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Maternal signature whistle use aids mother-calf reunions in a bottlenose dolphin, *Tursiops truncatus*

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ABSTRACT

Individual vocal signatures play an important role in parent-offspring recognition in many animals. One species that uses signature calls to accurately facilitate individual recognition is the bottlenose dolphin. Female dolphins and their calves will use their highly individualised signature whistles to identify and maintain contact with one another. Previous studies have shown high signature whistle rates of both mothers and calves during forced separations. In more natural settings, it appears that the calf vocalises more frequently to initiate reunions with its mother. However, little is known about the mechanisms a female dolphin may employ when there is strong desire for her to reunite with her calf. In this study we conducted a series of experimental trials in which we asked a female dolphin to retrieve either her wandering calf or a series of inanimate objects (control). Results show that she used her vocal signature to actively recruit her calf, and produced no such signal when asked to retrieve the objects. This is the first study to clearly manipulate a dolphin's motivation to retrieve her calf with experimental controls. The results highlight that signature whistles are not only used in broadcasting individual identity, but that maternal signature whistle use is important in facilitating mother-calf reunions.

Keywords: maternal care, signature whistles, bottlenose dolphin, mother-calf reunions, vocal learning.

INTRODUCTION

The recognition of individuals plays an essential role in the behaviour of social animals, allowing animals to recognize their offspring, identify their mates, and discern between friend or foe (Tibbetts and Dale, 2007). Such individual recognition is particularly important in colonial breeders, where mothers leave their offspring to find food, and in animals that are highly mobile and gregarious (Knörnschild and von Helverson, 2008; Sèbe et al., 2008). Using spatial location as a means of recognizing and finding individuals is not reliable in these contexts because mother-offspring separation periods may be large or the offspring may be relatively mobile (Knörnschild et al., 2013). One strategy particularly suited to circumvent these problems is vocal signatures, because they can be used to identify individuals over greater distances than vision or olfaction may allow. Vocal signatures facilitate mother-offspring recognition in a number of colonial breeders, including swallows (Medvin et al., 1993), fur seals (Charrier et al., 2001; Insley, 2001), penguins (Jouventin and Aubin, 2002), and sea lions (Charrier et al., 2009; Pitcher et al., 2012). Vocal signatures are also common in other gregarious species, such as bats (Balcombe and McCracken, 1992; Jin et al., 2015; Knörnschild et al., 2013), and sheep (Searby and Jouventin, 2003), where individual vocal signature calls are known to facilitate mother-offspring recognition.

Another taxon that uses individual vocal signatures to facilitate mother-offspring recognition is the bottlenose dolphin, *Tursiops spp.* (Sayigh, Tyack, Wells, Scott 1990; Sayigh 1992; Smolker et al. 1993). Common bottlenose dolphins (*Tursiops truncatus*) are known for their use of individually distinctive contact calls, termed ‘signature whistles’ (Caldwell and Caldwell, 1965). These are learnt signals that broadcast the whistle owners’ identity (Caldwell et al. 1990; Sayigh, Tyack, Wells, Scott, Irvine 1999; Janik et al. 2006). Signature whistles develop within the first few months to the first year of life and are stable over decades (Sayigh, Tyack, Wells, Scott 1990; Tyack 1997). Calves appear to develop the structure of their signature whistle by modelling it on other whistles in their acoustic environment (Tyack, 1997), such as those of their mothers (Sayigh, Tyack, Wells,

Scott, Irvine 1995) or of community members with whom they associate infrequently (Fripp et al., 2005). In marine mammal facilities this also includes the whistles of their trainers (Miksis et al., 2002).

As each individual's signature whistle forms a major part of only one animal's repertoire (King et al., 2013), this allows the signature whistle to act as a label for that particular individual when copied (King and Janik, 2013). Signature whistle copying is particularly well suited as a means of addressing (King et al., 2014) between animals that share strong social bonds, such as allied males and mother-calf pairs (King et al., 2013). However, outside of that context signature whistle copying appears to be relatively rare (Janik, 2000; King et al., 2013). Instead, animals tend to produce their own signature whistles when they become separated from their social group, which in turn elicits signature whistle calling in their social companions (Janik and Slater, 1998). Thus, as well as broadcasting individual identity, signature whistles also play an active role in maintaining group cohesion (Janik and Slater, 1998).

