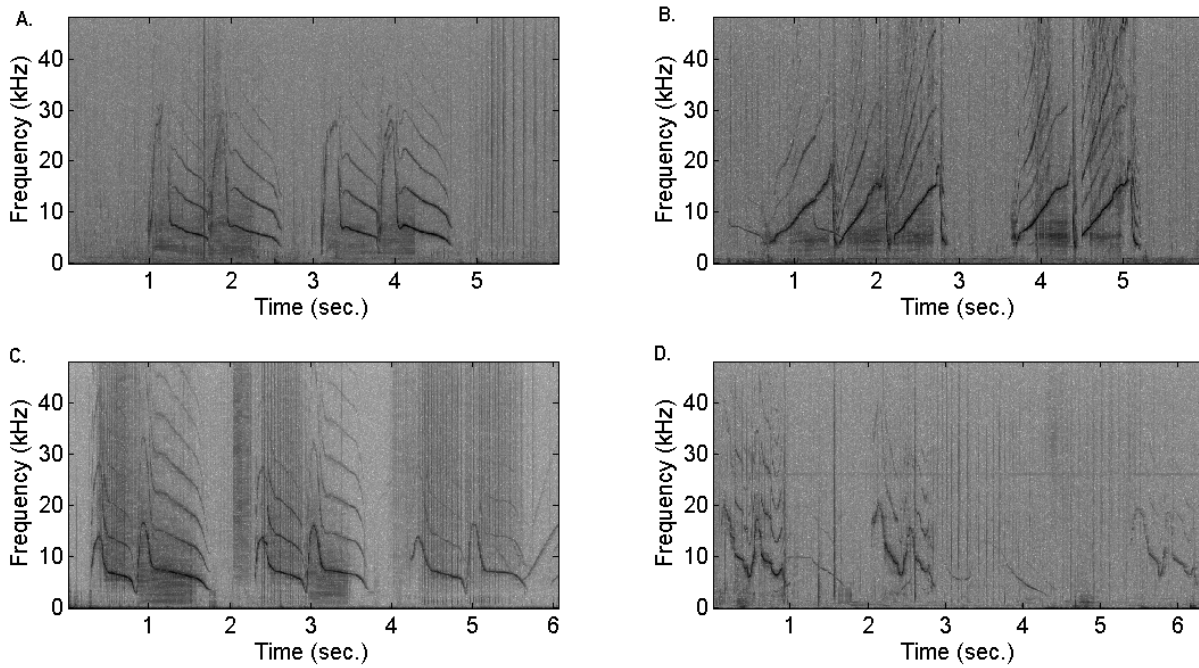
Figure 1. Spectrogram of the signature whistles of (a) Pandora, (b) Calusa, (c) Merina, and (d) Tursi; sampling rate is 96 kHz, FFT length 1024, Hanning window function.

Pre- and postpartum recordings were made with an array of four HTI-96 MIN hydrophones (frequency response: 0.002-30 kHz ± 1 dB) onto a TASCAM DR-680 multitrack recorder at a sampling rate of 96 kHz. During each recording session one hydrophone was placed in each corner of the target animal's pool, in an approximate rectangular formation, and distances between hydrophones ranged from approximately 8 to 28 m. Whistles were localized to an individual using the TOADY localization program (Quick *et al.* 2008). Localization was only possible when the whistle was detected on all hydrophone channels with a high signal-to-noise ratio. Localization error was calculated by asking a dolphin to whistle on signal at a known location at the dock, and then using custom-written MATLAB routines (L. Rendell) to calculate 2D averaged MINNA (minimum number of receiver array) localizations using the methods described in Wahlberg *et al.* (2001) and Schulz *et al.* (2006), and found to be 1.3 m (*n*=4) from the true location of the calling animal. Animals were either in the pool on their own, or when the two mothers were kept together they were consistently >1.5 m apart when the localized whistles were produced (see Table S1 for exception). Video recordings were made with a Canon VIXIA HF R42 video camera with acoustic input from one of the HTI-96 MIN hydrophones. When the females were kept together they were identified by zinc markings to their head and dorsal fin (pink for Pandora and white for Calusa). The position of the whistle as determined by acoustic localization was then compared with the position of the animal in the pool as per the video recordings. One-hour recordings were made 2-4 times per week over a 12 wk period that included five weeks prepartum

and seven weeks postpartum for each mother (Table S1). All acoustic recordings were taken at random times throughout the day for the duration of the 12 wk study period. Only minimal trainer interactions with the dolphins, consisting of occasional feeding sessions, occurred during these recordings. These were removed from the analysis.

