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Pre- and Post-Partum Whistle Production of a Bottlenose Dolphin (Tursiops truncatus) Mother-Calf Dyad

Audra Elizabeth Ames
University of Southern Mississippi

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PRE- AND POST-PARTUM WHISTLE PRODUCTION OF A BOTTLENOSE
DOLPHIN (*Tursiops truncatus*) MOTHER-CALF DYAD

by

Audra Elizabeth Ames

A Thesis
Submitted to the Graduate School
and the Department of Psychology
at The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Master of Arts

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May 2016
ABSTRACT

PRE- AND POST-PARTUM WHISTLE PRODUCTION OF A BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) MOTHER-CALF DYAD

by Audra Elizabeth Ames

May 2016

Whistle use pre- and post-partum in an Atlantic bottlenose dolphin (*Tursiops truncatus*) mother-calf dyad has rarely been studied. The current study is the first to investigate signature whistle production by the mother pre- and post-partum, as well as whistle use by other members of the social group during calf development, and how exposure to these whistles may affect the calf’s vocal repertoire. Findings showed that the mother increased her rates both pre- and post-delivery, while other group members produced their whistles at decreased rates until the calf’s second week of life. After the calf’s second week, whistle rates of the other members began to increase, while the mother’s production began to decrease. A discriminate analysis was used to determine the presence of adult contours in the calf’s repertoire. While adult contour imitation occurred in the calf’s whistle use, no favored whistle type appeared. In addition to adult contour imitations, the calf produced several other whistle types.
ACKNOWLEDGMENTS

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CHAPTER I
INTRODUCTION

The signature whistle of the Atlantic bottlenose dolphin (Tursiops truncatus) is a frequency-modulated, narrowband, tonal sound (Herman & Tavolga, 1980; Tyack, 1986) that is understood to have identifying qualities in contexts of separation (e.g., locating individuals, facilitating reunions, and maintaining group cohesion) (Herman & Tavolga, 1980; Janik & Slater, 1998; Janik, Sayigh, & Wells, 2006; Sayigh, 1992; Sayigh et al., 1998; Smolker, Mann, & Smuts, 1993; Tyack, 1986). Signature whistles may also play a role in mothers and calves reuniting (McBride & Kritzler, 1951; Smolker et al., 1993) and identifying each other (Janik et al., 2006; Sayigh et al., 1998).

There have been few studies conducted on the roles of maternal signature whistle production pre- and post-partum in bottlenose dolphins. Mello and Amundin (2005) found that the whistle rates of three dolphin mothers began to increase prior to parturition. In a study of signature whistles post-partum, Fripp and Tyack (2008) reported that dolphin mothers use their signature whistles at a higher rate for the first week of the calf’s life. Studies have suggested that these rates may be part of an imprinting process, establishing an early recognition system in the mother-calf dyad (Fripp & Tyack, 2008; Gnone & Moriconi, 2010; Gnone et al., 1997). Increases in pre-partum rates expose the calf to the sound in utero, preparing the calf to recognize the whistle soon after birth (Kuczaj & Winship, 2015; Mann & Smuts, 1998; Mello & Amundin, 2005).

The current study analyzed pre- and post-partum whistle production for a primiparous mother and additional dolphins present in the sound environment. Two developmental phenomena will be addressed: (1) imprinting, by which a calf learns to
identify and become attached to its mother (Fripp & Tyack 2008; Herman & Tavolga, 1980; Lorenz, 1937; Mann & Smuts, 1998), and (2) vocal learning, through which the calf develops her own vocal repertoire (Caldwell & Caldwell, 1979; Fripp et al., 2005; Sayigh, 1992; Sayigh et al., 1990; Sayigh et al., 1995; Tyack & Sayigh, 1997).

Imprinting Hypothesis

Lorenz (1937) described imprinting as an innate process by which the offspring of a species develops a conditioned response to its parent. Imprinting has been described as occurring rapidly in a very limited part of an animal’s life, and once the process is complete, it can be difficult to extinguish (Lorenz, 1937; Ramsay & Hess 1954).

Acoustic imprinting (i.e., imprinting on sounds produced by a parental model) has been found in bird species (Fischer, 1966; Insley, 2000; Jouventin, Aubin, & Lengagne, 1999; Lengagne, Aubin, Jouventin, & Lauga, 2000; Ramsey & Hess, 1954; Trillmich, 1981). In king penguins (*Aptenodytes patagonicus*), vocal cues are used to identify the calls of mates, parents, or young when reuniting in the wild (Jouventin, 1982; Jouventin et al., 1999; Lengagne et al., 2000). Jouventin et al. (1999) used a playback experiment to determine how king penguin chicks would respond to parental calls that contained manipulated acoustic parameters. The study found that chicks did not recognize calls with manipulated signals, even if they still contained the fundamental frequency of the parental call. When parameters only weakly associated with a parental call’s identification were manipulated, the call was still unrecognizable to the chick, indicating that only low harmonics contained the necessary information for chicks to identify their parents. These findings suggest that (1) a chick must be able to learn the parents’ call, (2) the call must
have unique frequency modulated variation, so that it is distinguishable by the chick, and
(3) the call must remain stable, so as not to confuse the chick (Jouventin et al., 1999).

Mammalian species also use vocal recognition when reuniting with offspring. Northern fur seal (*Callorhinus ursinus*) mothers separate from their pups to forage, and must identify their pups before reuniting (Insley, 2000). Studies of Galapagos fur seals (*Arctocephalus galapagoensis*) and sea lions (*Zalophus wollebaeki*) (Trillmich, 1981), and northern fur seals (Insley, 2000) indicate that this reunion is facilitated by acoustic calls produced by the mother-pup dyad. According to Trillmich (1981), pups develop an early recognition system that enables learning of specific acoustic cues emitted by the mother. Killer whale matrilines dramatically increase family-typical calls before and after the birth of a new calf, which may aid the calf in learning acoustic cues used to maintain proximity with family members (Weiß, Ladich, Spong, & Symonds, 2006). New bottlenose dolphin mothers whistle almost continuously for the few days following parturition (Caldwell & Caldwell, 1968), and so may provide a model for acoustic imprinting (Fripp & Tyack, 2008; Gnone & Moriconi, 2010; Herman & Tavolga, 1980; Mann & Smuts; 1998).