One of the most important functions of signature whistles is to facilitate mother-calf recognition and to help them maintain contact with one another when separated (Fripp and Tyack, 2008; Sayigh, 1992; Smolker et al., 1993; Tyack and Sayigh, 1997). Mothers imprint their signature whistles on the calf in the first few weeks of life (Fripp and Tyack, 2008; King et al., accepted) allowing calves to quickly learn to recognise their mother within their fluid social system. Signature whistle use by the mother or the calf may help reveal their locations to one another as well as stating their motivation to reunite. But exactly how this system works is not yet clear. So far, mother-calf signature whistle production has largely been studied during forced, but temporary, separations i.e. annual health assessment captures (Sayigh, Tyack, Wells, Scott 1990), where both

mothers and calves whistle at high rates (Esch et al., 2009; King et al., 2013; Sayigh, Tyack, Wells, Scott, 1990).

Evidence of naturally occurring separations in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) suggests that mothers do not whistle as reliably or as repetitively in separation contexts as do infants (Smolker et al., 1993). Signature whistle rates in the context of mother-calf separations have been shown to increase when the separation distance increases (Smolker et al., 1993), however it appears that it is the calf that whistles more frequently to initiate a reunion, rather than the mother (Smolker et al., 1993).

To date, only a single study has investigated how a female dolphin actively retrieves her calf when *she* wants to reunite (Kuczaj et al., 2015). In this study the authors reported that three female common bottlenose dolphins each "used her signature whistle and/or a secondary whistle" when asked to retrieve their calves. However, several methodological limitations leave these results open to a different interpretation, especially with respect to the individually-specific secondary whistle, which no other studies of dolphin communication have reported. Importantly, the Kuczaj et al. study lacked any visual classification of call types, a crucial component of many animal communication studies (Janik, 1999). Subsequent analysis has shown that in one of the three females studied, the secondary whistle identified was an introductory part of that animal's signature whistle (Jones 2014). Such partial signature whistles are well-known features of bottlenose dolphin communication, and are typically classified as exemplars of that animal's signature whistle and not a separate whistle type (Caldwell et al., 1990; Tyack, 1986). This standard coding makes particular sense in this instance, given that the individual in question showed no significant preference between her signature whistle and secondary whistle when retrieving her calf (Kuczaj et al., 2015). The secondary whistle of one of the other females (Ding) has also been recorded in other contexts (Jones 2014; Kuczaj et al. 2015), and while the secondary whistle of the third female may not have been previously reported in other contexts, the lack of experimental controls in the Kuczaj et al

(2015) study means it is impossible to know whether the adult females would have produced these same acoustic responses to any other trainers' requests (i.e., which did not involve retrieving a calf).

Another potential unknown is whether it was the mothers or their respective calves that produced the secondary whistles. Calves typically develop their own signature whistle within their first few months of life, so the secondary whistle may have been the calves' own signature whistle. Recent studies have also shown that bottlenose dolphins may copy one another's signature whistle as a mean of addressing specific social companions (King and Janik, 2013). For example, mothers and calves have been shown to copy one another's signature whistles during temporary (but forced) separations (King et al., 2013). The secondary whistle could therefore be the mother producing a copy of her calf's signature whistle. Thus, although there is some suggestion that females in the context of calf retrieval may use secondary whistles, alternative explanations cannot currently be ruled out.

To investigate the issue of mother-initiated reunions more systematically, we conducted a series of experimental trials in which we asked a female dolphin to retrieve a series of inanimate objects (control) or her wandering calf. We then used the standard method of visually scoring call types to determine the classification of individual whistles. Following the signature whistle framework we predicted that signature whistle use was the most efficient way to reunite with a calf and that she would therefore produce her signature whistle when asked to retrieve her calf but not when asked to retrieve other objects. By using experimental controls and visual classification we aimed to explore the idea of secondary context specific whistles more fully.

METHODS

Subject

The subject was a female common bottlenose dolphin named Merina (29 years old), who was born at the Dolphin Research Center (DRC). Merina had a female calf, Windley, who was 3-5 months old at the time of testing. The trials were conducted in a 502 m² natural seawater lagoon (28m by 15m) with depth dependent on tide (4.5-5.5 m).