Behavioral observations were conducted from the side of the pool for each calf during each postpartum acoustic recording session. The observation period lasted for 10 s every 30 s, where the calf's behavior was observed for 10 s and then recorded in the following 20 s time period. The observers noted the calf's behavior and proximity to other dolphins, including its mother, during the observation period. If the calf was not observed during that 10 s period (*i.e.,* it was not observable underwater due to its depth), then it was recorded as a 'no show'. This provided a catalogue of calf and mother locations and proximities every 30 s for the duration of the acoustic recording. Full descriptions of behavioral categories are provided in Table 1.

Table 1. Terms used to describe the proximity of the mothers in relation to the calves as part of the behavioral observations.

Term	Definition
With	Dolphin is in control of the calf (*e.g.*, slipstreaming)
Close	Dolphin is within 1 adult body length from the calf and is swimming with the calf
Intermediate	Dolphin is no more than 3 body lengths (*ca.* 25 ft) away from the calf
Far	Dolphin is farther away than Intermediate.

The vocal behavior of the two mothers were analyzed by inspecting the spectrograms (FFT length 1024, overlap 100%, Hanning window) in Adobe Audition v2.0 (Adobe Systems). All statistical procedures were conducted in R (R project for statistical computing; GNU project).
One observer (SLK) went through the recordings and noted all occurrences of the signature whistles of each of the mothers (Pandora and Calusa; Fig. 1), which where possible were localized to the female (Table S1). The signature whistles of the two control females (Merina and Tursi; Fig. 1) were also noted.

Visual classification was then used on a subset of data to confirm that this initial classification by the observer (SLK) was correct. For each dolphin, a batch of signature whistles were randomly

selected for the human classification task: 60 each for both Pandora and Calusa, and 20 each for the two control females (who had less overall recording time). All time axes were standardized to 3 s. The known signature whistles of 10 animals at DRC (including the two mothers and the two control females) were used to create a signature whistle template catalogue. Five naïve human observers, who were blind to context, were provided with a spectrogram of each whistle to be classified, and were asked to pick the signature whistle template (from the signature whistle template catalogue) which most closely matched that whistle. They were then asked to rate similarity of these two whistles using a similarity index ranging from 1 (dissimilar) to 5 (similar). The similarity ratings were compared between the judges using the Fleiss' Kappa statistic (Siegel and Castellan 1988) to determine the inter observer agreement. If agreement is similar to that expected by chance then the Fleiss' Kappa statistic (k) is 0, if observers are in complete agreement than k is 1. Agreement on the choice of signature whistle template was high among the fiver observers (Fleiss-Kappa statistic (k) = 0.62, $z = 6.2$, $P < 0.0001$) (Fleiss $et\ al.$ 2003) and in all cases corresponded to the signature whistle identified for each of the females by the original observer (SLK). The observers also showed strong agreement on the weighted similarity scores (Fleiss-Kappa statistic (k) = 0.95, $z = 63.4$, $P < 0.0001$) with an average score of >3.5 for all four females.

The signature whistle rate per minute (number of signature whistles divided by recording time in minutes) was calculated for each female for each recording session (excluding any feeding times that occurred during that session). Recordings were conducted when the animals were not involved in any other activities to ensure changes in behavioral state would not influence signature whistle rate. This made the context in which signature whistles rates were calculated comparable across all recording sessions. All signature whistles assigned to a female were used in this calculation. A proportion of those, which could be localized, were used to check whether signature whistle copying may have occurred.

Bottlenose dolphins are known to produce their signature whistles at higher rates when separated from social affiliates (Janik and Slater 1998, Sayigh $et\ al.$ 1999, King $et\ al.$ 2013). The removal of Molly from Pandora and Calusa immediately prior to the first recording session of week three (03 Feb 2015) resulted in significantly elevated signature whistle production during that session (Table S1). Given that this social change was unusual with respect to the rest of the study period we omitted this recording from the final analysis.

We used a linear mixed-effect model (lmer using lme4 package in R software (version 3.0.2)) to model the change in signature whistle production over the 12 wk recording period. The response

variable was signature whistle rate (per individual/per minute). The recording week (week 1-5 = prepartum and week 6-12 = postpartum) was included as a fixed effect and animal identity was included as a random effect. Forward model selection was performed using ANOVA with a *P*-value significance level of 0.05. An interaction term between animal identity and week was also incorporated to explore if the relationship between signature whistle production and week differed between the two mothers. There appeared to be no difference between the two mother's vocal behavior, as a model with a random intercept but no random slope (*i.e.* no interaction with fixed effects) was preferred by Akaike information criterion (AIC).

