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The Ontogeny of Whistle Production in Infant Atlantic Bottlenose Dolphins (*Tursiops truncatus*) During the First Thirty Days of Life

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The University of Southern Mississippi

THE ONTOGENY OF WHISTLE PRODUCTION IN INFANT ATLANTIC BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) DURING THE FIRST THIRTY DAYS OF LIFE

by

Brittany Leigh Jones

A Thesis
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of The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Master of Arts

Approved:

Dr. Stan Kuczaj____________________
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August 2014

ABSTRACT

THE ONTOGENY OF WHISTLE PRODUCTION IN INFANT ATLANTIC BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) DURING THE FIRST THIRTY DAYS OF LIFE

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The manner in which dolphin calves acquire their whistle repertoire is largely unknown. This paper focuses on whistle development in four bottlenose dolphin calves during the first thirty days of life in order to increase our understanding of the early emergence of whistles and whistle-like vocalizations. The acoustic parameters of whistle-type vocalizations (i.e., whistles and whistle-squawks) that coincided with a bubblestream emission from the focal calf and/or its mother were analyzed, as were the behavioral states of the mother-calf pair during the emission of such vocals. Mother and calf whistle rates are inversely related, with the mother whistling more often in the first ten days of the calf's life, and the calf whistling most often in the third ten days. Maternal whistles are most common when the calf and mother are less than one meter apart whereas the calf whistles are likely to occur when the calf is greater than one meter away from the mother. Only one of the four calves showed a generally stereotyped whistle contour in the first thirty days (day 27), a whistle that has the "tremulous and quavery" quality commonly attributed to young calf whistles (Caldwell & Caldwell, 1979). Whistle-squawks are much more common than adult-like, clear narrowband whistles throughout this developmental period. The maximum frequency, frequency range, and duration of calf whistles and whistle squawks increase with age, suggesting that the acoustic prowess of dolphin calves develops during the first month of life.

DEDICATION

I would like to dedicate my master's thesis to my beautiful niece Reese Olivia Kenney, in hopes that it will inspire her to always follow her dreams no matter how out of reach they may seem.

ACKNOWLEDGMENTS

I would like to express my utmost gratitude to my committee chair, Dr. Stan Kuczaj, for the opportunity to be involved in such an exciting project. It was through this project and Stan's guidance that I have found my passion for bioacoustics, and without his believing and trusting in me with this data set, this passion would never have been realized.

A special thank you must be extended to Dr. Holli Eskelinen for serving on my committee and more specifically for the countless time and effort she has spent as my mentor and friend. I would not be the person, researcher, or student I have become with out her motivation, encouragement, and guidance.

Thank you to Dr. Alen Hajnal for serving on my committee, for offering advice, and for always showing great enthusiasm throughout the duration of this project. I would also like to thank Dr. Christopher Baker for pushing me to follow my dreams and apply to graduate school.

I will forever be indebted to the members of the Marine Mammal Behavior and Cognition Laboratory for their constant support and encouragement in this endeavor. Specifically, Kelly Winship and Christina Perazio's tireless sessions of reliability coding and troubleshooting. I am even more appreciative of Kelley for her full-time job of keeping me relatively sane throughout this process!

Thank you to the staff at Dolphins Plus, Dolphin Cove, and Island Dolphin Care for allowing us access to their beautiful animals, and thanks also to their interns for their assistance in data collection.

Finally, I would like to extend an endless thank you to my family for their tireless support and enduring patience and love. I am extremely fortunate to have such a fantastic support system, and they are the inspiration and motivation behind every challenge I take on.

TABLE OF CONTENTS

CHAPTER

LIST OF TABLES

Table

LIST OF ILLUSTRATIONS

Figure

CHAPTER I

INTRODUCTION

Sound carries well underwater, and acoustic signals may be essential for bottlenose dolphin (*Tursiops truncatus*) communication and their ability to maintain contact in water with poor visibility (Caldwell, Caldwell, & Hall, 1973; Tyack, 1997). This unpredictable visual field may increase the amount dolphins rely on acoustic communication for relaying information about location and motivation to reunite (Janik & Slater, 1997; Smolker, Mann, & Smuts, 1993). Dolphin vocalizations include whistles, clicks, and burst pulses, each of which consists of more specific sound patterns (e.g., whistle-squawks) (e.g., Caldwell, Caldwell, & Tyack, 1990; Hill, 2002; Killebrew, Mercado, Herman, & Pack, 2001; McCowan & Reiss, 1995). However, little is known about what units are salient in dolphin communication systems (Kuczaj & Kirkpatrick, 1993). This paper focuses specifically on whistle-type vocalizations (i.e., signals that show frequency modulation when graphed over time; Dreher, 1961). Whistles are interesting because they have been hypothesized to express identification, location, and emotional state to conspecifics (e.g., Mello & Amundin, 2005; Tyack, 1986, 1993).

It has been commonly agreed upon that neonates produce whistles soon after birth but that such whistles are neither as complex nor as clear as most adult whistles (Caldwell & Caldwell, 1979; McBride & Kritzler, 1951). Caldwell and Caldwell (1979) described these unclear whistles from the underdeveloped whistle production system of a neonate (i.e., whistle-squawks) as similar to adult whistles heard during times of excitement. McCowan and Reiss (1995), Killebrew et al. (2001), and Caldwell and Caldwell (1979) all found an abundance of whistle-squawks and an absence of clear whistles in the first five days of life, which they suggested was evidence that neonates lack the muscle control and neuronal activation patterns governing muscle control to produce stereotyped whistles. Stereotyped whistles are whistle types that have consistent whistle parameters and a fixed contour (Caldwell & Caldwell, 1965; Caldwell et al.,1990). These types of whistles are often termed signature whistles and are thought to be individually unique to each animal. Caldwell and Caldwell (1979) reported that these stereotyped whistle contours are not fully developed until around three months of age. Originally, Sayigh (1992) suggested that this whistle crystallization (i.e., formation of a specific whistle contour) began after one month of age, but there seems to be large individual variability in whistle development as one calf produced its signature whistle as early as fourteen days old (Hill, 2002), but the full development of a stereotyped contour may extend into the second year of life (McCowan & Reiss, 1997).

A calf's vocal development may be critical for its survival. As calves mature, they become more likely to venture away from the mother's side, and the mother's ability to recognize her calf's calls may be essential for reunions between the two (Cook, Sayigh, Blum, & Wells, 2004; Mello & Amundin, 2005; Sayigh et al., 1999; Tyack & Sayigh, 1997;). Calf whistling may express their position to the mother and therefore facilitate their approach, or induce other responses from their mother based on emotion (e.g., fear, distress) expressed by the calf's whistle (Mello & Amundin, 2005; Smolker et al., 1993). Young animals of many species vocalize in response to separation or isolation (e.g., piglets [*Sus*]: Fraser, 1975; Weary & Fraser, 1995; guinea pigs [*Cavia porcellus*]: Monticelli, Tokumaru, & Ades, 2004; primates: Newman & Goedeking, 1992; Maestripieri & Call, 1996; Wiener, Bayart, Faull, & Levine, 1990; rodents [*Rodentia*]: Okon, 1971; cattle [*Bos primigenius*]: Marchant-Forde, Marchant-Forde, & Weary, 2002, bats [*Chiroptera*]: Moss, 1988; and bottlenose dolphins [*Tursiops truncatus*]: McCowan & Reiss, 1997).

Mann and Smuts (1999) reported maternal intolerance for separations during the first week of life. However, brief separations during the second week began generally increasing in duration and frequency as the calf matured (Mann & Watson-Capps, 2005). They hypothesized that dolphin calves imprint on their mothers during the first week of life and therefore mothers do not tolerate social separations until this process is complete. Imprinting, a form of learning during which infants of many species learn to recognize their mothers immediately after birth (Hess, 1959; Lorenz, 1937), is found in many species that are highly social and locomotive at birth, making dolphin calves a probable candidate for such early learning (Hess, 1959; Wells, 2003). Fripp and Tyack (2008) presented evidence of imprinting in bottlenose dolphins, as mothers whistled ten times as frequently immediately following the birth of their calf, and then decreased back to pre-birth whistle frequency by week three. This significant increase in whistle production likely enabled the calf to learn the identity of its mother, as the frequency of whistle production of non-mother females did not increase.

Vocal learning occurs when auditory input affects auditory output (Boughman & Moss, 2003; Hansen, 1979; Janik & Slater, 1997; McCowan & Reiss, 1997; Richards, Woltz, & Herman, 1984; Sewall, 2012; Tyack, 2008). This skill is relatively uncommon in the animal world and has only been found in some birds (*Aves*) (e.g., Kroodsma & Baylis, 1982), cetaceans (*Cetus*) (e.g., Janik & Slater, 1997; Tyack & Sayigh, 1997), seals (*Pinnipedia*) (e.g., Ralls, Fiorelli, & Gish, 1985), bats (e.g., Matsumura, 1979), elephants (*Elephantidae*) (e.g., Poole, Tyack, Stoeger-Horwath, & Watwood, 2005) and a few primate species (e.g., Campbell's mona monkey [*Cercopithecus campbelli*]*;* Lemasson, Hausberger, & Zuberbuhler, 2005). Bottlenose dolphins are adept at both social vocal learning and nonsocial vocal mimicry (Bain, 1986; Caldwell & Caldwell, 1972; Caldwell et al., 1990; Evans, 1967; Fripp et al., 2005; Janik & Slater, 1998; McCowan & Reiss, 1995, 1997; Miksis, Tyack, & Buck, 2002; Payne, Tyack, & Payne, 1983; Reiss & McCowan, 1993; Richards et al., 1984; Sayigh, 1992; Sigurdson, 1993; Tyack, 1986, 1993; Tyack & Sayigh 1997; Tyack & Whitehead, 1983). Janik and Slater (1997) proposed that vocal learning may have evolved as an adaptation for maintaining consistency in vocal output when communicating at various depths.

Not only do dolphin calves have a propensity for imitation, they also seem to be highly selective in what vocalizations they choose to imitate (Kuczaj, Yeater, & Highfill, 2012). Behavioral context, age, sex, relationship to the observer, novelty of the sound, and the calf's personality may affect whether or not a sound is imitated and whether mimicked sounds are admitted into a calf's vocal repertoire (Kuczaj et al., 2012; Sayigh, 1992). The best example of selective social learning in dolphin communication is found in the aforementioned theory of signature whistles (Kuczaj et al., 2012).