Prenatal Acoustic Exposure

Some mammal species show the ability to process sounds *in utero*. Armitage, Baldwin, and Vince (1980) implanted hydrophones into the amniotic sac of two ewes in order to discern the available sound environment of unborn lambs. External sounds emitted at volume levels similar to a normal conversation were picked up without interference from sounds internally produced by the mother’s cardiovascular system. Vince (1979) investigated the postnatal effects of prenatal sound in guinea pigs (*Cavia*
Pregnant guinea pigs were exposed to auditory stimuli alien to the species. Post-partum, the young guinea pigs were played these same auditory stimuli, and compared to controls that had not been similarly stimulated *in utero*. The exposed young responded with less heart rate acceleration than did the controls, indicating that the guinea pig offspring recognized the sounds they had been exposed to prenatally. Vince, Armitage, Walser, and Reader (1982) replicated this finding with Border Leicester and Soay sheep (*Ovis aries*). Lambs responded with higher heart rates to unfamiliar auditory stimuli than to auditory stimuli they had experienced in the womb. DeCasper and Fifer (1980) found that 3-day-old human newborns demonstrated a preference for their mother’s voice, despite very limited exposure post-partum. Partanen, Kujala, Tervaniemi, and Huotilainen (2013) reported that infants who were played *Twinkle, Twinkle, Little Star* during the last trimester responded to hearing it again at birth and at 4 months of age through stronger event-related potentials (ERP) (i.e., measured brain responses that are a result of a particular cognitive event).

There have been no such studies indicating that dolphin calves experience their sound environment *in utero*. However, dolphin calves are precocial, and may respond to their mother’s signature whistle shortly after birth. Prenatal exposure may be part of establishing an early recognition system, as well as assist the calf with its own developing repertoire. Tyack and Sayigh (1997) reported that some calves acquire a signature whistle within the first few days of life, and that one potential mechanism that makes this possible is prenatal exposure to the sound environment.
Whistle Development Hypothesis

Bottlenose dolphins vocally learn throughout their lives (e.g., King, Sayigh, Wells, Fellner, & Janik, 2013; Richards, Wolz, & Herman 1984; Tyack, 1986; Tyack & Sayigh, 1997). Vocal learning is the processes by which an individual modifies its vocal repertoire after exposure to a sound (Marler, 1976; McCowan & Reiss, 1997). Dolphin calves develop their vocal repertoire in part by imitating acoustic models in their sound environment (Caldwell & Caldwell, 1979; Fripp et al., 2005; King & Janik, 2013; King et al., 2013; Sayigh, 1992; Tyack, 1997). Fripp et al. (2005) investigated the signature whistles of dolphin community members in Sarasota, FL. to determine their influence on signature whistle development in calves. The authors found that calves were more likely to model their signature whistles after the whistles of dolphins that spent little time within 50 m of the mother-calf dyads. Sayigh et al. (1992) reported similar results when two calves within the Sarasota community developed whistles similar to those of unrelated females. While most dolphin calves develop signature whistles that differ from their parents (Fripp et al., 2005; Tyack, 1997), the mother’s signature whistle can influence the development of a calf’s vocal repertoire (Sayigh et al., 1990; Sayigh et al., 1995), especially if additional factors are present (e.g., stronger bond with the mother, limited exposure to other whistles) (Kuczaj, 2014).

Calves in captivity most often develop signature whistles that match models present in the sound environment. Caldwell and Caldwell (1979) reported that one captive male calf produced a signature whistle comparable to whistles produced by a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), while Tyack and Sayigh (1997) reported that a male calf modeled his signature whistle after two sub-adults in his
captive environment. Calves also use human training cues (e.g., marking stimuli, like whistles) as acoustic models (Miksis, Tyack, & Buck, 2002; Sayigh, 1992; Tyack, 1997), and if only a single model is available, calves will develop a signature whistle similar to that model (Caldwell & Caldwell, 1979; Tyack & Sayigh, 1997). When raised alone by its mother, Caldwell and Caldwell (1979) reported that one calf quickly developed a signature whistle similar to hers.

There are considerable discrepancies regarding when calves first produce their signature whistle. Calves begin to whistle on the day of birth (Morisaka, Shinohara, & Taki, 2005a), and most calves develop a signature whistle within the first 17 months of life (Caldwell & Caldwell, 1979; Fripp et al., 2005; Tyack & Sayigh, 1997). However, some bottlenose dolphin calves produce a discriminable signature whistle within the first few days of life, and this whistle remains stable throughout development (Sayigh, 1992; Tyack & Sayigh, 1997).

The current study aimed to verify the following hypotheses: (1) the mother’s signature whistle use will increase pre-partum and (2) the mother’s signature whistle rates will also increase post-partum, but wane after the first few weeks of the calf’s life. This study also addressed the signature whistle rates of other group members in the environment during the pre- and post-period. Finally, this study sought to discuss vocal learning in (1) whistle types used by the calf, (2) imitations of adult whistles, and (3) development of a favored whistle type in the repertoire of the calf.
CHAPTER II

METHODOLOGY

Facility, Equipment, and Subjects

Four months of data were collected opportunistically from November 14, 2013 until March 5, 2014 at the MRC habitat at Six Flags: Discovery Kingdom in Vallejo, California. The subjects were one primiparous, 9-year-old bottlenose dolphin mother (Bella) and her calf (Mirabella, aka “Mira”). Additional group members consisted of five other adult females (Chelsea, Jasmine, Mattie, Yoshe, and Ping). Ping and Yoshe remained physically, but not acoustically isolated in the south pool of the habitat for the entirety of data collection.

The data set for this study included video and hydrophone recordings from two months prior to two months after parturition. A Canon Vixia HF200 with a wide-angle lens with a Sony Audio Recorder PCM-M10 and CR-1 hydrophone input were placed in the center pool of the MRC habitat (Figure 1). The video recording device was placed in front of the observing window of the center pool, while the hydrophone was placed in the pool in a cylindrical tube adjacent to the viewing window. The center pool was an oval pool 43 feet wide, 60 feet long and 15 feet in depth. The adjacent pools were cylindrical pools 50 feet in diameter and 15 feet in depth.

Each pool can be closed off from the others via a gating system. When the mother-calf dyad was separated from the remaining group members, the sound environment remained available, as the gates separating the pools did not isolate the pair acoustically.
For the majority of the calf’s first month of life, Bella and Mira were physically isolated in the center pool. Prior to the calf’s birth, the gates separating the north and center pools remained open, allowing Chelsea, Jasmine, Mattie, and Bella to interact. On January 15, 2014, Mira began physical introduction to the other group members. Physical introduction was sporadic and limited to either Chelsea or Mattie individually until February 18th when Chelsea and Mattie were both allowed to physically interact with Bella and the calf, and February 19th when the gate to the north pool was opened allowing the dolphins (except for Yoshe and Ping) to swim freely between the center and north pools. Because the dyad was allowed additional access to the north pool on most days in the second month of life, the amount of their time in front of the observation window decreased. Subsequently, the amount of time spent on camera during video recording decreased as well.
Data

Data collection began 56 days prior to the birth of the calf. Data were sectioned into 28-day blocks, amounting to two blocks before the calf’s delivery and two blocks after. ~20 hours (~1,200 minutes) were selected from each 28-day block to equal the amount of total data collected in the fourth 28-day block, which represented the lowest amount of data collected for the study. A total of ~80 hours of data were analyzed. Files that were video or hydrophone data only were not analyzed due to absence of sound data or due to a differentiation in sampling rate between hydrophone only (48 kHz) and video files with hydrophone input (24 kHz).