Signature whistle rate and the number of signature whistles produced by each of the mothers during each recording session/week leading up to and after the birth of their calves is provided in Table S1. Postpartum signature whistle production significantly increased immediately following the birth of the calves and remained high for four weeks (Table S1 and Fig. 2). All of the signature whistles that were classified as Pandora's or Calusa's, and that matched the criteria for acoustic localization, were localized to the respective mothers. Thus, the increase in signature whistle rate was a result of an increase in calling by the mothers and not a result of signature whistle copying by other dolphins at the facility (Table S1).
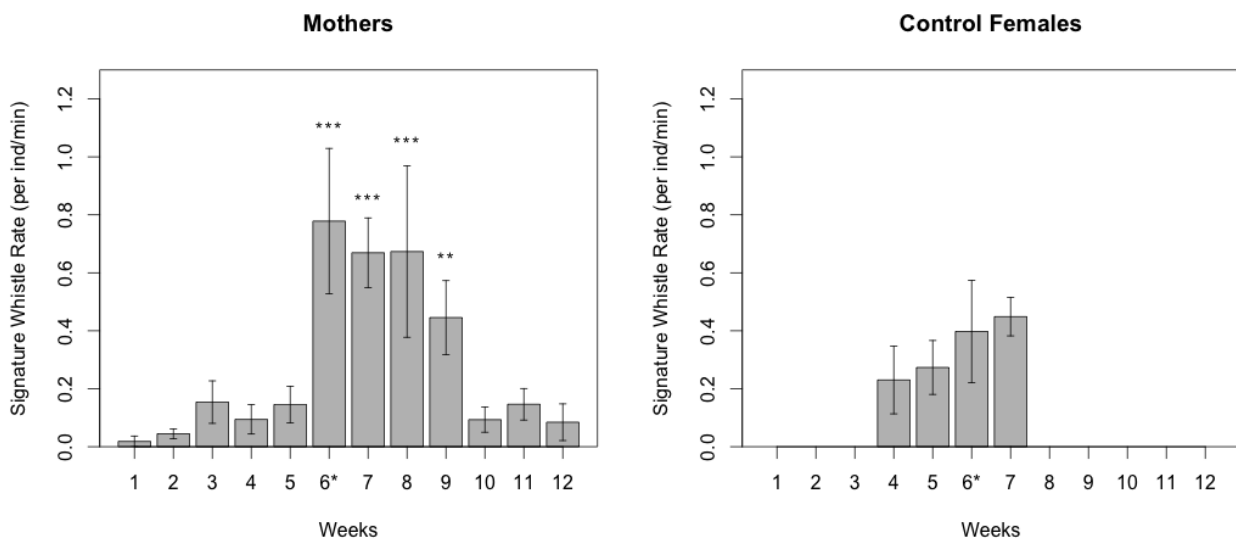

Figure 2. Average signature whistle rate per female/min with standard errors for the 12 recording weeks. The left panel presents combined data for the two mothers and the right panel presents data for the two control females. The 6* denotes the week the calves were born, therefore prepartum signature whistle production occurs in weeks 1-5, and postpartum signature whistle production

occurs in weeks 6-12. Asterisks indicate significantly high whistle rates (**P<0.01; ***P<0.001), and their corresponding P-values are provided in Table S2A.

Average signature whistle rate increased significantly from 0.14 whistles/min in week five to 0.78 whistles/min immediately after the birth in week six (LMER, t = 4.752, P < 0.0001). This represents over a five-fold increase in signature whistle production. Postpartum signature whistle rate remained significantly high for the first four weeks after the birth of the calves, and then returned to prepartum levels (Fig. 2; Table S2A & S2B). In comparison, the signature whistle rates of the two control females did not change significantly in week six after the two calves were born (LMER, t = 0.676 P = 0.5). In fact, signature whistle rate for the two control females did not change significantly over weeks four to seven of the recording period (Fig. 2; Table S2C). The signature whistle rate for these females was 0.27 whistles/min in week five and 0.35 whistles/min in week six.