Kuczaj (1998) suggested that species that participate in vocal learning should be the most likely to engage in sound play. Play is generally considered a pleasurable activity that benefits well-being and development (Bekoff & Byers, 1981; Burghardt, 2005; Fagen, 1981; Kuczaj et al., 2006; Kuczaj & Makecha, 2008). Sound play seems to be a convergent learning strategy that facilitates the development of adult-like signals (Kuczaj, 1998) and has been found in a number of bird and mammal species (Doupe & Kuhl, 1999; Elowson, Snowdon, & Lazaro-Perea, 1998; Garvey, 1977; Kroodsma, 1982; Lieberman, 1984; Locke, 1990, 1993; Macken & Ferguson, 1983; Marler, 1970; Pepperberg, Brese, & Harris, 1991; Pepperberg & Neapolitan, 1988; Reiss & McCowan, 1993; Snowdon, 1990; Snowdon, French, & Cleveland, 1986). Babbling, a common type of sound play, can include repetitive calling, replication of parts of the adult repertoire, or iteration of subunits not found in an adult repertoire (Elowson et al., 1998). Repetitive states of expression in children are associated with pleasurable experiences, which suggests an innate reinforcement system for overproduction and sound play (Marler, 1970). The ability for play to reinforce practicing a behavior that may be important for survival would provide an evolutionary advantage for this process (Kuczaj, 1998). Neonate bottlenose dolphins have been found to practice by overproducing a variety of whistle segments before they are able to produce stereotyped adult-like whistles (Tyack & Sayigh, 1997).

The focus of this report is to describe the ontogeny of whistle production in dolphin calves by describing whistle quality, whistle parameters, and associated mother calf behaviors associated with this development. Individual differences, behavioral and acoustic milestones, and observations suggesting the presence of imprinting, sound play, and vocal learning are also explored.

CHAPTER II

METHODS

Four captive Atlantic bottlenose dolphin calves housed at three managed care facilities, Dolphins Plus, Island Dolphin Care, and Dolphin Cove in Key Largo, Florida, were filmed opportunistically over the first thirty days of life (Table 1). Focal-follow was the methodology used during each filming session, with the neonate being the focal subject. Please see Table 2 for focal hours for each subject.

Table 1

Subject Specifications

Calf	Dame	Sire	Facility	Date of Birth	Sex	Housed with During Study	Dates Analyzed
Zoe	Jessica	Bob	Dolphins Plus	7/14/10	F	Bob, Jessica, Nica, Elvis, Squirt, Lotus, Bella Fiji	7/14/10 – 8/12/10
Isaac	Samantha	Kimbit	Dolphin Cove	6/1/11	M	Samantha, Kimbit, Alfonz, Leo	6/1/11 – 6/30/11
Baby Bit	Dinghy	Little Bit	Dolphins Plus	9/13/11	F	Dinghy, Sarah, Julie, Grace	9/13/11 – 10/12/11
Tashi	Squirt	Bob	Dolphins Plus	8/13/12	M	Squirt, Bob, Bella, Louts	8/13/12 – 9/11/12

Materials and Apparatus

A Canon G9 (12.6 mega pixels) and a Canon G12 (10.0 mega pixels with HD) digital camera were used with respective underwater housings, Canon WP-DC21, Canon WP-DC34, connected to custom made monopods for underwater filming. These cameras each sample at 46 kHz, which results in a Nyquist frequency, cut off at 23 kHz. This is a sufficient sampling rate for this project as dolphin whistles on average range from 5kHz to 14kHz (Caldwell et al., 1990).

Table 2

Focal Hours for Each Calf (HR:MM:SS)

	Time Frame (Days)						
Calf	**1 – 10**		**11 – 20**		**21 – 30**		**Total Focal Hours 30 Days**
	On	**Off**	**On**	**Off**	**On**	**Off**	
Zoe	4:59:33	4:42:54	3:54:01	1:14:33	00:54:29	00:52:02	16:37:32
Isaac	3:45:55	1:35:11	00:18:55	00:28:34	2:46:33	00:50:06	9:45:14
Baby Bit	1:11:33	4:04:59	3:11:53	2:52:24	2:12:29	1:56:38	15:29:56
Tashi	3:18:00	4:09:47	2:20:45	1:08:57	2:38:35	1:13:19	14:49:23

Analyses

QuickTime™ was used for video behavioral analyses. Ethograms accompanied each of the videos, where every data point results from an occurrence of a bubblestream emitted from either the mom or the calf. The videos were recorded during two different contexts, during a feeding session, and during off-time when the animals are freely swimming without food present (Table 2). This allowed for an analysis of overall behavior and whistles common throughout their typical day. Any behavioral differences that seem to result from this change in context are addressed in the discussion. Given the difficulty of determining which animal is producing a whistle, this methodology has been used by a number of studies as a conservative approach to analyzing the whistle repertoire of dolphin calves (Killebrew et al., 2001; Morisaka, Shinohara, & Taki 2005a, 2005b; Reiss, 1988; Smolker et al., 1993). While it is recognized that whistles can be produced without the accompaniment of a bubblestream (Fripp, 2005), the benefits of this approach are: (a) it decreases the chances that a whistle is wrongly assigned to a calf, and (b) dolphins need not be isolated to collect the data (see McCowan, 2006 for further discussion).

Behavioral context of the mother, calf, and other conspecifics within one meter of the calf starting five seconds before, during, and five seconds after each whistle were coded using the coding scheme attached (see Table 3). Lastly, whistles were analyzed using RavenPro 1.4, acoustical analysis software from the Cornell Lab of Ornithology, which graphs the frequency of the sound as a function of time, subsequently creating a picture of the whistle (i.e., spectrograms). Raven spectrogram parameters were set at Window type, Hann, and Size, 512 samples (512 DFT), with a 50% overlap and 256 hop size and a 3db filter bandwidth. Breaks in the whistle contour of the spectrogram were used as the indicator of where the whistle began or ended (Watwood, Tyack, & Wells, 2004). Whistles were defined as a continuous trace on the spectrogram that was not interrupted by breaks greater than .25 seconds (Sayigh, Esch, Wells, & Janik, 2007). Whistle-squawks were differentiated from whistles if the whistle had any type of broadband, blurred, or screechy quality (see Killebrew et al., 2001 for examples).

Table 3

Basic Behavioral Coding Scheme

Behavior	Behavior Code	Behavior Definition
orient	MorC/CorM	looking at, echolocating towards, or turning towards. Include what the animal was orienting towards (ex. Camera, calf, mom)
retrieval	MretC	the calf is solo- mom leaves the dock towards the calf and returns into frame or to the dock with him <1m
check on	McoC	calf solo, mom leaves the dock towards the calf and returns without the calf <1m
tactile	MrosCpec	non-aggressive touching- Initiator+body part, Receiver+body part (first three letters of the body parts that were touching)
burst swim	BUR	immediate shift in swim speed from slow or normal to fast/racing
change direction	CD	a sharp change in direction from the natural swimming path (seemingly a reaction, or to have some intent)
divert	MdivC(dock)	mother intentionally moves the calf away from an object+ object (e.g., dock, camera, dolphin)
repetitive swim	Crs	swimming in consistent repetitive pattern more than 1x
chase	MchC	rapid, persistent pursuit of another dolphin
rake	RK	sliding open jaws/teeth on other dolphin
bite	BI	abrupt forceful contact with another using teeth
breathe	BRT	breaking the surface of the water with the melon to briefly expose the blowhole out of the water
bubbles	BS/BB	multiple bubbles coming from the blowhole over a period of time (stream), one larger emission of bubbles at the same time (burst)
nurse	N	calf's rostrum is within a few inches of the mother's mammary slits for more than 2 seconds
not visible	Mnv	if mother or calf are not in frame record which animal and then NV

Duration, initial frequency, final frequency, minimum frequency, maximum frequency, range of frequency, and number of inflections (see Figure 1 for definitions) (Morisaka et al., 2005a) were recorded for each whistle. Whistle-squawk parameters occasionally could not be recorded when the unclear, blurred portion of the vocalization made the precise parameter location unclear. These parameters were considered unknown and omitted from that characteristic's analyses. Each of the aforementioned categories was analyzed by using statistical analysis software, SPSS.

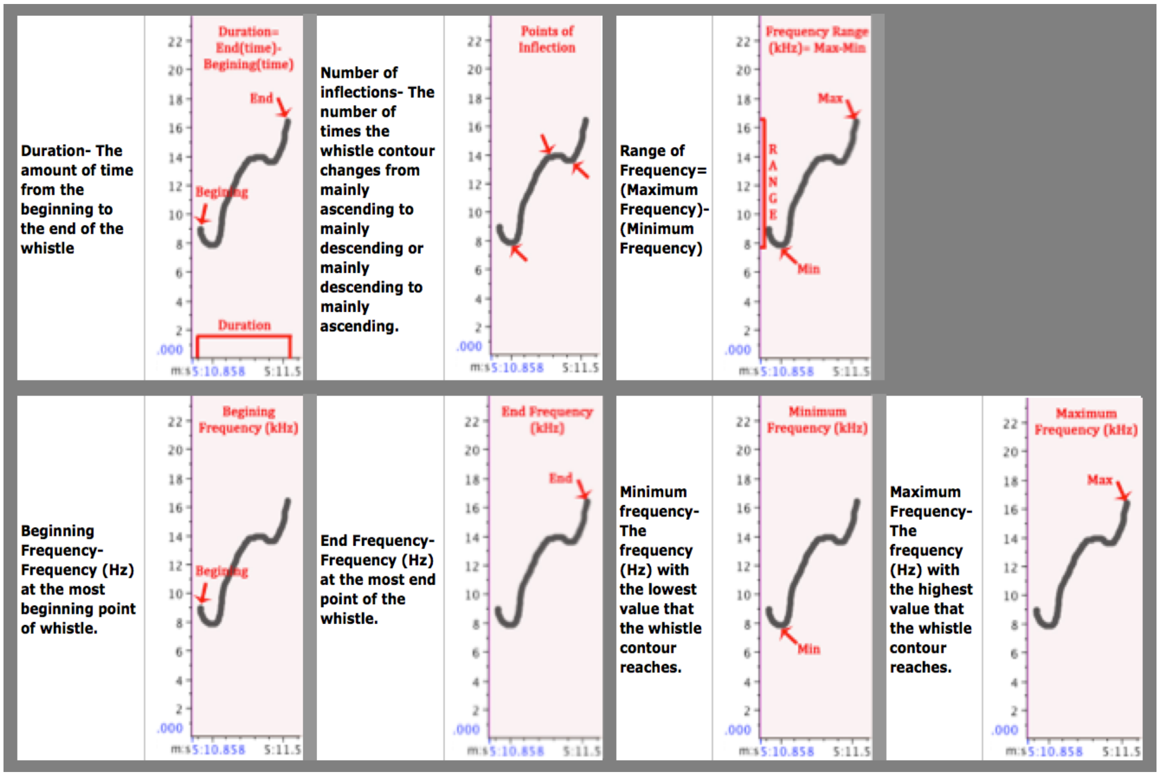


Figure 1. Whistle parameter definitions. The seven parameters analyzed for each whistle emission.