The 28-day durations were segmented further into 14-day blocks. This was necessary to analyze two-week trends occurring in the data. As a result, two 14-day segments were produced for each of the original 28-day durations, for a total of 8 blocks of time for comparison (see Table 1 for a list of each block’s relationship to the calf’s birth).

Table 1

*Blocks of Time in Relation to the Calf’s Birth*

<table>
<thead>
<tr>
<th>28-Day Block</th>
<th>Dates of Data Collection</th>
<th>14-Day Block</th>
<th>Relation to Birth</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>11/14/13-11/27/113</td>
<td>1</td>
<td>Two months pre</td>
</tr>
<tr>
<td></td>
<td>11/28/13-12/11/13</td>
<td>2</td>
<td>Six weeks pre</td>
</tr>
<tr>
<td>2</td>
<td>12/12/13-12/25/13</td>
<td>3</td>
<td>One month pre</td>
</tr>
<tr>
<td></td>
<td>12/26/13-1/8/14</td>
<td>4</td>
<td>Two weeks pre</td>
</tr>
<tr>
<td>3</td>
<td>1/9/14-1/22/14</td>
<td>5</td>
<td>Two weeks post</td>
</tr>
<tr>
<td></td>
<td>1/23/14-2/5/14</td>
<td>6</td>
<td>One month post</td>
</tr>
<tr>
<td>4</td>
<td>2/6/14-2/19/14</td>
<td>7</td>
<td>Six weeks post</td>
</tr>
<tr>
<td></td>
<td>2/20/14-3/5/14</td>
<td>8</td>
<td>Two months post</td>
</tr>
</tbody>
</table>
In August of 2014, the signature whistle of each group member (excluding Ping) was recorded. To collect the signature whistles, all members of the population were simultaneously stationed poolside with heads above water. Animals were each asked to swim to a trainer at the opposite end of the pool, where a hydrophone was located. Once the dolphin swam to the trainer, she was given a discriminative stimulus (SD) cuing her signature whistle. This process limited additional sound production by other group members and increased the likelihood that the focal animal was producing the whistles recorded. Video and hydrophone recordings were collected using the same devices used in data recording for the study. Spectrograms of whistles produced from these recordings were used to create the adults’ signature whistle categories used for contour matching. Window settings for these spectrograms were replicated in the adult whistle analysis.

It should be noted that the signature whistle for one adult female (Ping) was not recorded in August of 2014. At this time, Ping was unfamiliar with the signature whistle SD. Therefore, her signature whistle was not directly featured in analyses. It is likely that Ping’s whistle appeared in the data set as an additional whistle type (e.g., whistle A; see limitations), but a link between any additional whistle types could not be associated with Ping.

Calf Whistle Analysis

During a calf’s early life, adult and calf whistles can be identified individually based on their acoustic characteristics (i.e., the calf’s vocalization will be less frequently modulated and also contain some pulse sounds much of the time) (Caldwell & Caldwell, 1979; Caldwell, Caldwell, & Tyack, 1990; Fripp & Tyack, 2008; Gnone et al., 1996; Killebrew, Mercado, Herman, & Pack, 2001). Because calf whistles eventually lose their
tremulous quality, it can later be difficult to distinguish calf from adult whistles. Adults may also produce whistles that contain calf-like qualities, as was observed in the data collected prior to the calf’s birth. Therefore, only whistles corresponding with a bubble stream produced by the calf were considered a calf whistle (see limitations regarding this methodology). A total of 350 calf whistles were identified. Parameters, including beginning frequency, end frequency, minimum frequency, maximum frequency, frequency range, duration, and number of inflection points (Azevedo, Oliveira, Dalla Rosa, & Lailson-Brito, 2007) (see Table 2 for parameter definitions) were extracted from each whistle using Raven Pro 1.5 (Cornell University) (see adult whistle analysis for settings). These parameters were then compared to the same parameters extracted from adult signature whistles for calf whistle classification.

Table 2

Definitions of Whistle Parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beginning Frequency</td>
<td>Frequency at which whistle begins</td>
</tr>
<tr>
<td>End Frequency</td>
<td>Frequency at which whistle ends</td>
</tr>
<tr>
<td>Maximum Frequency</td>
<td>The highest frequency of the whistle</td>
</tr>
<tr>
<td>Minimum Frequency</td>
<td>The lowest frequency of the whistle</td>
</tr>
<tr>
<td>Frequency Range</td>
<td>The difference between the minimum and maximum frequency</td>
</tr>
<tr>
<td>Duration</td>
<td>The length of the whistle in seconds from the initial to final frequency</td>
</tr>
<tr>
<td>Inflection Points</td>
<td>A point in the whistle at which the contour changes direction (e.g., ascending to descending)</td>
</tr>
</tbody>
</table>
Adult Whistle Analysis

Signature whistles were categorized based on the whistles collected in August of 2014. All whistles were identified using Raven Pro 1.5, with a Hann window size of 512 (512 DFT); with 50% overlap and 256 hop size. Whistles were coded per minute, per video, per day of data collection. Continuous and non-continuous multi-looped whistles were counted as a single signature whistle emission (Caldwell et al., 1990; Tyack, 1997). Whistles not matching a signature category, and that were also not positively identified as a calf whistle, were classified as “other”, or as whistle A or whistle B, two prominent whistle types within the data set (see Figure 2 for representations of whistle categories). Whistle types A and B were considered adult whistles because of their presence pre-partum and lack of tremulous qualities associated with calf whistles. “Other” whistle types included variant whistles and whistles that could not confidently be categorized as a signature pre-partum. Post-partum, the “other” classification also included whistles that may have been produced by the calf, but were not visually associated with a bubble stream.

For signature whistle analysis, whistle groups were divided by min per two-week block of time. Whistle types “other” (pre-partum), A and B were divided by adult dolphin, per minute, per two-week block. The calf was accounted for in “other” (post-partum) per dolphin-minute-block rates. In order to reduce potential biases in whistle categorization, 20% of the data set was used to measure inter-rater reliability. Two hours of data were chosen at random from each block of time for raters to score. Raters were considered reliable if they met an 80% agreement criterion. Raters had a 98% agreement on signature whistle categorization, 92% agreement in “other” whistle types pre-partum,
and 90% agreement in “other” whistle types post-partum. With calf whistles, raters met criterion at 84%. A discriminate analysis of adult signature whistle parameters (Table 2) was used as a measure of correct group classification in addition to inter-rater reliability. This allowed for a quantitative evaluation of visually matched whistles. 78% of the original whistle classifications were grouped correctly. The remaining 22% may possibly account for outliers or contour variations that resulted in misclassification.
Figure 2. Spectrograms of adult whistle contours used for classification; representations of (a) Bella’s signature whistle, (b) Chelsea’s signature whistle, (c) Jasmine’s signature whistle, (d) Mattie’s signature whistle, (e) Yoshe’s signature whistle, (f) whistle A, and (g) whistle B. The Y-axis in each image was cropped at 20 kHz.
CHAPTER III

RESULTS

Adult Whistle Production

Bella’s signature whistle was emitted 1,839 times over the course of the study. This accounted for 64% of the signature whistles produced by the five adult females analyzed (Table 3). One-way ANOVAs were run to determine significance in signature whistle production between dolphins ($F (4, 910) = 81.16, p < .001$). Games-Howell post hoc tests revealed that Bella’s signature whistle ($M = 0.37, SD = 0.44$) was used significantly more than other adult females in the group ($p < .001$). Jasmine ($M = 0.03, SD = 0.06$) and Yoshe ($M = 0.02, SD = 0.05$) produced whistle rates that were significantly different from Bella, Chelsea, and Mattie ($p < .05$), but not significantly different from each other ($p = .065$). Similarly, Chelsea ($M = 0.09, SD = 0.13$) and Mattie ($M = 0.06, SD = 0.11$) produced rates that significantly differed from Bella, Jasmine and Yoshe ($p < .05$), but not from each other ($p = .318$).