Individual signature whistle rates for the 12 wk study period are shown in Figure S1. The two control females are only represented in weeks four to seven. It appears Calusa's signature whistle rate increased in week eight (third week postpartum), which corresponds with Pandora initiating a calf switch and refusing to switch back (pers. obs. E Guarino). The postpartum behavioral observations show that mothers were in control of their own calves for the first two weeks postpartum (week 6 and 7a) and then were in control of each other's calves when they were re-introduced at the end of the second week postpartum (7b) (Fig. 3). Pandora instigated the calf switching, and although Calusa tried a number of times to retrieve her calf, Pandora would not allow it (pers. obs. E Guarino). Both mothers nursed each other's calves, rather than their own, for the remainder of the study. This is reflected in the behavioral observations in Figure 3, which show that the calves spent the vast majority of their time slipstreaming (as shown by the dark bars) first with their mothers and then their adopted mothers (i.e., aunts) in the first five weeks postpartum (week 6-10). Then towards the end of the study period we start to see both calves moving more independently of their adopted mothers, frequently moving within 1-3 body lengths away (week 11-12 in Fig. 3).
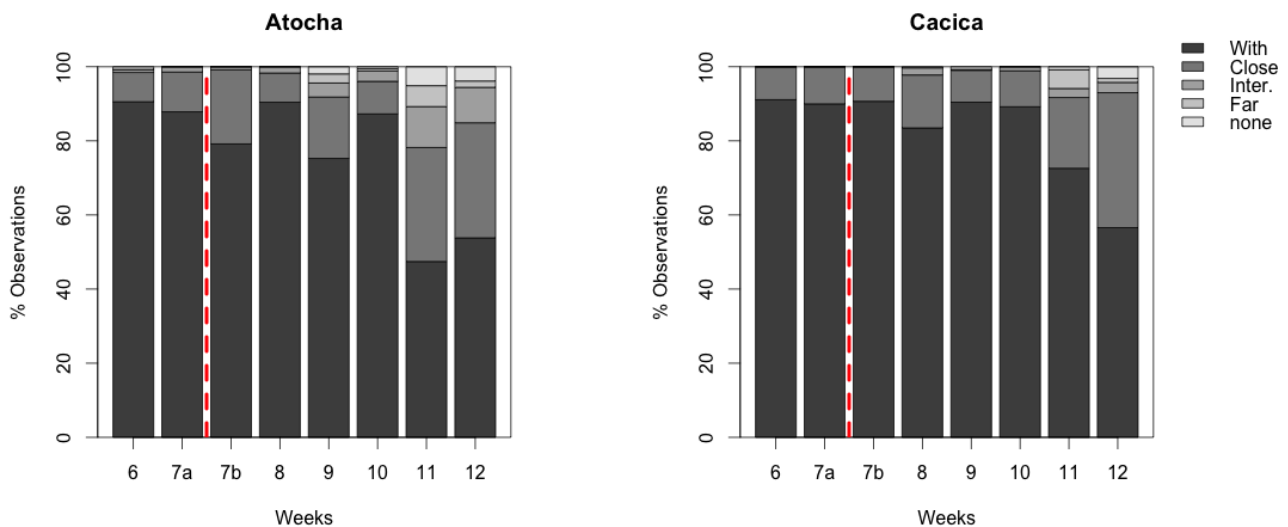
Figure 3. Postpartum observations of the proximity of each calf with both its mother and its aunt. The barplots show the proportion of observations for each level of proximity (full term descriptions provided in table 1). The mothers were re-introduced (with their associated calves) at the end of week seven, and subsequently switched calves. Thus the figure depicts the proximity of calf with its mother (week 6 and 7a) and then proximity to its aunt (weeks 7b to 12). The red dotted line highlights when each calf switched from its mother to its aunt.

Our data offer further support to the imprinting hypothesis postulated by Fripp and Tyack (2008), where calves imprint on their mothers' signature whistles immediately after parturition, which may facilitate the calf's recognition of its mother's call before mother-calf separations occur. This is one of the few studies, to our knowledge, to show in detail the underlying mechanisms immediately following parturition that facilitates long-term mother-offspring recognition in a species with precocial young. We have shown that female bottlenose dolphins increase their rate of signature whistle production five-fold immediately after the birth of their calves, with rates remaining high for four weeks postpartum. This was a similar finding to that of Fripp and Tyack (2008), who observed a ten-fold increase in signature whistle rate in the first week after parturition. However, in their study elevated signature whistle rates only lasted for the first two weeks postpartum before declining to prepartum levels for the mother of the one surviving calf (Fripp and Tyack 2008). The difference in the duration of the imprinting period between our study and Fripp and Tyack's (2008) study could be explained in one of three ways. Firstly, the period of imprinting may be flexible and we should expect variation both between and within individuals (*i.e.* from calf to calf). Secondly, we had an unusual situation where two weeks following the birth of the calves, the females switched calves and did not switch back. Pandora instigated the switch, and even though Calusa tried a number of times to retrieve her calf, Pandora seemed to not allow it. Whistle rates are known

to increase during stressful periods (Esch *et al.* 2009), and given that the increased whistle rate in week 8 appears to largely be driven by Calusa (Figure S1) the elevated signature whistle rates in the third and fourth week postpartum may be a result of the potentially stressful situation of 'losing' a calf. Thirdly, the calf switch may have essentially re-set the imprinting clock, leading to an additional two weeks of increased maternal signature whistle production.