Acoustical analyses were done using a series of chi-square goodness of fit tests, one MANOVA, which assessed differences in the seven previously defined whistle parameters as they were affected by the interaction of individual calf and time period. This was followed up by post hoc analyses of two univariate

ANOVAs assessing differences in whistle parameters across individual calves and overall changes in those parameters across the three time periods.

CHAPTER III

RESULTS

Mother and calf whistle rates were inversely related ($r = -.702$, $p <. 05$) during the first thirty days of life (Figure 2).

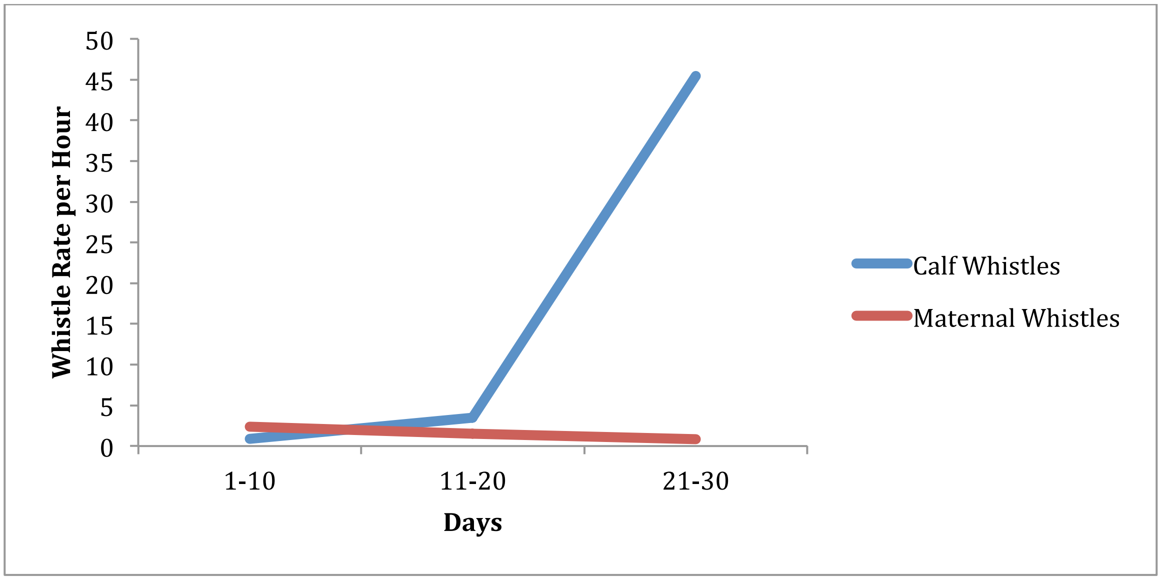


Figure 2. Whistle rates for mom and calf. Frequency of mom and calf whistles per hour over three sampling periods (n = 10 days each).

Calf whistling occurred significantly more often when the mother was greater than one meter away, χ^2 (2, N = 620) = 1020.72, $p < .05$. Conversely, maternal whistles occurred significantly more frequently when the calf was less than one meter away from the mom, χ^2 (2, N = 84) = 81.93, $p < .05$ (see Figure 3).

In congruence with the above finding, the calf was significantly more frequently in the “solo” spatial configuration when they whistled χ^2 (6, N = 668) = 3368.862, $p < .05$, and significantly more in the “beside” configuration when the mother whistled χ^2 (6, N = 107) = 195.439, $p < .05$.

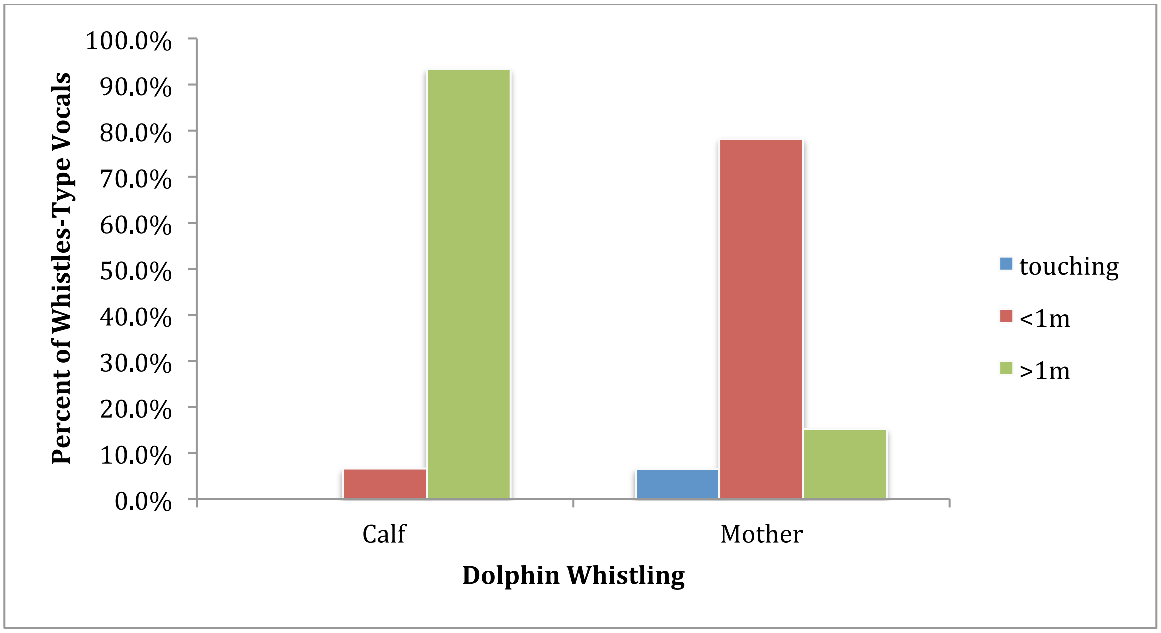


Figure 3. Mother calf proximity. Percent of whistle type vocalizations emitted during each of the spatial proximity categories when a calf whistled compared to when a mother whistled.

Mothers were significantly more likely to be stationed at the dock preceding a calf whistle than during or following the whistle, χ^2 (2, N = 531) = 19.627, $p < .05$. Interestingly, during a calf whistle, the calf significantly changed direction, χ^2 (2, N = 395) =36.248, $p < .05$, and participated in burst swim behaviors, χ^2 (2, N = 58) = 9.5533, $p < .05$, when compared to pre- and post-whistle behavior rates. Immediately following the calf's whistle the mom was significantly more likely to leave the dock to retrieve the calf, χ^2 (2, N = 74) = 119.755, $p < .05$, and whistle on bubblestream herself, χ^2 (2, N = 9) =8.667, $p < .05$, when compared to the five seconds preceding or simultaneously with a calf's whistle.

Timelines

Timelines for each mother calf pair describing qualitative changes and developmental milestones across the first thirty days of life are provided in Figures 4-7.

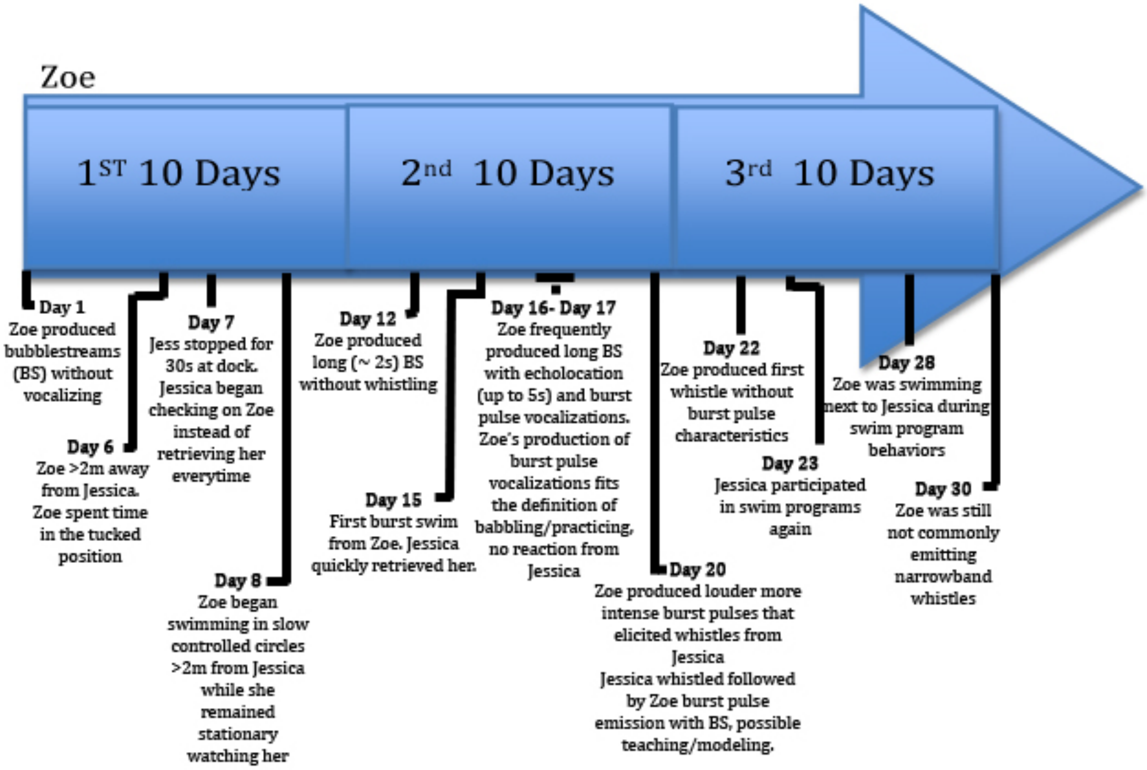


Figure 4. Zoe timeline. Qualitative behavioral and acoustic milestones for the mother calf pair; Jessica and Zoe.