Signature Whistle Identification

Signature whistles are typically defined as the most common whistle produced by an animal when isolated from its group (Caldwell et al., 1990). In the current study, signature whistles were identified by recording the most common whistle type produced by Merina and Windley when they were separated from one another during a medical assessment. Recordings were made in-air and in water with an HTI-96 MIN hydrophone (frequency response: 0.002-30 kHz \pm 1 dB) onto a TASCAM DR-680 multitrack recorder at a sampling rate of 96 kHz. The signature whistles of Merina and Windley are provided in Figure 1.

Trials

Experiments were conducted with Merina at DRC between February and May 2014. Using a combined hand and verbal signal, a trainer asked Merina either to retrieve her calf ('go get the baby') or to retrieve an object that had been thrown into the lagoon immediately prior to the trial ('go get the object'). Merina was only asked to 'go get the baby' when her calf was in another part of the lagoon and not nearby. It should be noted that whereas the objects and Windley were usually at similar distances from Merina at the start of the trial (ranging from 5m to 8m), Windley was free to move away or towards Merina, and therefore the distance between Merina and her calf could change as soon as the trial started, and could not be explicitly controlled for.

The trial ended when Merina returned to the trainer's station with her calf or with the object, at which time the trainer blew a whistle and provided her with positive reinforcements of fish and social interaction. A range of familiar objects was used in the trials, such as a ball, hoop, frisbee, target pole and a selection of shapes made from pvc piping. Trials were randomised in their presentation, and were conducted both in Feb-March 2014 and in May 2014. This allowed us to investigate whether the performance of the target animal changed as her calf got older by comparing the trials in these two different blocks of time.

Trials were recorded with a Canon VIXIA HF R42 video camera with acoustic input from the Aquarian H1a hydrophone. Vocalisations of the animals were recorded with an Aquarian Hydrophone H1a (frequency range: 1 Hz ~ 100kHz, sensitivity: $-190 \pm 4\text{dB re } 1\text{V}/\mu\text{Pa}$ at 20Hz-4kHz) at a sampling rate of 48 kHz and were synchronised with the video recordings.

Acoustic Localisation

The 'go get baby' trials conducted in 2014 were only recorded with one hydrophone. DRC houses approximately 27 animals in seawater lagoons, which are separated from one another by underwater fencing and therefore the majority of animals are in acoustic contact. To show explicitly that it was Merina vocalizing during these trials, and not another dolphin copying Merina's signature whistle we repeated some additional 'go get baby' trials with a hydrophone array in January-March 2015, when Windley was 16 months old. These recordings were made with an array of four HTI-96 MIN hydrophones (frequency response: $0.002\text{-}30\text{ kHz} \pm 1\text{ dB}$) onto a TASCAM DR-680 multitrack recorder at a sampling rate of 96 kHz. During each recording session four hydrophones were placed into the lagoon in an approximate rectangular formation, and distances between hydrophones ranged from approximately 8 to 28 metres. Whistles were localized to an individual using the TOADY localization program (Quick et al., 2008). Localisation 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 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). The mean localization error was calculated to be 1.3 m (n=4) from the true location of the calling animal. Video recordings were made with a Canon VIXIA HF R42 video camera with acoustic input from one of the HTI-96 MIN hydrophones. The position of the whistle as determined by acoustic localisation was then compared with the position of Merina in the lagoon as per the video recordings. During these localisation trials there were no other animals in the lagoon with Merina and Windley, however, they remained in acoustic contact with animals in adjacent pools.

Analysis

The vocal behaviour of Merina during the trials was analysed 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). The start time, end time and duration of all vocalisations were noted using the marker function in Adobe Audition by a researcher who was blind to the timing of the trials. Afterwards, the salient information from the trial videos, such as the trial start time (as indicated by a hand and verbal signal from the trainer) and the trial end time (as indicated by the trainer's whistle) were also noted.