Nonetheless, even if the imprinting period lasts two weeks or up to four weeks, it appears to be of much longer duration than required in other species. For example, mutual recognition is established within hours or days following parturition in both Australian seal lions (*Neophoca cinerea*; Pitcher *et al*. 2010) and sheep (Sèbe *et al.* 2007). However, bottlenose dolphins are known to encode individual identity in the unique frequency modulation pattern of their signature whistle (Janik *et al.* 2006) rather than relying on the by-product distinctiveness of voice features (Boughman and Moss 2003). Bottlenose dolphin calves are not born with a signature whistle but develop their own within the first few months of life (Sayigh *et al.* 1990, Tyack 1997). It therefore remains unknown whether female bottlenose dolphins can recognize their calves acoustically, before signature whistle are developed. It may therefore be imperative that a calf recognizes its mother's signature whistle in order to facilitate reunions in the event of separations, necessitating the need for extended periods of vocal imprinting. Another interpretation for the increase in maternal signature whistle rate postpartum is heightened arousal due to the birth of the calves. However, increased arousal and imprinting need not be mutually exclusive.

Importantly, we also recorded elevated signature whistle rates by new mothers when the calves were female, indicating that an increase in maternal signature whistle rates postpartum is not specific to male calves. That being said, males may still model their own signature whistle on their mothers whistle, but it is likely imprinting benefits both sexes by allowing the calves to recognize their mother's unique call. In addition, Pandora's signature whistle (Fig. 1A) appears to be similar to her mother's (Fig. 1C), whereas Calusa's signature whistle (Figure 1B) does not appear to be similar to her mother's (Figure 1C). Thus the factors influencing signature whistle development certainly warrants further investigation.

In line with earlier studies (Fripp and Tyack 2008), the signature whistle rate of non mothers did not change significantly as a result of calf births in this study (Table S2C), indicative that the increase in maternal signature whistle use is directed towards the calf. The control females in adjacent lagoons did increase their signature whistle rate immediately after the birth of the calves (Fig. 2 & Table S1), perhaps in response to the increased rate of calling by the new mother or due to

increased arousal from the birth and presence of a new calf. However, contrary to the pattern with the mothers, this increase in signature whistle rate was temporary and only lasted on the first day or two after the birth. If the mother was increasing her rate of signature whistle production to communicate with other group members then we would expect reciprocal vocal behavior in those animals across the entire study period. In addition, previous studies were unable to distinguish between increased signature whistle calling by the mother or copying of the mother's signature whistle by other group members due to the novelty of a new calf (Fripp and Tyack 2008). Bottlenose dolphin's are able to copy each other's signature whistles in order to label or address one another (King and Janik 2013, King *et al*. 2013). With the use of a hydrophone array and acoustic localization we were able to show that copying did not occur and that the elevation in postpartum signature whistle rate was due to the mothers calling more. We should also note that we observed no increase in prepartum signature whistle use as suggested in another study (Mello and Amundin 2005).

Interestingly, previous studies speculated that we should see a decline in maternal signature whistle production once mothers begin tolerating social separations and calves become more mobile (Mann and Smuts 1998). Our behavioral data revealed that the calves did not start becoming more independent until week six postpartum (week 11 of the study), yet maternal signature whistle production declined after week four postpartum (week 9). This supports the idea that irrespective of calf independence and/or social separations, there is an optimum time, <1 mo, in which imprinting should occur. It may well be that the first week or two is most critical but the overall duration of imprinting is flexible (Fripp and Tyack 2008, Mann and Smuts 1998). After this period, female dolphins will continue to use their signature whistles to initiate reunions with their calves, particularly when they become more independent, but the rate of signature whistle production is similar to prepartum levels.

Finally, we recognize that our study is based on a small sample size with just two females that experienced unusual circumstances in the third week postpartum when they switched calves. Conducting a study with this much detail for multiple animals across multiple facilities requires extensive planning and time investment. We hope that our study, coupled with Fripp and Tyack's earlier work (2008), will encourage researchers to explore the intricacies of postpartum signature whistle production in greater detail by using larger sample sizes and the inclusion of both male and female calves. Future work such as this would provide valuable insight into the temporal parameters of this imprinting period.

Acknowledgements

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