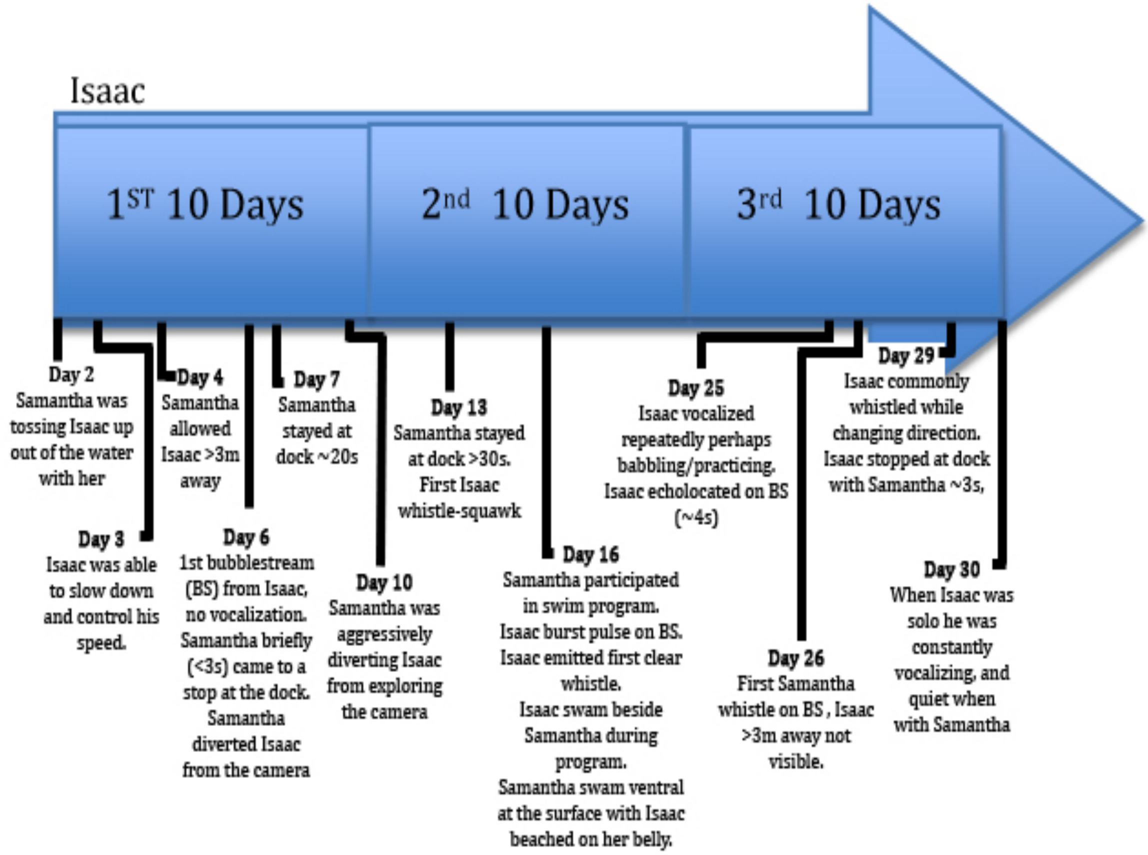


Figure 5. Isaac timeline. Qualitative behavioral and acoustic milestones for the mother calf pair; Samantha and Isaac.

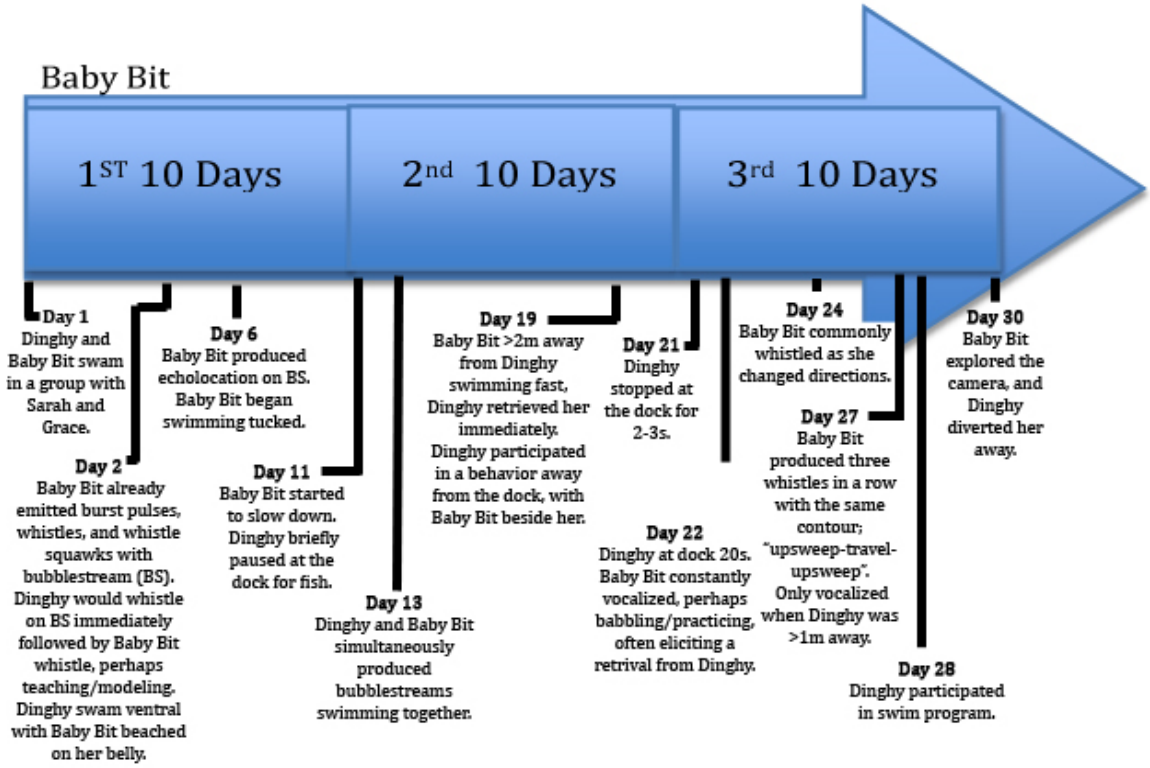


Figure 6. Baby Bit timeline. Qualitative behavioral and acoustic milestones for the mother calf pair; Dinghy and Baby Bit.

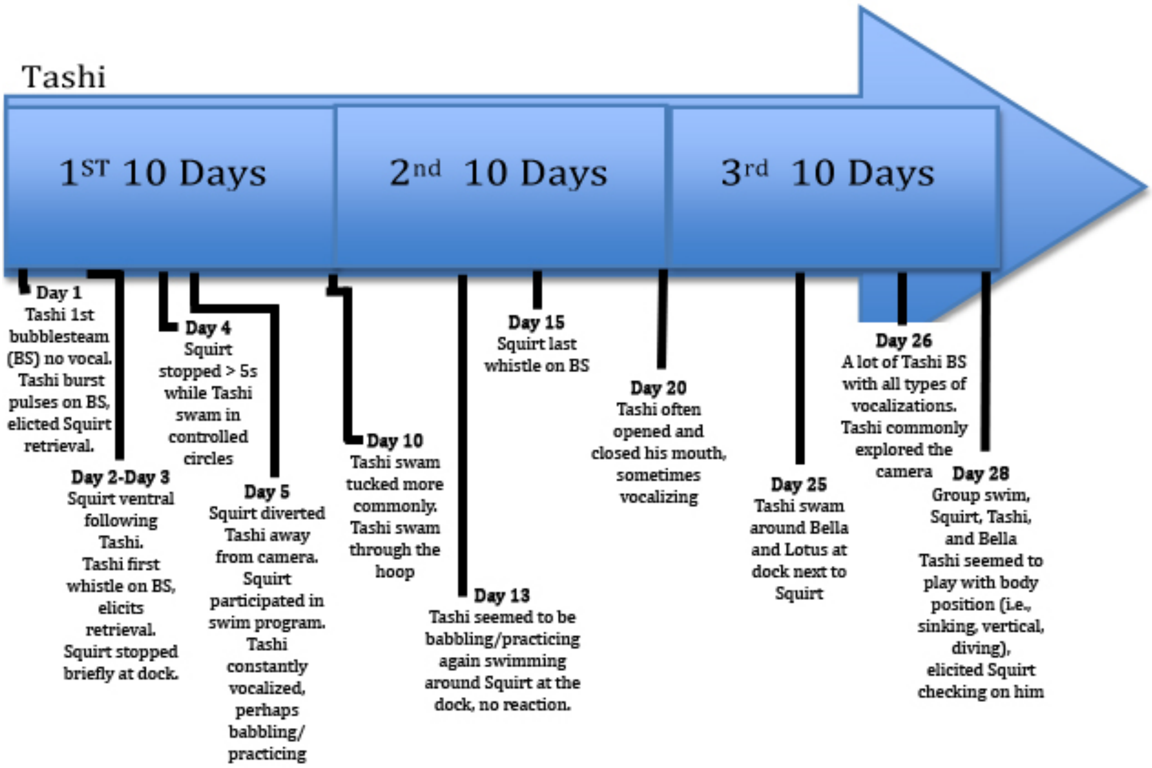


Figure 7. Tashi timeline. Qualitative behavioral and acoustic milestones for the mother calf pair; Squirt and Tashi.

Figure 8 depicts the typical acoustic developmental trends exhibited by the calves in this study over the first thirty days of life. As there was large individual variation in calf development across the four animals, please refer to Figures 3-6 for more detailed results for each animal.

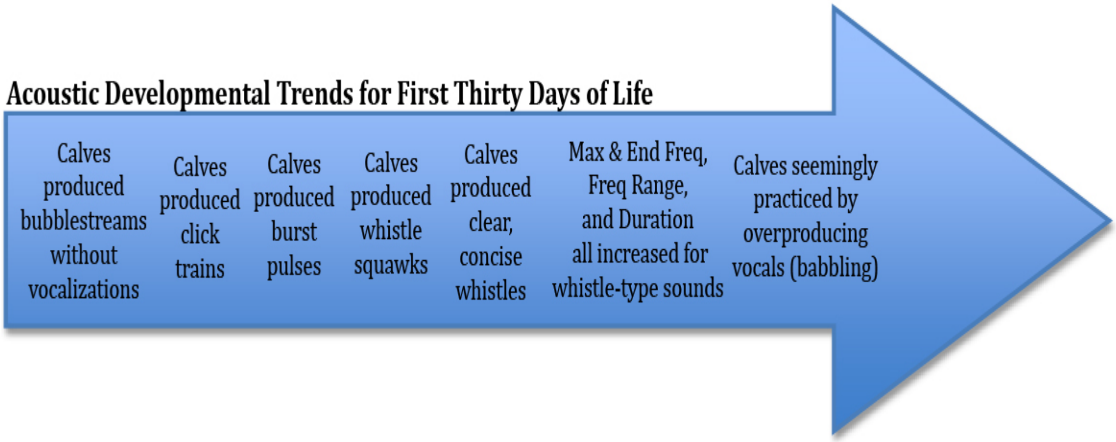


Figure 8. Acoustic development trends timeline. General developmental trends for calf acoustic development.

Parameter Analyses

Zoe (n = 3) and Samantha (n = 1) were omitted from further analyses because of their small whistle sample sizes.

Whistling rates for calves were significantly greater in the third ten days of life, χ^2 (2, N = 620) = 877.251, $p < .05$ (see Figure 9) than the first or second ten days. Inversely, the maternal whistle rate was significantly greater in the first ten days than the second or third ten days, χ^2 (2, N = 94) = 49.287, $p < .05$ (Figure 10).