Visual classification was used to determine whether the whistles produced during the trials were Merina's signature whistle. Visual classification is widely used in animal communication studies and has been shown to be more reliable than computer based classification methods, particularly when analysing dolphin whistles (Janik, 1999; Sayigh, Esch, Wells, Janik, 2007). One observer (S.L.K) went through the trials and identified all occurrences of any stereotyped and/or repeated whistle. A total of 84 slides were then created in Microsoft Powerpoint each containing two spectrograms; one of either a whistle produced during the trial or a randomly selected whistle produced by other animals at the facility, and the other a template of Merina's signature whistle. All time axes were standardised to 2 seconds and no information on caller identity was given. Five naïve human observers, who were blind to context, were provided with the slides, and were asked to rate the similarity between each pair of whistles. Similarity was based on a five point similarity index ranging from 1 (dissimilar) to 5 (similar). The similarity ratings were compared between the judges using the Fleiss' Kappa statistic (Siegel & Castellan 1988) to determine the inter-observer agreement. The scores of the 5 different judges were significantly similar (Fleiss-Kappa statistic (unweighted) = 0.35, $z = 17.4$, $P < 0.0001$) (Fleiss et al., 2003). Any whistle that scored a mean similarity value of ≥ 3.6 was deemed to be very similar (Sayigh, Tyack, Wells, Scott, Irvine 1995) to Merina's signature whistle template and was thus confirmed as Merina's signature whistle in the

analysis. The mean similarity score given to the whistles of other animals at the facility when compared to Merina's signature template was 1.3. A selection of whistle contours taken from Merina's signature whistles produced during the 'go get baby' trials and of the signature whistles of the other animals housed at DRC are presented in the supplementary material.

We used a GLM with a binomial family to analyse the presence or absence of Merina's signature whistle in the two different trial types. The binary response was 1 if Merina produced her signature whistle in the trial and 0 if she did not. The predictor variable was trial type (baby versus object retrieval).

We then used GLM with a poisson family to investigate how Merina's signature whistle use varied between 'go get baby' trials. The response variable was the number of Merina's signature whistles produced from the start to the end of the trial. The predictor variables were time block (Feb/March versus May) and the duration of the trial in seconds (continuous). There was no significant difference between the two data collection periods as the predictor variable time block was removed under model selection. Model selection was performed using Akaike information criterion (AIC) and stepwise selection with a p-value significance level of 0.05.

RESULTS

Trials

A total of 79 trials were repeated with Merina: 50 'go get baby' trials where she was asked to retrieve her calf, and 29 'go get object' trials where she was asked to retrieve an object. Of these, 50 trials (32 GGB and 18 GGO) were conducted in February and March 2014 and 29 trials (18 GGB and 11 GGO) were conducted in May 2014.

During these trials Merina always physically went to retrieve either Windley or the relevant object. Merina also frequently produced her signature whistle when asked to retrieve her calf, but rarely produced her signature whistle when asked to retrieve an object (Figure 2). This difference in vocal behaviour to the two trial types was significant (Binary GLM, $\chi^2_1 = 4.039$, $P < 0.0001$).

To balance the experimental design we randomly selected 29 GGB trials and ran the model again with the 29 GGO trials. The results remained significant (Binary GLM, $\chi^2_1 = 3.868$, $P = 0.0001$). The mean number of signature whistles produced by Merina was 1 (range from 0 to 6) during the 'go get baby' trials and 0.2 (range from 0 to 3) during the 'go get object' trials. The mean time from the start of the trial to Merina first producing her signature whistle was 1.6 s (range from 0.1 to 8) for 'go get baby' trials and 7.6 s (range from 5 to 11) for 'go get object' trials.

Average trial durations were similar across trial types, with a mean duration of 14.7 seconds (range: 6 to 54) for 'go get baby' trials and a mean duration of 14.8 seconds (range: 5 to 39) for the 'go get object' trials. Thus average trial duration did not directly influence signature whistle production. However, Merina did produce significantly more signature whistles during the 'go get baby' trials when the trial duration was longer (Poisson GLM, $\chi^2_1 = 3.190$, $P = 0.001$). Because the trial was over as soon as Merina returned to station with her calf, the duration of the trial was determined by how quickly Merina could recruit her calf. Merina also produced her signature whistle in three of the 'go get object' trials, which all had relatively long durations (mean: 25 seconds). However,

unlike the calf retrieval trials where Merina continued to produce her signature whistle throughout the trial until she had retrieved Windley, all of the signature whistles produced in the object retrieval trials occurred near the beginning (within 11 seconds of the trial starting).