Table 3

Identified Signature Whistle Totals and Percentage of Appearance

<table>
<thead>
<tr>
<th>Dolphin</th>
<th>Total</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bella</td>
<td>1,839</td>
<td>64%</td>
</tr>
<tr>
<td>Jasmine</td>
<td>181</td>
<td>6%</td>
</tr>
<tr>
<td>Chelsea</td>
<td>433</td>
<td>15%</td>
</tr>
<tr>
<td>Yoshe</td>
<td>100</td>
<td>4%</td>
</tr>
<tr>
<td>Mattie</td>
<td>304</td>
<td>11%</td>
</tr>
<tr>
<td>Total</td>
<td>2,857</td>
<td></td>
</tr>
</tbody>
</table>

One-way ANOVAs with Games-Howell post hoc tests were also run to compare each dolphin’s signature whistle use over time. Results of Bella’s signature whistle
production rates ($F(7, 175) = 51.33, p < .001$) showed the largest increase during block 3 ($M = 1.23, SD = 0.41, p < .001$). Block 1 ($M = 0.12, SD = 0.18$) showed no significant differences between block 4 ($M = 0.05, SD = 0.10$), and blocks 7 ($M = 0.18, SD = 0.12$) and 8 ($M = 0.12, SD = 0.09$) ($p > .05$). The most dramatic decrease in Bella’s signature whistle use occurred between block 3 and block 4 ($p < .001$). After the calf’s birth, Bella’s signature whistle production began to rise again during block 5 ($M = 0.50, SD = 0.44$) showing a significant increase from block 4 ($p = .002$). Rates did begin to slowly decrease after the calf’s first two weeks of life, however, there was no significant difference between blocks 5 and 6 ($M = 0.31, SD = 0.19, p = .588$). Bella’s signature whistle emission decreased significantly from block 5 to blocks 7 and 8 ($p < .05$). At the end of the calf’s second month of life (block 8), Bella’s signature whistle production had returned to levels similar to what was exhibited two months prior to the calf’s birth (block 1). Bella’s whistle means per minute of each day during block 4 were also compared (see adult whistle production). There was no significant change across individual days in block 4 according to Games-Howell post hoc tests ($p > .05$) (Figure 3).

Additional one-way ANOVAs were used to examine the non-maternal signature whistle rates produced by the other group members. Games-Howell tests of Jasmine’s signature whistle ($F(7, 175) = 8.58, p < .001$) exhibited a significant rise in signature whistle emission between blocks 1 ($M = 0.002, SD = 0.01$), 7 ($M = 0.05, SD = 0.07$), and 8 ($M = 0.11, SD = 0.10$) ($p < .05$). Chelsea’s signature whistle rates ($F(7, 175) = 11.22, p < .001$) also showed a significant increase between block 1 ($M = 0.01, SD = 0.03$) and blocks 7 ($M = 0.18, SD = 0.15$) and 8 ($M = 0.18, SD = 0.11$) ($p < .001$). Yoshe’s signature
Figure 3. Bella’s daily signature whistle rate during block 4. Mean rate was calculated per minute-day.

whistle \( (F(7, 175) = 11.64, p < .001) \) exhibited a significant increase, but only during the last two weeks of the calf’s second month of life (block 8) \((M = 0.09, SD = 0.09, p < .05)\).

Mattie’s signature whistle production \( (F(7, 175) = 11.03, p < .001) \) showed significant increases in emission during blocks 6 \((M = 0.10, SD = 0.11)\), 7 \((M = 0.18, SD = 0.17)\), and 8 \((M = 0.12, SD = 0.14)\) when compared to blocks 1 \((M = 0.01, SD = 0.02)\), 2 \((M = 0.01, SD = 0.03)\), and 3 \((M = 0.01, SD = 0.02)\) \((p < .05)\). See Figures 4.1-4.6 for line graphs of the signature whistle trends described.
Figure 4.1. Bella’s signature whistle rate across two-week blocks of time. Mean rates were calculated per minute-block.

Figure 4.2. Jasmine’s signature whistle rate across two-week blocks of time. Mean rates were calculated per minute-block.
Figure 4.3. Chelsea’s signature whistle across two-week blocks of time. Mean rates were calculated per minute-block.

Figure 4.4. Yoshe’s signature whistle across two-week blocks of time. Mean rates were calculated per minute-block.
Figure 4.5. Mattie’s signature whistle across two-week blocks of time. Mean rates were calculated per minute-block.

Figure 4.6. Comparison of all rates.

One-way ANOVAs and Games-Howell post hoc tests for whistle A ($F(7, 175) = 71.2, p < .001$) and “other” whistles ($F(7, 175) = 58.12, p < .001$) also expressed lower rates for both categories pre-partum. Whistle A emission rose significantly between blocks 4 ($M = 0.004, SD = 0.01$) and 5 ($M = 0.10, SD = 0.08$) ($p < .001$). The greatest
increase in whistle A production occurred during block 6 ($M = 0.22, SD = 0.07, p < .001$), followed by a significant decrease in block 7 ($M = 0.03, SD = 0.02, p < .001$), and increase during block 8 ($M = 0.11, SD = 0.06, p < .001$). “Other” whistle rates ($F(7, 175) = 58.12, p < .001$) began to rise after the birth of the calf, with a significant increase occurring between blocks 4 ($M = 0.19, SD = 0.12$) and 5 ($M = 0.42, SD = 0.17$) ($p < .001$), and blocks 5 and 8 ($M = 0.86, SD = 0.27$) ($p < .001$). Signature whistle rates of additional group members were less common in the data set than “other” whistles (Figure 5). Whistle B ($F(7, 175) = 7.68, p < .001$) was emitted significantly more in block 8 ($M = 0.86, SD = 0.27$) ($p < .001$) than time block 1 ($M = 0.12, SD = 0.16$) (see Figures 6.1-6.3 for whistle A, whistle B, and “other” trends).

Figure 5. “Other” whistle type in comparison to remaining predominant whistle categories.
Figure 6.1. Whistle A across two-week blocks of time. Mean rates were calculated per minute-dolphin-block.