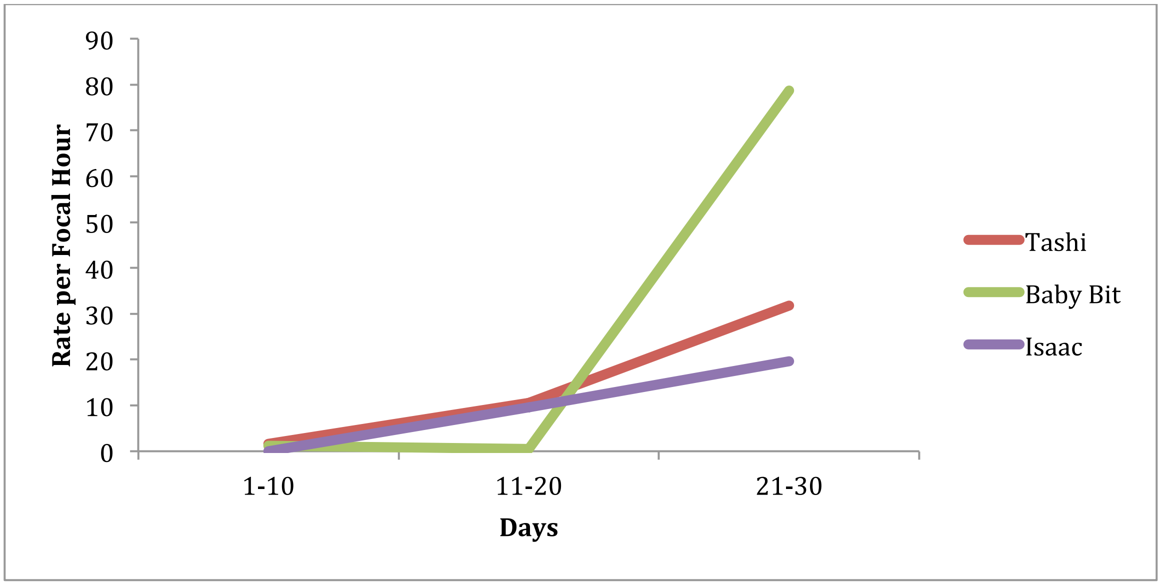


Figure 9. Calf whistle rate. The whistle rate for each calf over the three time periods.

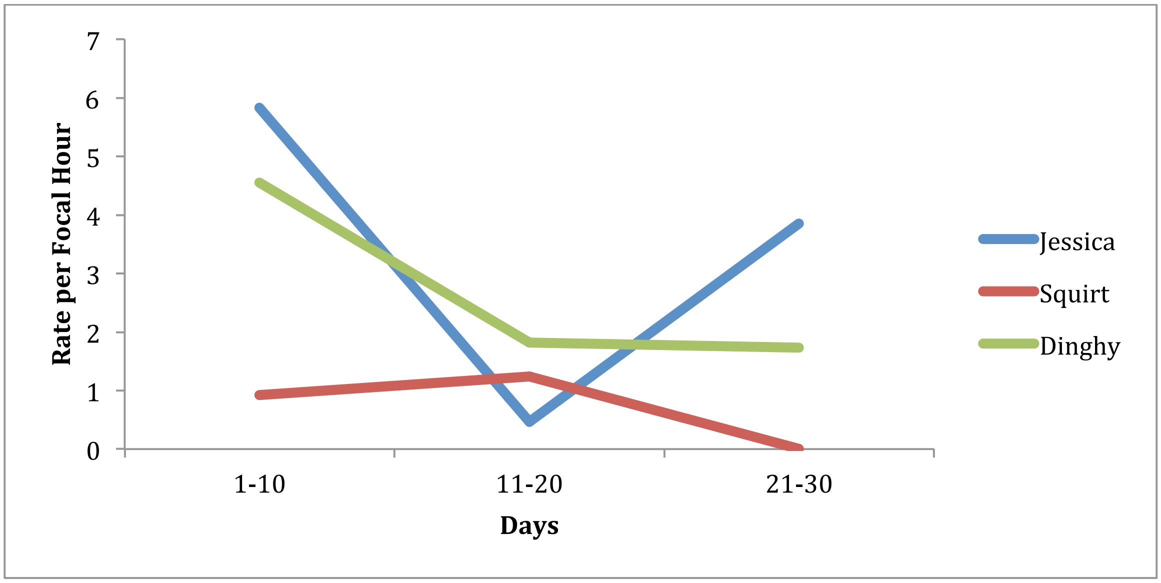


Figure 10. Maternal whistle rate. The whistle rate of each mother over the three time periods.

Calves across the first thirty days of life produced significantly more whistle-squawks than clear whistles, χ^2 (1, N = 620) = 102.426, $p < .05$ (see Figures 11 and 12).

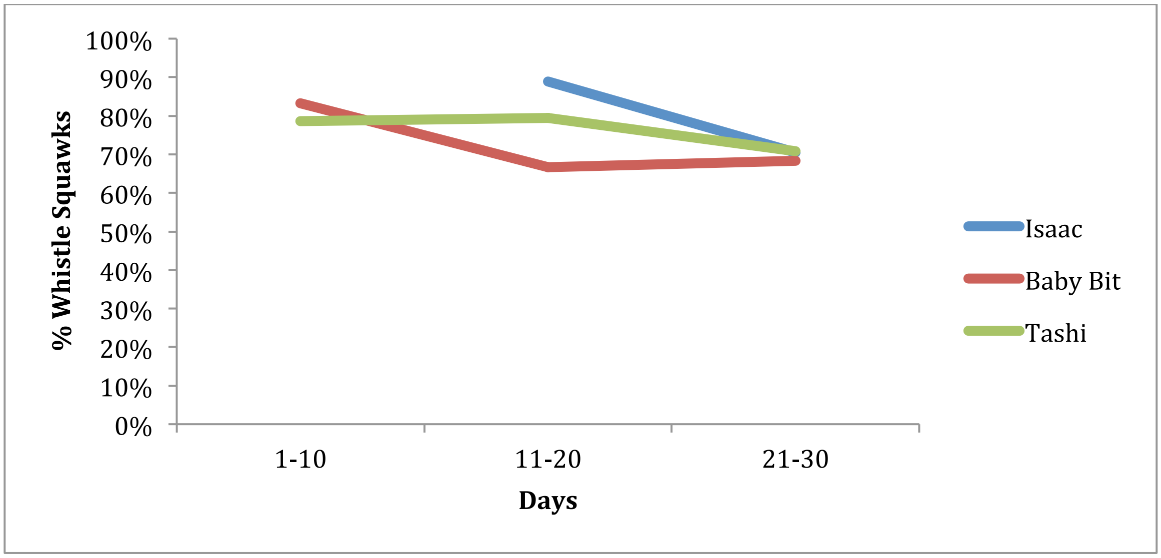


Figure 11. Percentage of whistle-squawk vocalizations produced by each calf over the three ten day sampling periods

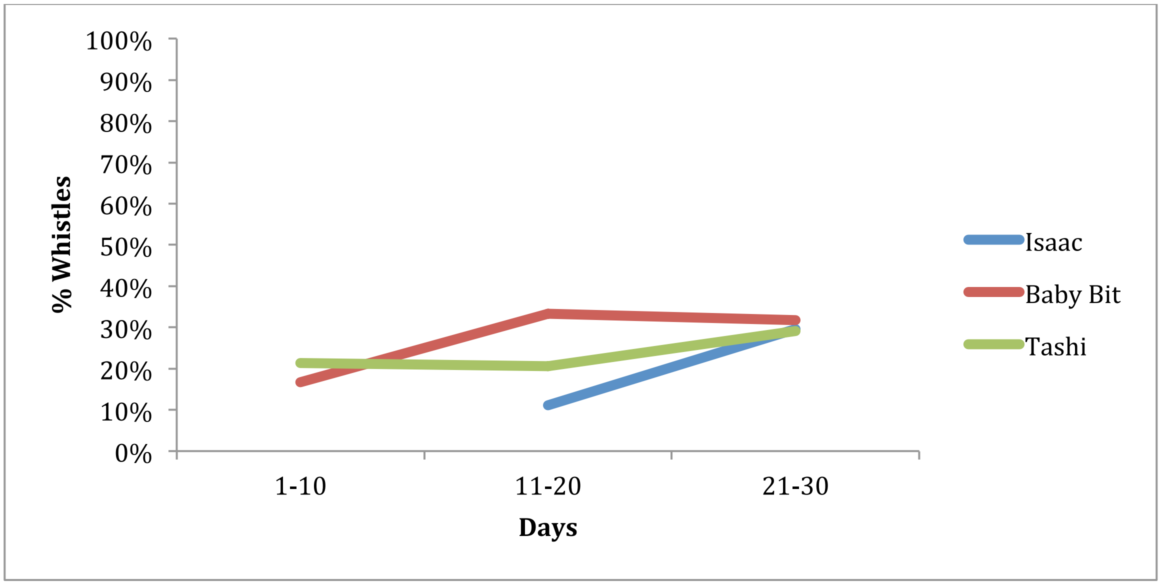


Figure 12. Percentage of whistle vocalizations produced by each calf over the three ten day sampling periods

Figure 13 details the whistle contour types and frequency that were used by a mother more than once. Two of the three mothers used in this analysis showed a significant preference for one whistle type over all others. Jessica utilized Type A significantly more than all other whistle contours, χ^2 (6, N = 39) =

195.28, and Dinghy used Type C significantly more frequently than all other contours, χ^2 (6, N = 43) = 196.141, $p < .05$. Squirt used one stereotyped whistle (i.e., Type F), and other times split Type F into two separate parts (i.e., Type D and Type E) that were often emitted in succession with a gap >.25 s and, therefore, were analyzed as two separate whistles. Whistle contours that were only emitted one time throughout data analysis were considered “other”- Jess (2.4%) Ding (0%), Squirt (8.4%)- and were omitted from Figure 13.