Merina sometimes produced single loop signature whistles (example in Figure 3) during the calf retrieval trials, which were correctly classified as her signature whistle in the visual classification task. Excluding Merina's signature whistle, there were no other stereotyped or repeated whistle types produced in either of the two trial types. In fact, for the majority of the 'go get object' trials (69%) no whistle of any type was produced. We found no evidence of any whistle that resembled Windley's signature whistle being produced during the trials nor evidence of any potential copies of Windley's signature whistle by Merina.

Acoustic Localisation

We successfully localised Merina's whistles in three 'go get baby' trials from recordings made in January-March 2015. During these trials, when asked to go and retrieve her calf, Merina's signature whistle was produced 3, 1 and 4 times respectively. All of the whistles classified as Merina's signature whistle were localised to Merina's position in the lagoon, as corroborated by the video recordings. The localisation plot in figure 4 shows the position of Merina (where the hyperbolas cross) when she produced her signature whistle during one of these trials.

At the start of this trial Merina was positioned at the dock and was asked by the trainers to 'go get' her calf. Merina immediately swam in the direction of Windley and produced her signature whistle. Merina was not stationary when she whistled so the hyperbolas cross at her relative position. Within 10 seconds Merina returned to the dock with Windley.

DISCUSSION

By clearly manipulating the mother's motivation to retrieve her calf, and utilizing appropriate experimental controls, the current study has demonstrated that a female bottlenose dolphin will use her signature whistle--and only her signature whistle--to facilitate calf retrieval.

When exploring the function of calls in this way, careful consideration must be given to whether the calls are being produced by the focal animal or whether call production could be a result of vocal copying by other individuals. Bottlenose dolphins are excellent vocal mimics and may copy one another's signature whistle as a mean of addressing specific social companions (King and Janik, 2013; King et al., 2014). In addition, this copying is known to occur between animals that share strong social bonds, such as mothers and calves (King et al., 2013). However, it is very unlikely the whistles produced here are signature whistle copies. Firstly, although we were unable to localise whistles to Merina for the majority of trials, human observers showed strong agreement that the whistle produced in the trials was Merina's signature whistle. For the majority (60%) of the 'go get baby' trials Merina only produced one signature whistle when asked to retrieve her calf. The only animal that was subject to the different contexts in these trials was Merina. Therefore if other animals were producing signature whistle copies we would not expect a significant difference in call use between contexts. Secondly, the localisation plots for the small number of trials we were able to replicate with an array the following year, clearly show that Merina was the animal vocalising during these calf-retrieval contexts.

Alternatively, one might posit that Merina's use of her signature whistle may have been a result of increased motivation by Merina due to anticipating positive reinforcement. However, if this was the case then we would have expected her to also whistle more during the object retrieval trials. We found no evidence of an acoustic signal being associated with the objects in this study. Dolphins certainly have the ability to use sounds to refer to objects (Richards et al., 1984) and to emit them

when manipulating objects (Reiss and McCowan, 1993). However, Merina only produced her signature whistle in a very small number of the object retrieval trials.

Indo-Pacific bottlenose dolphin mothers and calves are known to use their signature whistles to facilitate the localisation of one another when travelling apart i.e. they reveal their locations to one another as well as stating their motivation to reunite (Smolker et al., 1993). In the current study, given the smaller dimensions of the lagoon in comparison to natural settings, Windley was always reliably nearby. The fact that Merina often retrieved Windley without vocalising may offer support to the notion that when the calf is visible, or its position is known, the mother heads straight over and physically retrieves it; when the calf is not visible, or its position is unknown, then the use of the mother's signature whistle is a clear signal that she wants her calf to return. Interestingly, there was no evidence of the calf replying with her own signature whistle during the calf retrieval tasks. This is perhaps surprising given that previous studies have shown that mothers and calves will both produce their signature whistles during separations and reunions (Smolker et al. 1993; Tyack & Sayigh 1997; Fripp & Tyack 2008). However, such exchanges between mothers and calves may only occur when animals are forcibly separated from one another (Sayigh, Tyack, Wells, Scott 1990; King et al. 2013) or separation distances are relatively large (Smolker et al., 1993). Again, given the relatively small size of the lagoon, the mother would have found her calf fairly quickly, negating the need for the calf to reply vocally and indicate its location.