Figure 6.2. Whistle B across two-week blocks of time. Mean rates were calculated per minute-dolphin-block.
Figure 6.3. “Other” whistles across two-week blocks of time. Mean rates were calculated per minute-dolphin-block. Post-partum dolphin count includes the addition of the calf.

Calf Whistle Classification

A discriminate analysis was used to predict the classification for each calf whistle. A model was derived from classification coefficients produced in SPSS version 21 from parameters extracted from each adult signature whistle as well as parameters from each calf whistle sampled. The model included nine possible groups: five groups corresponding with each adult group and four groups corresponding with each block during which the calf could have produced a whistle (i.e., blocks 5, 6, 7, 8). Parameters for each classification group were quantitatively different (see Table 4 for the parameter means of each group). Classification coefficients from the discriminate analysis were then used to create a prediction model in Microsoft Excel. Each calf whistle was tested for group prediction against this model. Table 5 shows the distribution of groupings and proportion of whistle types for calf whistles across the blocks 5-8.
Table 4

Parameter Means of Whistle Groups Used to Create the Discriminate Analysis Model for Calf Whistle Classification

<table>
<thead>
<tr>
<th>Whistle Type</th>
<th>Begin (kHz)</th>
<th>End (kHz)</th>
<th>Min (kHz)</th>
<th>Max (kHz)</th>
<th>Range (kHz)</th>
<th>Duration (s)</th>
<th>Inflection Points</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bella</td>
<td>5.30</td>
<td>14.44</td>
<td>5.13</td>
<td>14.44</td>
<td>9.31</td>
<td>0.47</td>
<td>1.40</td>
</tr>
<tr>
<td>Jasmine</td>
<td>4.87</td>
<td>14.30</td>
<td>4.86</td>
<td>14.30</td>
<td>9.49</td>
<td>0.20</td>
<td>0.19</td>
</tr>
<tr>
<td>Chelsea</td>
<td>5.87</td>
<td>13.64</td>
<td>5.50</td>
<td>13.65</td>
<td>8.15</td>
<td>0.35</td>
<td>1.05</td>
</tr>
<tr>
<td>Yoshe</td>
<td>6.35</td>
<td>5.71</td>
<td>5.01</td>
<td>9.84</td>
<td>4.84</td>
<td>0.46</td>
<td>1.74</td>
</tr>
<tr>
<td>Mattie</td>
<td>7.04</td>
<td>10.98</td>
<td>6.26</td>
<td>11.04</td>
<td>4.78</td>
<td>0.19</td>
<td>0.81</td>
</tr>
<tr>
<td>Whistle 5</td>
<td>4.65</td>
<td>8.50</td>
<td>4.19</td>
<td>9.09</td>
<td>4.90</td>
<td>0.54</td>
<td>2.57</td>
</tr>
<tr>
<td>Whistle 6</td>
<td>5.30</td>
<td>9.02</td>
<td>4.78</td>
<td>9.52</td>
<td>4.79</td>
<td>0.42</td>
<td>1.58</td>
</tr>
<tr>
<td>Whistle 7</td>
<td>6.21</td>
<td>9.21</td>
<td>5.90</td>
<td>9.29</td>
<td>4.16</td>
<td>0.47</td>
<td>0.80</td>
</tr>
<tr>
<td>Whistle 8</td>
<td>7.05</td>
<td>10.40</td>
<td>6.58</td>
<td>10.65</td>
<td>4.20</td>
<td>0.36</td>
<td>1.16</td>
</tr>
</tbody>
</table>

Table 5

Whistle Type, Totals, and Proportions of Calf’s Repertoire

<table>
<thead>
<tr>
<th>Whistle Type</th>
<th>Block 5 Prop*</th>
<th>Block 6 Prop</th>
<th>Block 7 Prop</th>
<th>Block 8 Prop</th>
<th>Total Prop</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whistle 5</td>
<td>0.54</td>
<td>0.24</td>
<td>0.20</td>
<td>0.09</td>
<td>0.33</td>
</tr>
<tr>
<td>Whistle 6</td>
<td>0.22</td>
<td>0.42</td>
<td>0.20</td>
<td>0.16</td>
<td>0.28</td>
</tr>
<tr>
<td>Whistle 7</td>
<td>0.01</td>
<td>0.00</td>
<td>0.10</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Whistle 8</td>
<td>0.04</td>
<td>0.09</td>
<td>0.50</td>
<td>0.30</td>
<td>0.12</td>
</tr>
<tr>
<td>Chelsea</td>
<td>0.01</td>
<td>0.01</td>
<td>0.00</td>
<td>0.06</td>
<td>0.02</td>
</tr>
<tr>
<td>Mattie</td>
<td>0.06</td>
<td>0.14</td>
<td>0.00</td>
<td>0.33</td>
<td>0.14</td>
</tr>
<tr>
<td>Yoshe</td>
<td>0.07</td>
<td>0.05</td>
<td>0.00</td>
<td>0.00</td>
<td>0.05</td>
</tr>
<tr>
<td>Bella</td>
<td>0.05</td>
<td>0.03</td>
<td>0.00</td>
<td>0.01</td>
<td>0.03</td>
</tr>
<tr>
<td>Jasmine</td>
<td>0.01</td>
<td>0.03</td>
<td>0.00</td>
<td>0.03</td>
<td>0.02</td>
</tr>
<tr>
<td>Total:</td>
<td>0.41</td>
<td>0.38</td>
<td>0.03</td>
<td>0.19</td>
<td></td>
</tr>
</tbody>
</table>

*Proportion of whistle in each block of time.

Progression in calf whistle development was evident in some whistle types more than others. For example, adult signature type contours produced by the calf began to resemble the contours of the adult signature whistles. Figures 7.1-7.9 are spectrograms of
whistle types produced by the calf over time, as well as comparisons of calf whistles classified as adult contours.

\textit{Figure 7.1}. Spectrograms of whistle 5 in blocks 5-8. The Y-axis in each image was cropped at 14 kHz. Whistle images were taken from the first or only whistle available in each block.

\textit{Figure 7.2}. Spectrograms of whistle 6 in blocks 5-8. The Y-axis in each image was cropped at 14 kHz. Whistle images were taken from the first or only whistle available in each block.
Figure 7.3. Spectrograms of whistle 7 in blocks 5, 7, and 8 (note that these are the only emissions of whistle 7). The Y-axis in each image was cropped at 14 kHz.

Figure 7.4. Spectrograms of whistle 8 in blocks 5-8. The Y-axis in each image was cropped at 14 kHz. Whistle images were taken from the first or only whistle available in each block.
Figure 7.5. To the left, calf whistles classified as Chelsea’s signature whistle type from blocks 5, 6, and 8 (note that no calf whistles were classified as an adult type in block 7). To the right, are two single loops of Chelsea’s signature whistle.

Figure 7.6. To the left, calf whistles classified as Yoshe’s signature whistle type from blocks 5 and 6 (note that no calf whistles were classified as Yoshe’s type during blocks 7 and 8). To the right, is one multi-looped representation of Yoshe’s signature whistle.
**Figure 7.7.** To the left, calf whistles classified as Bella’s signature whistle type from blocks 5, 6, and 8. To the right, two multi-looped representations of Bella’s signature whistle.