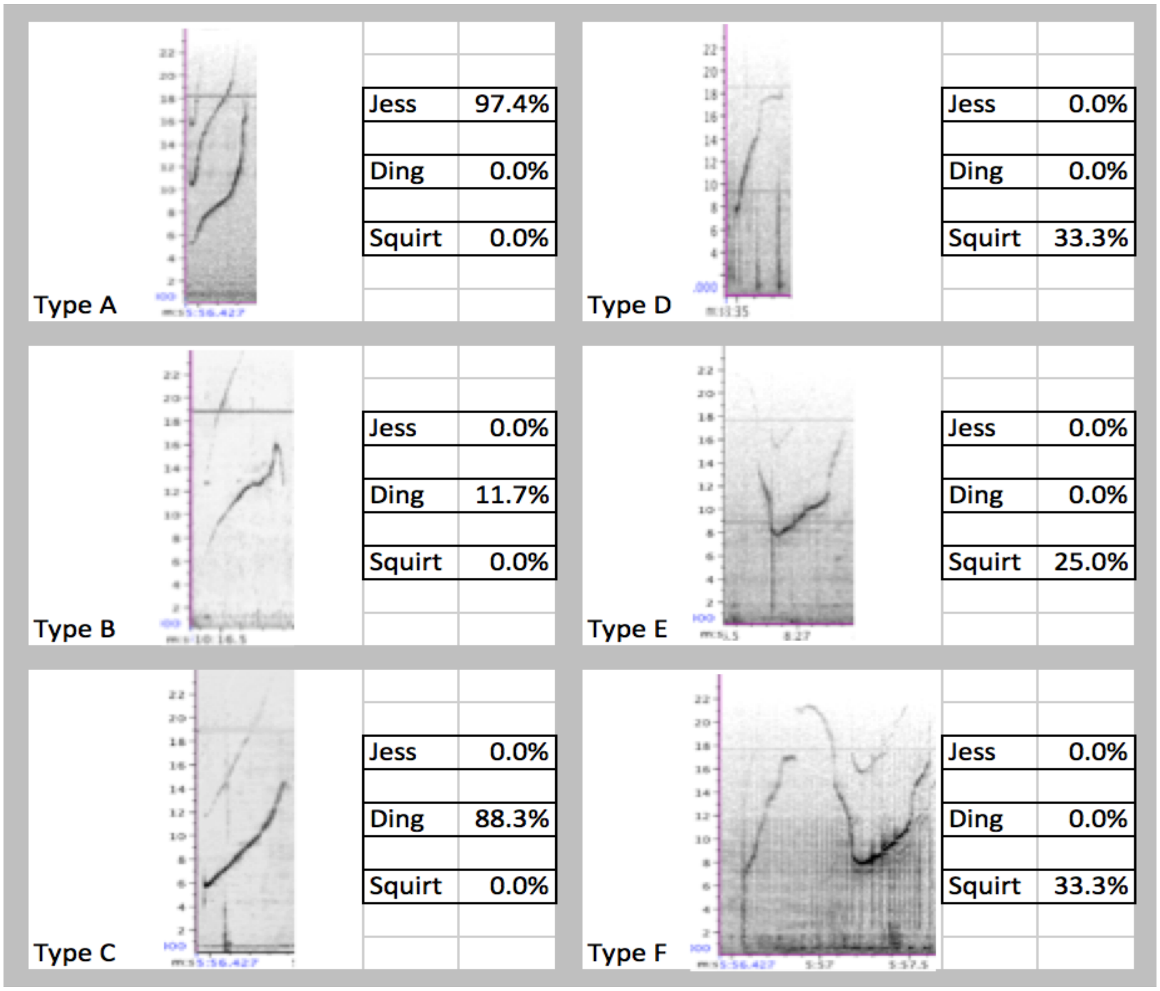


Figure 13. Whistle contour types. Percentage of maternal whistle emissions for each of six whistle contours.

Table 4

Maternal Whistle Parameter Descriptive Statistics

Whistle Parameter	**Minimum**	**Maximum**	**Mean**	**Std. Deviation**
Beginning Frequency	3.15	22.48	6.0014	2.53179
End Frequency	4.01	21.61	13.6474	3.43718
Maximum Frequency	7.82	22.39	15.2495	3.24653
Minimum Frequency	2.86	9.05	5.0161	1.19332
Frequency Range	2.15	17.43	10.2334	3.17604
Duration	.14	1.10	.4186	.16705
Inflection Points	.00	5.00	1.0753	.87522

Table 5 provides the descriptive statistics for the seven whistle parameters for all calf whistles during the first thirty days of life. Over the first thirty days of life the whistle frequencies ranged from .47 kHz to 20.64 kHz, the duration ranged from .05 s to 1.35 s, and the number of inflection points ranged from 1 to 13.

Table 5

Calf Whistle Parameter Descriptive Statistics

Whistle Parameter	**Minimum**	**Maximum**	**Mean**	**Std. Deviation**
Beginning Frequency	.62	19.17	7.4650	2.64210
End Frequency	.73	20.27	11.4617	4.04570
Maximum Frequency	1.10	20.64	13.3429	2.80372
Minimum Frequency	.47	13.78	6.5129	2.20063
Frequency Range	.41	17.59	6.8300	3.14770
Duration	.05	1.35	.4679	.21544
Inflection Points	1.00	13.00	1.8638	1.38089

A one-way MANOVA revealed a significant multivariate main effect for the interaction between time period and animal, Wilks' $\lambda = .912$, F (12, 580) = 2.272,

$p < .05$, partial eta squared = .045. End frequency, maximum frequency, minimum frequency, and duration were all significantly different ($p < .05$).

Given the MANOVA's significance, the between subjects effects for individual differences of three calves for seven whistle parameters was also significantly different, Wilks' $\lambda = .373$ $F\,(12, 580) = 28.694$, $p < .05$, partial eta squared = .376. Mean end frequency, minimum frequency, frequency range, and number of inflection points were all significantly different across the four animals ($p <. 05$). Figures 14-16 document 12 whistle-type examples representative of the whistle quality and development, including the first whistle and the final whistle recorded for each animal across their first thirty days of life. Individual differences in whistle contour and quality are largely apparent. Findings show that Isaac was the only calf who appeared to produce a repeated whistle contour during the first thirty days of life.

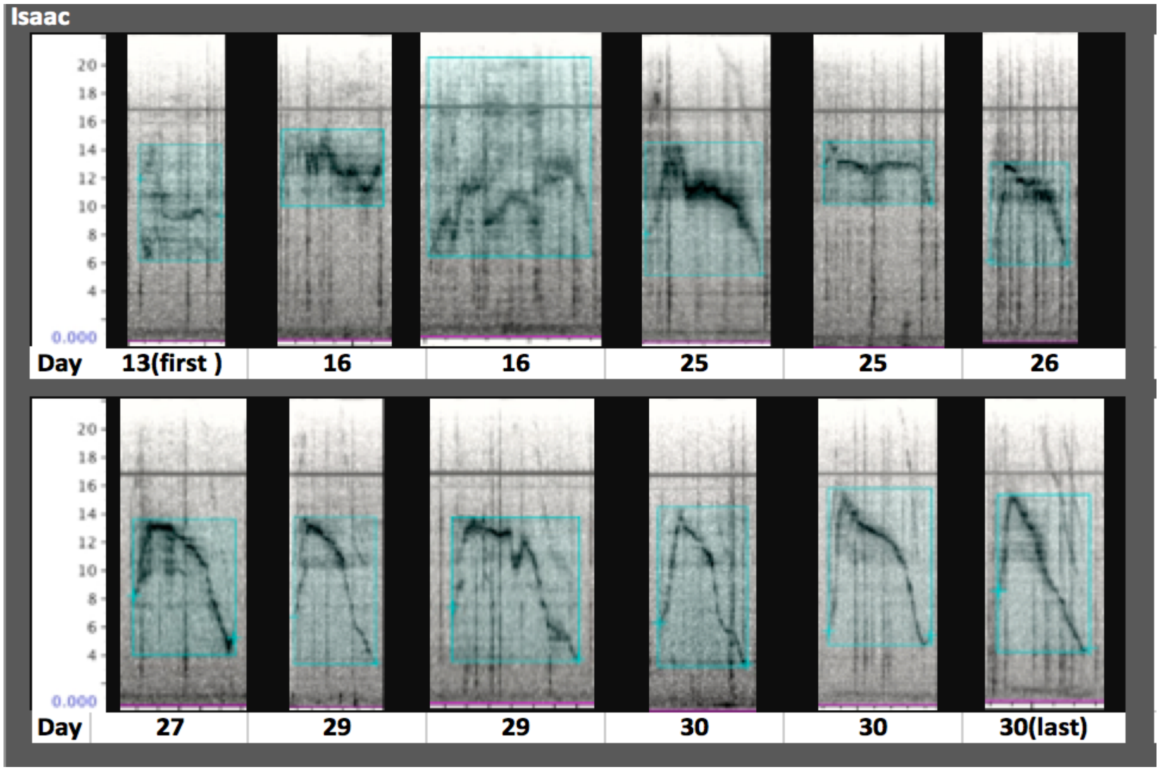


Figure 14. Isaac whistle development examples.

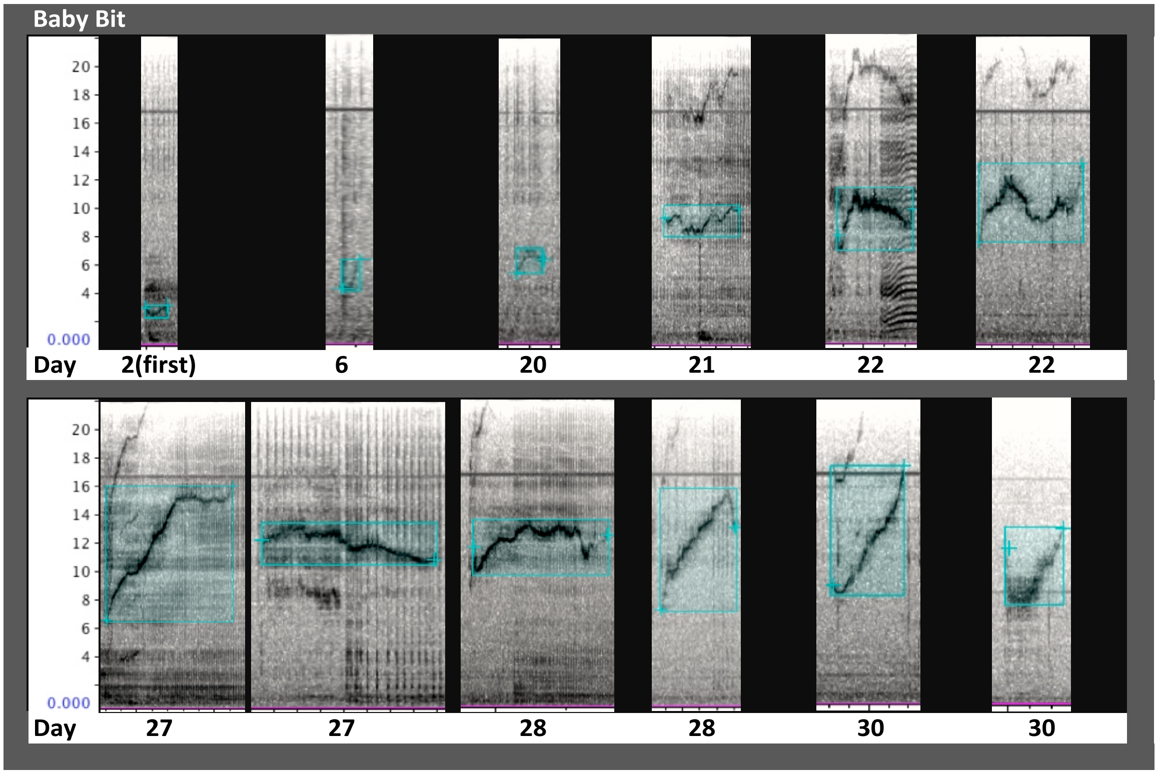


Figure 15. Baby Bit whistle development examples.