Thus, maternal signature whistle use not only broadcasts the mother's location but also her motivation to reunite with her offspring. For example, Merina produced more signature whistles during longer trials, during which Windley either did not approach her mother or was actively swimming away -- a behaviour that becomes more frequent as calves get older and wander further from their mothers (Mann and Smuts, 1998). As such, although it was previously inferred that it was the calf that whistles more frequently to initiate a reunion (Smolker et al., 1993), our results support the idea that it is the animal that wishes to reunite that calls more.

We also found no evidence of Merina producing copies of Windley's signature whistle. A recent study has shown that bottlenose dolphin mother and calves will copy one another's signature whistles during temporary (but forced) separations (King et al., 2013). However, these calves were at least 1 year old when the copies were recorded. When calves are fairly young it is likely that it is the mother's signature whistle that induces the strongest response in the calf (Fripp and Tyack, 2008; King et al., accepted). Copying may be more likely to occur when calves are older and/or weaned from their mother. The age at which copying may first occur between mother-calf pairs certainly warrants further exploration.

Finally, our findings both support and refute the conclusions of the Kuczaj et al. (2015) study. Although our study was a repeated-measures design with one individual, we found no evidence of a context specific secondary whistle, a discrepancy that may be explained by the methods used. Our use of a visual classification task and experimental controls showed that Merina produced only her signature whistle when retrieving her calf, with no evidence of a secondary whistle. It may be that the age of the calf influences the mother's vocal behaviour, however, the trials in Kuczaj et al. (2015) occurred during the first two years of the calf's life, and our trials were carried out when Windley was 3-5 months old and 16 months old respectively. It is therefore unlikely that the age of the calves accounted for the difference in results between the two studies. To summarise, we found no evidence of a context specific secondary whistle, and we find the data presented in Kuczaj et al. (2015) to be inconclusive. As such, it remains unclear whether some females may use additional whistle types in the context of calf retrievals, and future studies should aim to explore maternal whistle use in greater detail.

However, the finding from this study does support, and add to, our current understanding that signature whistles provide a means of locating and maintaining contact with specific individuals in bottlenose dolphins (Caldwell & Caldwell 1965; Tyack 1986, 1997; Caldwell et al. 1990; Janik & Slater 1998; Sayigh, Tyack, Wells, Scott, Irvine 1999; Janik et al. 2006; Janik & Sayigh 2013; King

& Janik 2013; King et al. 2014). The fission fusion nature of the bottlenose dolphin social system inevitably leads to frequent separations and reunions between mothers and their calves (Smolker et al., 1993). Signature whistles have been shown to be pivotal in mother-offspring recognition (Sayigh, Tyack, Wells, Scott 1990; Sayigh 1992; Smolker et al. 1993; Sayigh, Tyack, Wells, Scott, Irvine 1999; Fripp et al. 2005; Fripp & Tyack 2008). We previously knew that calves would frequently whistle to initiate a reunion with their mother (Smolker et al., 1993). Our study now highlights the importance of maternal signature whistle use in facilitating mother-calf reunions.

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Figures

Figure 1. Spectrogram of (a) Merina’s signature whistle and (b) Windley’s signature whistle (sampling rate is 96 kHz, FFT length 1024, Hanning window function)

Figure 2. The vocal response of Merina when asked to retrieve her baby (GGB) or to retrieve an object (GGO); the figure shows the number of trials during which Merina produced her signature whistle (grey) and did not produce her signature whistle (white).

Figure 3. Example of a full signature whistle and a single loop signature whistle produced by Merina (sampling rate is 96 kHz, FFT length 1024, Hanning window function).

Figure 4. Localization plot showing the position of Merina when she produced her signature whistle during the ‘go get baby’ trial. The ‘x’ indicates the position of Windley, the rectangle indicates the position of the trainers at the docking station, and the positions of all four hydrophones are also shown (h1-4).