**Figure 7.8.** To the left, calf whistles classified as Mattie’s signature whistle type from blocks 5, 6, and 8. To the right, two multi-looped representations of Mattie’s signature whistle.
Figure 7.9. To the left, calf whistles classified as Jasmine’s signature whistle type from blocks 5, 6, and 8. To the right, one multi-looped representations of Jasmine’s signature whistle.
CHAPTER IV

DISCUSSION

Adult Whistle Production

As anticipated, Bella’s signature whistle rates showed significant trends during the course of the study. Rates significantly increased prior to Mira’s birth, with the most prominent increase in production occurring one month prior to the end of the gestation period. There was a significant decrease in Bella’s stereotyped whistle two weeks prior to the birth of the calf for reasons unknown. Mello and Amundin (2005) reported significant increases in daily rates in the days prior to the births of the calves in their study, with the most significant increases occurring several days prior to parturition. Bella’s rates showed no significant trend in that time frame when daily rates were examined.

Within the first two weeks of the calf’s life, Bella’s signature whistle production significantly rose again. This was anticipated based on findings from Fripp and Tyack (2008), which established that the highest rates for signature whistle production in their study occurred during the first two weeks following parturition. Bella’s stereotyped whistle was not produced more in the two weeks post-partum than during the one-month prior, however. Individual differences in mothers’ whistle production may explain the inconsistencies between the current study and the literature. Mello and Amundin (2005) found significant increases in dolphin signature whistle production prior to the birth of calves in their study. However, in a study conducted at the same facility (Kolmården Djurpark in Kolmården, Sweden), Fripp and Tyack (2008) reported no significant increase in whistle rates produced during their “pre-birth” condition. Two of three
subjects in the Mello and Amundin (2005) study were not subjects studied by Fripp and Tyack (2008), but it is unknown to the author whether the third subject was.

One study does include a brief discussion of additional group members’ signature whistle rates pre- and post-partum (Fripp & Tyack, 2008). Signature whistles of the other adult females followed a dissimilar trend when compared to Bella’s signature rate. Two of the females (Jasmine and Chelsea) began to increase production during the first two weeks of the calf’s life. The remaining two females (Yoshe and Mattie) did not show significant increases until after these two weeks. These findings are consistent with Fripp and Tyack (2008) that also showed no significant increases in non-maternal signature whistles from the “pre-birth” period to the first week of life.

Imprinting

Bottlenose dolphin mothers may not tolerate their calf’s separation from the dyad until sometime during its second week (Fripp & Tyack, 2008; Mann & Smuts, 1998; Sayigh, 1992). These social separations may not be tolerated until a recognition system for the dyad is in place. It is likely that signature whistle production exists as a part of the imprinting process through which calves establish recognition of their mothers (Fripp & Tyack, 2008; Gnone & Moriconi, 2010; Herman & Tavolga, 1980; Mann & Smuts, 1998; Mello & Amundin, 2005). After an early recognition system has been solidified, the mother may continue whistling at high rates to reinforce the learning process (Fripp & Tyack, 2008).

This hypothesis is corroborated by the increase in other animals’ whistles after the calf’s first two weeks of life. Bella’s signature whistle production did decrease between the calf’s first and second two weeks of life, while other animals’ rates increased. This
may suggest that other animals produce their signature whistles at lower rates so that the calves’ exposure to the mothers’ signature whistle is not masked. However, there may be alternative explanations as to why additional group members produce rates less abundantly pre- and post-partum (see vocal learning hypothesis).

From birth through the first month of life, dolphin calves have a strong tendency to follow accelerating objects (Connor, Wells, Mann, & Read, 2000; Mann & Smuts, 1998), which may result in the calf’s swimming away with other group members (Kuczaj & Winship, 2015; Mann & Smuts, 1998; Tavolga & Essapian, 1957). Mother dolphins may repeat their signature whistles to identify which dolphin the calf should follow or to alert the calf of its separation from the dyad. In order for the calf to readily identify the mother’s signature whistle, some exposure would need to occur in utero (Kuczaj & Winship, 2015; Mann & Smuts, 1998; Mello & Amundin, 2005). Thus, when the calf is born, it has already been exposed to the sound it needs to follow. Superb fairy-wren (Malurus cyaneus) embryos are taught vocal passwords during their incubation period, so that parents avoid the risk of brood parasitism (Colombelli-Ne´grel et al., 2012). Fairy-wren eggs will hatch, and chicks must produce a call similar to that of their mothers in order to receive resources. Fairy-wren females produce higher incubation call rates in the presence of Horsfield bonze cuckoo (Chalcites basalis) songs near their nests (Kleindorfer, Evans, & Colombelli-Ne´grel, 2015), which may override embryo exposure to irrelevant sounds and minimize a female’s perceived risk of brood parasitism. Likewise, bottlenose dolphin mothers may increase signature whistle use pre-partum if high amounts of additional sound are present in the acoustic environment. However, in the case of fairy-wrens, females produce a call that is to be repeated by chicks so that
they can be recognized. This does not seem to be the case with bottlenose dolphins, as many calves do not produce whistles that are similar to their mothers’ (Bojanowski, Veit, & Todt, 2000; Fripp et al., 2005; McCowan & Reiss, 1995b; Sayigh et al., 1990; Sayigh et al., 1995), nor are calves known to produce a signature whistle at birth (Caldwell & Caldwell, 1979; Fripp et al., 2005; Sayigh, 1992; Tyack & Sayigh, 1997). So while high signature whistle rates pre-partum may assist in an early recognition system in the dolphin calf, the system appears to support calf recognition of the mother’s call and not the opposite.

Alternative Hypotheses

Mello and Amundin (2005) suggested that mothers may increase their whistle rates due to restlessness prior to birth and during labor. If this is the case, then it should be expected that a mother’s signature whistle show little increase once her pregnancy has subsided. In the current study, block 3 (pre-partum) and block 5 (post-partum) were the most significant increases recorded, and were not significantly different from each other. If restlessness is a viable explanation, then Bella’s restlessness before birth must have been present after birth as well, or the two increases are unrelated. While it is possible that reasons for increases pre- and post-partum exist exclusively, in this scenario it seems highly unlikely.

Esch, Sayigh, Blum, and Wells (2009) reported that high signature whistle rates may be indicative of stress in bottlenose dolphins. Cortisol increases during gestation, peaking near delivery (Tizzi, Accorsi, & Azzali, 2010). If signature whistles are an additional stress response, then it is reasonable to predict that stress is the source of increased rates. Again, it would be necessary to provide evidence that Bella was stressed...
after birth. In light of the new calf, a primiparous mother may be stressed after delivery. But this would not explain increased rates following parturition in a multiparous mother (Gnone & Moriconi, 2010). Furthermore, the sudden decrease in Bella’s whistle rates following period three provides evidence against these hypotheses as any relative stress or restlessness should peak close to birth.