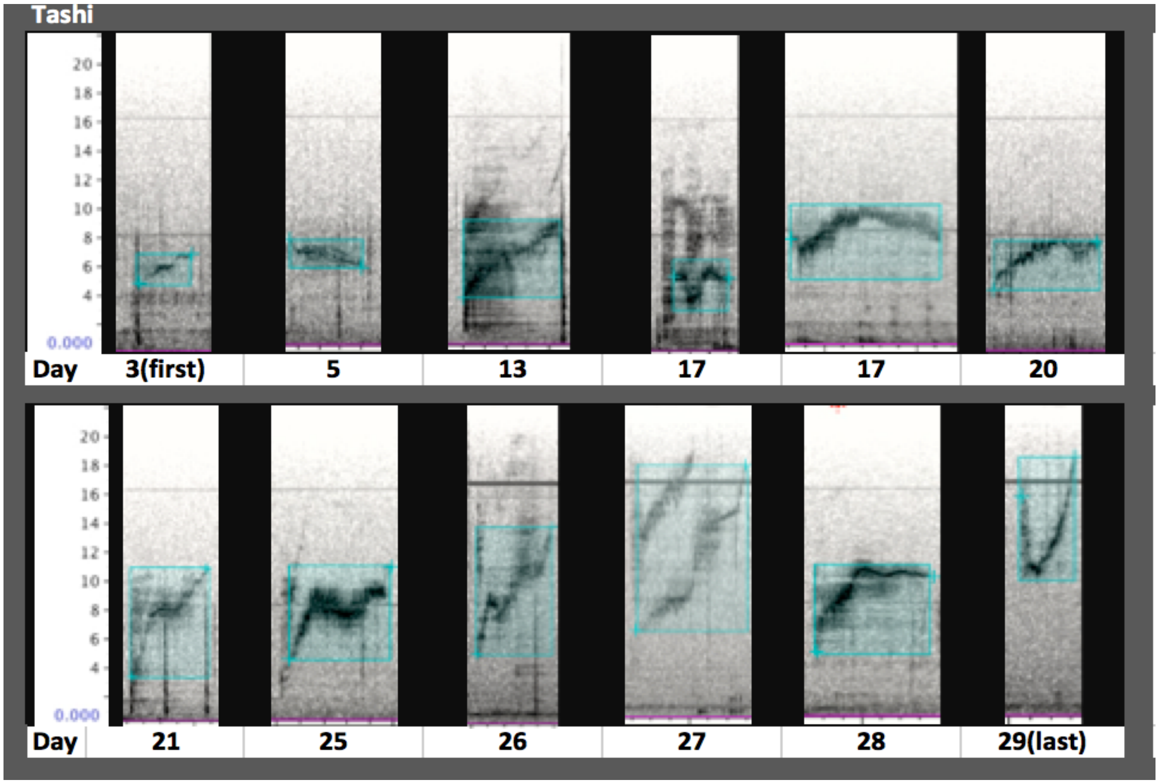


Figure 16. Tashi whistle development examples.

Finally an univariate ANOVA analyzing the seven calf whistle parameters across the three time periods, not including the effect of individual differences, was significantly different, Wilks' λ = .831, *F* (12, 580) = 4.675, *p* < .05, partial eta squared = .088. Tests of between subjects effect show an overall significant difference over the first thirty days of life for end frequency, maximum frequency, minimum frequency, frequency range, and duration (*p* < .05).

Figure 17 visually depicts the whistle parameter changes over time. Post hoc analyses provided more finite detail regarding where the differences occurred across the three ten day periods. End frequency (kHz) was significantly higher in both the second ten days and the third ten days when compared to the first ten days (*p* < .05). Maximum frequency (kHz) was significantly higher in both the second and third ten days when compared to the first ten days (*p* < .05). Frequency range and duration were both significantly greater in the third ten days than in the first ten days, *p* < .05.

Additionally, beginning frequency and minimum frequency were highly correlated at r = .771, end frequency and maximum frequency were highly correlated at r =. 639, and maximum frequency and frequency range were highly correlated at r =. 719.

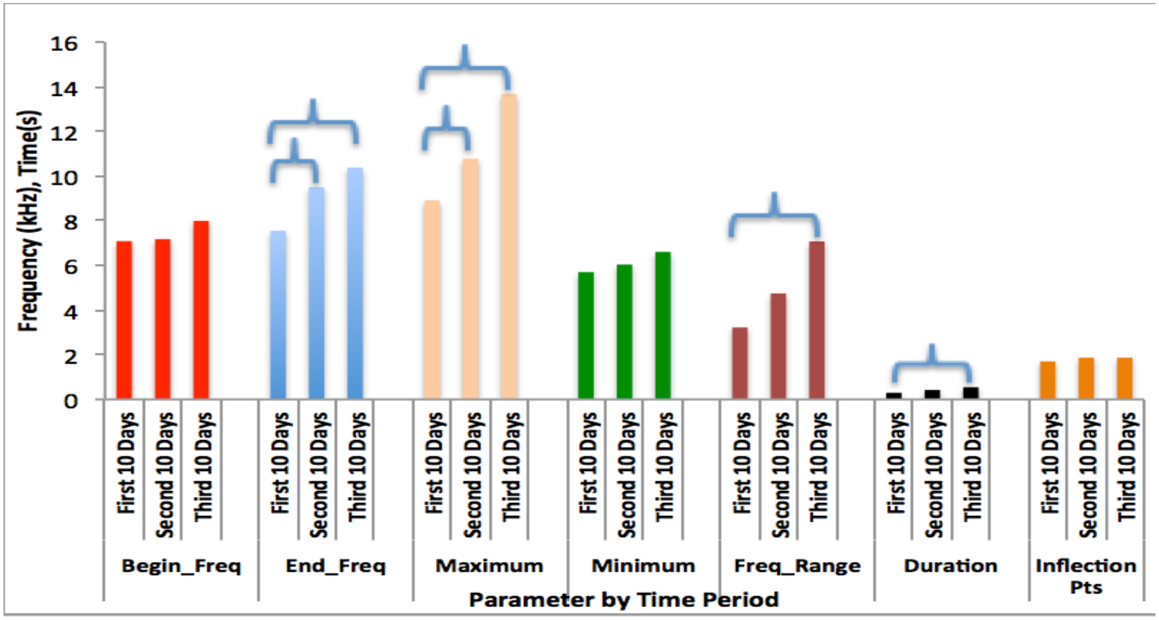


Figure 17. Whistle parameter development across time. Means for combined calf whistle parameters for each ten day period the first thirty days of life. ⏞ Significant differences between two time periods.

CHAPTER IV

DISCUSSION

Whistle Development and Behavior

Mothers whistled significantly more during the first ten days than the other two time periods, and these whistles corresponded most commonly with the calf swimming beside her. These results are consistent with Fripp and Tyack's (2008) hypothesis that imprinting may occur during the first week of life. In this study, mothers were, on average, six times more likely to whistle in the first ten days of their calf's life than in the third ten days, while Fripp and Tyack (2008) found a tenfold decrease in whistle rates from week one to week three.

Calves, on the other hand, increased their whistle rate significantly across the first thirty days and rarely whistled when within one meter of their mom. When the calf was solo (i.e., at least one meter away from its mother) 91% of their whistles occurred. These findings augment Tyack's (1997) results indicating that calves whistled more frequently during separations than mothers, and are consistent with Smolker et al.'s (1993) suggestion that calf whistles facilitated reunions and conveyed information about location to the mother.

The maternal behavioral patterns were the most diverse when comparing the five seconds preceding the whistle (one check on and one physical calf retrieval) to the five seconds after the calf whistle (four check on behaviors and 69 calf retrievals). This difference suggests that certain calf whistles may elicit this retrieval by the mother and is consistent with the aforementioned idea that it is the calf, rather than the mother, who is responsible for facilitating reunions after separation (Smolker et al., 1993). These retrievals typically occurred during the on-feed condition as the mom was stationed at the dock and would leave the dock immediately following the calf whistle.

In the ten-second time interval surrounding a calf whistle (i.e., five seconds pre and five seconds post), the calves had a high occurrence of changing swim direction. This behavioral increase was also specifically found during the “on-feed” condition as the mom was typically stationed at the dock where she was being fed, allowing the calf to explore its environment. We speculate that the increased whistle rates during changing direction may allow the mother to acoustically track the calf’s swim pattern. Breath was also a common behavior found surrounding calf whistles. This may be related to the underdeveloped respiratory system of the calves as Dearolf, McLellan, Dillaman, Frierson, & Pabst (2000) suggest that respiration development may be important to whistle development.

While Hill (2002) found that one calf developed its signature whistle as early as 14 days old, the only calf in this study that seemed to develop a stereotyped whistle contour was Isaac, around day 27. Baby Bit, after day 27, produced a few segments of repeated whistle contours, but unlike Isaac this was not a consistent whistle contour across whistling bouts or across days. She may have practiced reproducing the same whistle more than once prior to the development of a repeated signature whistle. The other three calves in this study were consistent with Caldwell and Caldwell (1979) and Sayigh (1992), as they did not seem to form clear signature whistles during the first month of life. In fact

Zoe did not develop a consistently frequency modulated whistle at all, and (with the exception of three whistles) only produced burst pulses and echolocation during the first thirty days of her life. It is unclear why her whistle development deviated from the other calves as Zoe commonly emitted bubblestreams that were not correlated with vocalizations and those that corresponded with burst pulses and clicks suggesting that it was not a methodological error, but instead was an example of individual variation in development.

When the behavioral and acoustic milestones are compared across the mom and calf pairs, the following developmental trends emerged. Three of the four calves emitted bubblestreams, two of which whistled within the first two days of life. Our data is consistent with Reiss's (1988) findings that burst pulse vocalizations are produced before whistle-type vocalizations and whistle-squawks precede clear whistle emissions.

While whistle emission does not typically begin until after day five (Killebrew et al., 2001; McCowan & Reiss, 1995; Morisaka et al., 2005a; Reiss, 1988) the majority of the calves in this study produced clear whistles during the first five days of life. That being said, whistles without burst pulse characteristics, while present, were rare during the first five days of life (n = 5). Whistle-squawks were consistently more prominent when compared to clear, concise whistles, but whistles generally increased from about 20% to about 30% of whistle-type vocalizations over the thirty-day time period. While our findings are consistent with others who have previously suggested that most tonal sounds produced during at least the first five days of life are typically categorized as whistle-squawks (Killebrew et al., 2001; McCowan & Reiss, 1995; Morisaka et al., 2005a; Reiss, 1988), these data suggest that calves have the ability to produce clear whistles as early as the first 48 hours of life, but they are unable to do so consistently.