The sudden drop off in Bella’s production two weeks prior to Mira’s birth (block 4) is extremely puzzling, as it almost defies each hypothesis addressed throughout this study. For example, if the mother’s signature whistle is associated with in utero learning, then it should be expected to remain at elevated rates in the days before labor. This does not necessarily discount the imprinting hypothesis altogether, but the argument for in utero learning is weakened. Again, individual differences in dolphins may explain why Mello and Amundin (2005) saw increased rates during the same time frame. However, if the dolphins studied by Fripp and Tyack (2008) showed similar behavior to Bella, this may explain why the authors did not find increased rates pre-partum.

Studies have shown that animals alter sound production when group consistency changes (Jones & Sayigh, 2002; Quick & Janik, 2008), or when sound becomes overabundant to prevent the sound environment from becoming polluted with noise (Quick & Janik, 2008). If the other group members’ decreased signature whistle production was due to noise avoidance, it could explain the other dolphins’ increase in signature whistles in blocks 5 and 6. It should be expected then, that the other dolphins’ production would have increased when Bella also decreased whistle production during block 4. Because this increase did not exist, noise pollution may not be a reasonable explanation for the decreased signature rates of the other animals. It should be noted that
other vocalization types present in the sound environment (e.g., pulsed sounds) were not analyzed in this study, so while other dolphin’s signature rates were lower, there could have been an abundance of additional vocalizations further indicating that noise pollution was not a concern for this group. In fact, miscellaneous whistles categorized as “other” rose through the course of the study, even after the calf’s addition to the group was accounted for.

Vocal Learning

In order to investigate the role that whistle rates played in the calf’s developing repertoire, it was necessary to explore the calf’s production of whistle types. Whistles classified as Mattie’s were the most common among the adult whistle types present in the calf’s repertoire. However, Bella’s signature was not a model for a commonly produced calf whistle.

A favored whistle type would have been apparent if one whistle group was produced consistently at a high proportion in each block of time. No such trend occurred after each calf whistle was classified. Whistles 5 and 6 were the most produced groups out of the calf’s total whistles, but this was relative to the blocks of time they were produced in. Whistle 5 dominated production in block 5, which also happened to be the two-week period from which the most whistles were sampled. Likewise, whistle 6 was the most common whistle in block 6, which happened to be the two-week period during which the second most whistles were sampled. The use of whistle 5 and whistle 6 became less common as the calf got older, indicating that these whistle types did not remain popular. Inversely, whistle 8 increased in its proportion of use through the four two-week periods, as it was most common in blocks 7 and 8. Given these findings, there may be
some indication that the whistle types pertaining to each two-week block were a function of the calf’s development during that time.

Madsen, Jensen, Carder, and Ridgway (2012) found that whistle production was a function of a vibrating source within dolphins (i.e., the phonic lips), similar to mammalian vocal cords. It is possible that in young calves, phonic lip development affects the production of certain whistles in the calf’s repertoire. Phonic lips are supported by ligaments and connective tissue (Madsen et al., 2012), which may be underdeveloped in calves (Killebrew et al., 2001). Morisaka et al. (2005a) reported that a calf began producing whistle parameters at higher frequencies, but that a gradual shift occurred over time as the calf lowered the parameter frequencies it was using. This may signify continued development that produces natural changes in dolphin vocal structures as they mature.

It is difficult to determine from the first two months of Mira’s life whether she would have eliminated some whistles from her repertoire, incorporated new sounds, or produced whistles already available at higher rates as she developed. It is also difficult to discern what the function may have been of some of these whistle types. For example, the calf may have mimicked whistles for the purposes of addressing the adult females (Gish, 1979; Janik, 2000; King & Janik, 2013; King et al., 2013; Tyack, 1986), or she may have spontaneously produced these sounds (Reiss & McCowan, 1993). It is also possible that calves play with sounds as a way to acquire and develop their repertoire (Kuczaj & Makecha, 2008). Apart from Yoshe’s whistle type, the calf produced adult signature types through her first two months, suggesting that these whistles were at least a small part of Mira’s repertoire. Limited exposure to these whistles may have provided the calf
with sounds to explore, diversifying her repertoire (Kuczaj, 2014; Kuczaj & Winship, 2015). It is interesting that the calf did not repeat a whistle matching Yoshe’s signature during the second month of life, as the calf was not physically introduced to Yoshe in the first two months. The lack of Yoshe’s physical presence and the low rates of her signature whistle production would seem to make her signature an ideal model for the calf according to some studies (Bojanowski et al., 2000; Fripp et al., 2005). This may provide evidence that dolphin calves more consistently replicate whistles of animals they are in physical contact with. Whether Yoshe’s signature whistle type reappeared in the calf’s repertoire later on is unknown.

There may be a more parsimonious explanation as to why Mira did not mimic Bella’s signature whistle more during the study. Tchernichovski, Mitra, Lints, and Nottebohm (2001) reported on what they called the “too much factor”, by which zebra finch (Taeniopygia guttata) males produce songs less similar to songs that are overabundant in the sound environment. The authors speculated that wild zebra finch males may use a portion of the overabundant song, but would incorporate more components of less abundant songs, creating their own individually distinct sound. If a similar phenomenon occurs in dolphin calves, then Bella’s overproduction of signature whistles may serve as a model for a sound the calf should not use as her own distinctive whistle. The rates of the additional adult females in this study also support this hypothesis. Additional signature whistles may have been produced at lower rates for much of the study as less abundant models, giving the calf some direction towards sounds that were dissimilar to her mother’s whistle. Signature whistles of other group members
may have also been produced at low levels to ensure that a specific whistle type was not produced more than Bella’s, thereby becoming the overexpressed sound.

Evidence indicates that calves create their signature whistles based on models not often present in the sound environment (Bojanowski et al., 2000; Fripp et al., 2005; Tyack & Sayigh, 1997). Fripp et al. (2005) found that dolphin calves simulate signature whistles of animals not often affiliated with the mother-calf dyad. The authors also reported that calves do not build their whistles from random sounds they emit, and they do not anti-model, or create sounds that are the opposite of what they hear. Ultimately, a dolphin calf may replicate a sound that it hears less often in the sound environment for signature whistle use, but the calf’s repertoire may still incorporate common occurring sounds to some degree.

It does not appear that Bella’s high whistle rates influenced an early appearance of Mira’s favored whistle type, as one was not found in the calf’s first two months. It has been suggested that signature whistles may not appear in a calf’s repertoire until the calf begins to become more independent from the dyad (Sayigh et al., 1990). At two months, Mira may not have experienced the type of distance from the dyad this process may require. Furthermore, there may exist more pressure on female calves when forming an individual whistle, requiring more time in selecting the appropriate sound (Sayigh et al., 1990; Sayigh et al., 1995).

Calves have a propensity for vocal learning as they can easily incorporate sounds into their repertoire after brief exposure (Bojanowski et al., 2000; Fripp et al., 2005; Sayigh et al., 1990; Sayigh et al., 1995; Tyack & Sayigh, 1997), as was the case in the current study. The calf repeated whistles that were not as common in the sound
environment as Bella’s whistle, and did not simulate Bella’s whistle as often as other signatures. The incorporation of the adult signature types into the calf’s repertoire may have allowed the calf to attend to any consistencies in the sounds that may reflect a group component. Thus when a calf encounters a unique sound that may meet group requirements, the calf may select this sound as its signature choice.

Limitations

The bubble stream method, a conservative technique used to localize dolphins that may be vocalizing, has been consistently viewed through a lens of controversy (see Fripp, 2005, 2006; McCowan, 2006). Vocalizations produced simultaneously with bubble streams are not representative of an adult dolphin’s vocal repertoire and may only be contextually dependent in use (Fripp, 2005). One study that used bubble streams as a system for identifying signature whistles in adult dolphins found that dolphins share a predominant whistle type across social groups, discounting the signature whistle hypothesis (McCowan & Reiss, 2001). Findings from studies that have relied on bubble stream methodology have been scrutinized (McCowan & Reiss, 1995a, 1995b, 2001). However, bottlenose dolphin calves purportedly produce vocalizations with associated bubble streams in much of early life (Gnone et al., 1996; McBride & Kritzler, 1951, McCowan & Reiss, 1995b). Many studies that have investigated the ontogeny of calf vocal development have employed this method in some way when identifying calf sounds (Bojanowski et al., 2000; Bowles, Grebner, Musser, Nash, & Crance, 2015; Favaro, Gnone, & Pessani, 2013; Fripp & Tyack, 2008; Gnone & Moriconi, 2010; Hooper, Reiss, Carter, & McCowan, 2006; Killebrew et al., 2001; McBride & Kritzler, 1951; McCowan & Reiss, 1995b; Mello & Amundin, 2005; Miksis et al., 2002; Morisaka et al., 2005a,
2005b; Reiss, 1988). Despite this understanding, whistles identified as Mira’s may not have been representative of her full vocal repertoire. For example, calf whistles in which the calf was not on camera could not be included in the analysis because any corresponding bubble stream would have been occluded. Thus, the calf may have produced higher or lower proportions of certain whistle types during periods off camera that were not accounted for.

It has been noted that human judges may yield biased visual matches (see McCowan & Reiss, 2001). Again, many studies have used human judges in whistle matching tasks (Fripp & Tyack, 2008; Fripp et al., 2005; Janik, 1999; Janik & Slater, 1998; McCowan & Reiss, 2001; Mello & Amundin, 2005; Sayigh, Esch, Wells, & Janik, 2007; Tyack, 1986). Studies that have compared human judgment to quantitative analyses have found that human judges are superior to computerized methods of contour matching (Janik, 1999; Sayigh, Esch, Wells, & Janik, 2007). In the present study, human judges had 98% agreement on adult contour matches during inter-rater reliability. The discriminate analysis showed a 78% correct classification of adult whistles based on quantitative measures. But, because contours were matched visually, signature whistle imitations may have been included in the original whistler’s rate. However, if increases in Bella’s signature whistle were due to an influx of imitations produced by other animals in the habitat, this would be an entirely different phenomenon than what was anticipated in the current study.

The hydrophone malfunctioned during the day of and two days prior to the birth of the calf. Recordings from these days were unavailable as a result, and any analyses of this time period do not include these days. Any significant increase in Bella’s whistle
rates during the few days prior to delivery that may have been present was unaccounted for in the data set. This may explain why Mello and Amundin (2005) were able to report significant findings in the days prior to delivery, and the results of this study showed no such finding. However, Mello and Amundin (2005) showed increases in production rates beginning several days prior to birth. There were no significant changes between days in block 4, and no sign that an upward trend was beginning on the last day of data collection before the birth of the calf.

Ping’s whistle was the only signature excluded from the study. If her whistle did have some effect on the calf’s repertoire, it could not be indicated. Out of the two additional prominent whistle types in the data (whistle A and B), it may be possible that whistle A was Ping’s signature as whistle B may have been a commonly shared whistle type among the dolphins in this group. McCowan and Reiss (see Figures in 1995a, 1995b, 1997, 2001) discuss a whistle type of similar contour in social groups at Marine World/Africa USA (now Six Flags Discovery Kingdom). Subjects of the social groups reported in these studies included Chelsea and Jasmine, so it is possible that the same whistle type was still in use during the present study.

Finally, the discriminate analysis of the calf’s vocal repertoire included nine possible whistles. Subsequent classification was therefore limited to these nine whistles. Different classifications may have occurred if additional whistle types were included in the model (e.g., whistle A or B). Calf whistles were also classified by parameters, whereas adult whistles were categorized by contours before parameter extraction. It is possible that some calf whistles matching adult contours were included in different groups based on whistle parameters. Using human judges as classifiers for calf whistles
in early life is not a methodology that is featured in the literature however, and the author felt that the nature of this task would yield highly subjective results.

Conclusions

The high rates of the mother’s signature whistle use, coupled with the low rates of the signature whistles produced by other animals in the environment, would suggest that some learning process of the mother’s signature whistle takes place *in utero*. Once the calf is born, there may be a critical period during which the calf imprints on the mother’s whistle, and any subsequent exposure to the whistle may be due to reinforced learning. Thus, high rates of maternal signature whistle production pre- and post-partum take place as part of a learning process. This is supported by the decreased rates of additional dolphins in the environment, which limits the calf’s exposure and consequent recognition of other whistles. How the calf selected sounds as part of her repertoire was less clear, but her use of whistles similar to sounds present in the sound environment does support calves’ ability to vocally learn. It seems that calves will incorporate sounds they are exposed to, even briefly, into their repertoire during early life. Whether these sounds remain permanent in the repertoire is not clear, and future studies should investigate the stability of calf whistle repertoires over time. It may also be necessary to investigate whether the increased rates produced by dolphin mothers pre- and post-partum are related to the same phenomenon, or if there may be alternate explanations for the existence of both.

It is important to know the specifics of whistle production in a mother-calf dyad as this process may be crucial to the survival of the calf. In the wild, however, we sometimes cannot tell what is going on beneath the surface of the water. Studies that
allow for the intimate collection of data on mother-calf dyads in captivity can assist in illuminating some processes not easily studied in wild groups.
APPENDIX A

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER: 14050803
PROJECT TITLE: Observational Studies of Bottlenose Dolphins at Six Flags: Discovery Kingdom
PROJECT TYPE: New
PRINCIPAL INVESTIGATOR(S): Stan Kuczaj
DEPARTMENT: Psychology
FUNDING AGENCY/SPONSOR: Full Committee Approval
IACUC COMMITTEE ACTION: September 30, 2016
PROTOCOL EXPIRATION DATE: 5/12/2017

Frank Moore, Ph.D.
IACUC Chair

Date
REFERENCES


fairy-wrens reveals intruder cuckoo nestlings. *Current Biology*, 22(22), 2155-2160.


doi:10.1006/anbe.2000.1569