While Isaac may have developed a stereotyped whistle contour by the end of his first thirty days of life, the majority of these whistles still had the “blurring” quality characteristic of whistle-squawks (see Figure 14). This suggests that the ability to produce clear narrowband whistles and the ability to produce a general stereotyped whistle contour may be independent of one another, and their development may overlap. Isaac seemed to produce a stereotyped general whistle contour before perfecting a clear, concise whistle.

On the other hand, maternal whistle contour was highly stereotyped and specific to the individual. Only whistle types with more than one occurrence were included in the type classification, all others were considered “other” (N = 4). Jessica and Dinghy both had considerably stereotyped whistle contours. Squirt also seemed to have a stereotyped whistle contour (see Type F). What is interesting is that she seemed to break Type F up into parts (Type D and Type E) and commonly emitted them as two whistles (i.e., >.25 s break between them) (Sayigh et al., 2007). Although she varied the inter-whistle interval, when Type E and Type D were emitted in succession the pattern was always the same, Type E always followed Type D. When these two contours were connected (i.e., <.25 s break between them) they were considered one whistle contour (Type F). Type D was also used as a stand-alone whistle by Squirt, whereas Type E was always emitted immediately following a Type D whistle. It is unclear why she varied her whistle in this way.

Variation in maternal style was found across mother calf pairs. Calf proximity to the mothers, greater than three meters away, for extended periods was recorded as early as day five to as late as day 22. Although there was large variation across the pairs, all mother calf pairs demonstrated this indicator of calf independence in the first month of life. All mothers gradually increased the amount of time spent away from their calf during the first thirty days of life, but did not tolerate long separations (> 20 s) until at least day five. This gradual increase in the longevity of separations was consistent across both recording conditions (i.e., on feed and off feed). Interestingly, this did not correlate strongly with whistle development, as Baby Bit, who had already whistled by day two, was not allowed more than three meters away from Dinghy for extended periods of time until day 22.

Janik (2000) found that a mother's whistle was frequently followed by her newborn calf's whistle, as if she provided the calf a model to imitate. Three of the four mother calf pairs were observed participating in this type of potential modeling or teaching behavior during off feed recordings. While swimming beside their calves the moms would whistle concurrently with a bubblestream and then immediately following that whistle their calf would also whistle on bubblestream. Dinghy and Squirt were first observed demonstrating this behavior in the first two days of their calves' lives. It is interesting that three out of four mother calf pairs were observed participating in this modeling behavior as it appeared as though the mother's whistle was eliciting a whistle response from the calf. The response whistle emitted from the calf varied greatly in terms of whistle quality and contour shape from the mom's whistle, so it seems unlikely that they are teaching the calf their specific whistle, but are more likely providing a model for whistling in general. Jessica and Zoe were not observed partaking in this behavior until day 20.

Similarly, Tyack and Sayigh (1997) found that bottlenose dolphin infants practice whistling by overproducing a number of different whistle segments before they are able to produce adult-like whistles. This ability for them to use their own auditory input to develop and shape their auditory output is suggestive of vocal learning. This practice behavior was consistently found in observations of all four calves beginning as early as day five. Other vocalizations on bubblestream were often heard both preceding and following a calf whistle. These bouts of constant vocalizing were often a mix of burst pulses, whistle-squawks, and whistles and were consistently a multitude of different whistle qualities and contours, which fits the criteria of infant babbling (Snowdon, 1997). Locke (1993) and Snowdon (1997) found that infant babbling in humans and pygmy marmosets initiated infant-caregiver interaction. While there was a significant increase in the retrieval behaviors produced by the mom following a calf's whistle compared to preceding a calf's whistle, the vast majority of calf vocalizations during these bouts occurred during the on feed condition, but did not elicit a reaction from their mother. Future research may look at which vocalizations provoked this response compared to non-approach soliciting whistles.

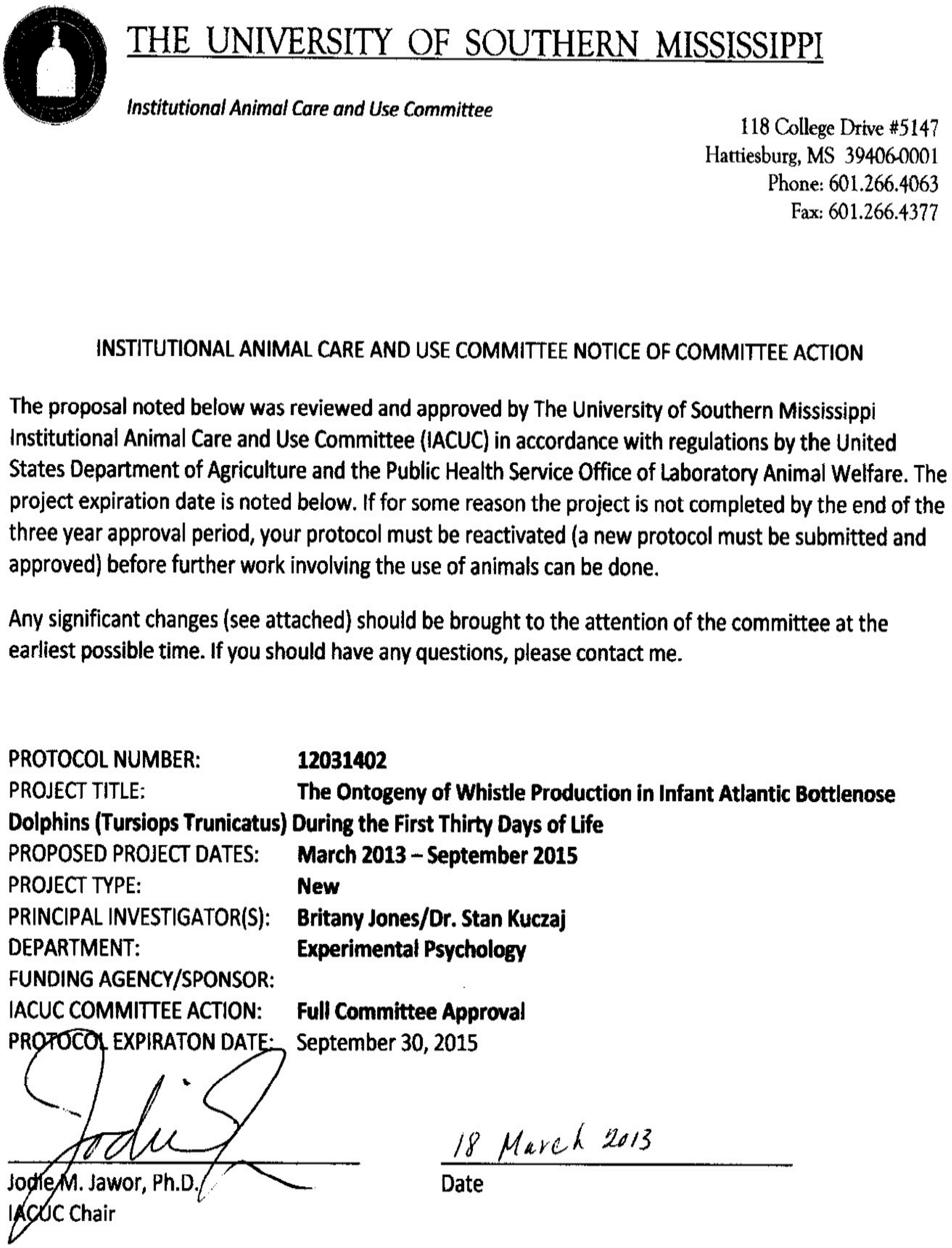
Whistle Parameter Development

An overall significant interaction effect between individual and time period suggests individual differences across whistle development, subsequently ruling out the idea of a whistle contour that is common to all calves after birth. End frequency and maximum frequency both showed an increase in kilohertz over time, and were positively correlated to one another. Beginning frequency and minimum frequency did not show significant changes over time and were also positively correlated. This data set also suggests that calf whistles tend to increase in duration as they develop (see Dearolf et al., 2000), but also that they are able to cover a larger frequency range. Additionally, maximum frequency underwent the greatest change over the first thirty days, with relatively large differences between all three time periods. It seems as though calves are able to improve their ability to reach higher frequencies as they mature. This directly opposes Wang, Wursig, and Evans' (1995) findings that there is a negative correlation between maximum frequency and body size. While we were unable to provide body size measurements for these calves, all three of the calves appeared to increase in size across this period of time and therefore would show a positive correlation with maximum frequency. It is unfortunate that body measurements were unable to be recorded, as Hammerschmidt, Newman, Champoux, and Suomi (2000) found that in rhesus macaques, (*Macaca mulatta*), weight better predicted change in coo vocalizations than age. It is important that maximum frequency, frequency range, and duration be studied more closely to determine how they develop over longer periods of time.

In summation, calf whistle emissions began as early as the first 48 hours of life. This ability was commonly preceded by the production of burst pulse vocalizations, and the majority of whistles had a screechy, unclear quality facilitated by a broadband component (i.e., whistle-squawks). Maternal whistle rate started high and decreased over the first thirty days of life and was most commonly associated with the calf in close proximity. Calves showed the opposite trend as they increased their whistle rate over time and seemed to correlate their whistles with separation from their mother. Anecdotal evidence is provided for potential instances of imprinting, teaching, and sound play. Maximum frequency, frequency range, and duration were positively correlated with calf age, suggesting that as the vocal apparatus and respiratory systems mature, calves are able to reach higher frequencies and emit longer, clearer whistle-type vocalizations. There appear to be distinct individual differences in whistle makeup for calves during the first thirty days of life. Finally, it appears that stereotypy and whistle clarity may develop independent of one another, suggesting that signature whistle development may begin before clear adult-like whistle quality is consistent. Future studies on saliency of whistle parameters, vocal learning, and longitudinal whistle development projects are important next steps in fully understanding the development of this seemingly complex communication system.

APPENDIX A

INSTITUTIONAL REVIEW BOARD NOTICE OF COMMITTEE ACTION



THE UNIVERSITY OF SOUTHERN MISSISSIPPI

Institutional Animal Care and Use Committee

118 College Drive #5147
Hattiesburg, MS 39406-0001
Phone: 601.266.4063
Fax: 601.266.4377

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:	**12031402**
PROJECT TITLE:	**The Ontogeny of Whistle Production in Infant Atlantic Bottlenose Dolphins (Tursiops Trunicatus) During the First Thirty Days of Life**
PROPOSED PROJECT DATES:	**March 2013 – September 2015**
PROJECT TYPE:	**New**
PRINCIPAL INVESTIGATOR(S):	**Britany Jones/Dr. Stan Kuczaj**
DEPARTMENT:	**Experimental Psychology**
FUNDING AGENCY/SPONSOR:	
IACUC COMMITTEE ACTION:	**Full Committee Approval**
PROTOCOL EXPIRATON DATE:	September 30, 2015

Jodie

Jodie M. Jawor, Ph.D.
IACUC Chair

18 March 2013
Date

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