



Maternal and Alloparental Discipline in Atlantic Spotted Dolphins (*Stenella frontalis*) in the Bahamas

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Abstract – Maternal and alloparental disciplinary behavior were examined in a community of Atlantic spotted dolphins (*Stenella frontalis*) on Little Bahama Bank, Bahamas. An operational definition of discipline was created and analyses were performed of underwater behavior by spotted dolphins. Results indicated that both mothers and alloparents performed discipline towards juveniles and calves in their community. Both males and females were observed performing and receiving discipline. Disciplinarians were significantly more likely to be adults than juveniles, and receivers of discipline were significantly more likely to be calves than juveniles. Pursuit, contact, and display behaviors were used in discipline, however pursuit behaviors were most often observed. Variables such as age class, sex, and parity were not found to influence how discipline was implemented, nor outcome. The durations of all disciplinary pursuits analyzed were under thirty seconds.

Keywords – Spotted dolphins, Discipline, Allomaternal care, Maternal care

Discipline is a broad category of behavior that involves punishment and the threat of punishment, and encompasses parental and alloparental behavior. Discipline is traditionally defined as punishment or penalty imposed for an unwelcome behavior with intent to extinguish that behavior (Clutton-Brock & Parker, 1995; Hill, 2009; Webster's Merriam Dictionary, 2011). Discipline has been thoroughly studied in human behavior, however little discipline research has focused on other organisms (Hoffman & Saltzstein, 1967; Kircaali-Iftar, 2005; McLoyd & Smith, 2002; Regalado, Sareen, Inkeles, Wissow, & Halfon, 2004). In animals, behaviors that decrease the survivorship of the individual or group often elicit punishment or discipline, and the receiver is often a subordinate to the punisher (Clutton-Brock & Parker, 1995). Factors such as sex, age, and kinship have been observed to influence how punishment/discipline is executed (Clutton-Brock & Parker, 1995). Discipline has been examined in animal behavior studies as a facet of maternal behavior (Herzing, 1996; Hill, Greer, Solangi, & Kuczaj, 2007; Hill, 2009; McCowan & Reiss, 1995). This suggests disciplinary behavior may function to increase the fitness of an individual or group by reducing the frequency of behaviors that decrease survival or reproduction (Clutton-Brock, 1991; Clutton-Brock & Parker, 1995; Hill, 2009). Few studies have defined discipline; however existing definitions are similar in meaning. Herzing (1996) defined discipline for Atlantic spotted dolphins (*Stenella frontalis*) as an individual reprimanding another individual for punishment or to re-establish order. Hill (2009) also defined maternal discipline for cetaceans, describing it as a type of behavior in which the mother aims to reduce the frequency of a specific behavior occurring in their calf.

A variety of discipline behaviors have been described for several delphinid species (Herzing, 1996; Hill et al., 2007; Hill, 2009; McCowan & Reiss, 1995). Captive beluga whale and bottlenose dolphin mothers pinned their calves to the bottom of the pool and held calves either above or below the water's surface (Hill, 2009; Hill et al., 2007; McCowan & Reiss, 1995). A specialized vocalization was

reported by McCowan and Reiss (1995) in captive bottlenose dolphins (*Tursiops truncatus*) as a precursor to disciplinary behavior. Researchers reported mothers and “aunting females” used this vocalization in concert with disciplinary behavior to retrieve calves after separations from adults (McCowan and Reiss, 1995). Mann and Smuts (1998) found that wild bottlenose dolphin mothers chased their calves when calves swam away from their mother during the first week of life. Wild Atlantic spotted dolphin mothers chased their calves as well, often inverting their bodies during the chase (Herzing, 1996). Within the chase, mothers were observed to use echolocation on the genital area of the calf, and sometimes hit the calf with their rostrum. In the present study, videos were analyzed to examine discipline in a community of Atlantic spotted dolphins. Disciplines were examined for 1) Category in which behavior of dolphin falls, 2) Behaviors used by different individuals, and 3) How type of discipline and individual performing discipline were related to the outcome of discipline. Since the study considers discipline within the framework of parental care, analyses focused on older individuals disciplining calves or juveniles.

Method

Study Site

The study area was located on Little Bahama Bank, north of Grand Bahama Island (Figure 1). The white sand bank encompasses an area of 480 km² and ranges from 6 to 16 ms in depth. It is surrounded by deeper water greater than 500 m in depth. This location is unique with shallow, clear water that allowed researchers to identify and record dolphins using video and still photography (Herzing, 1996; 1997).

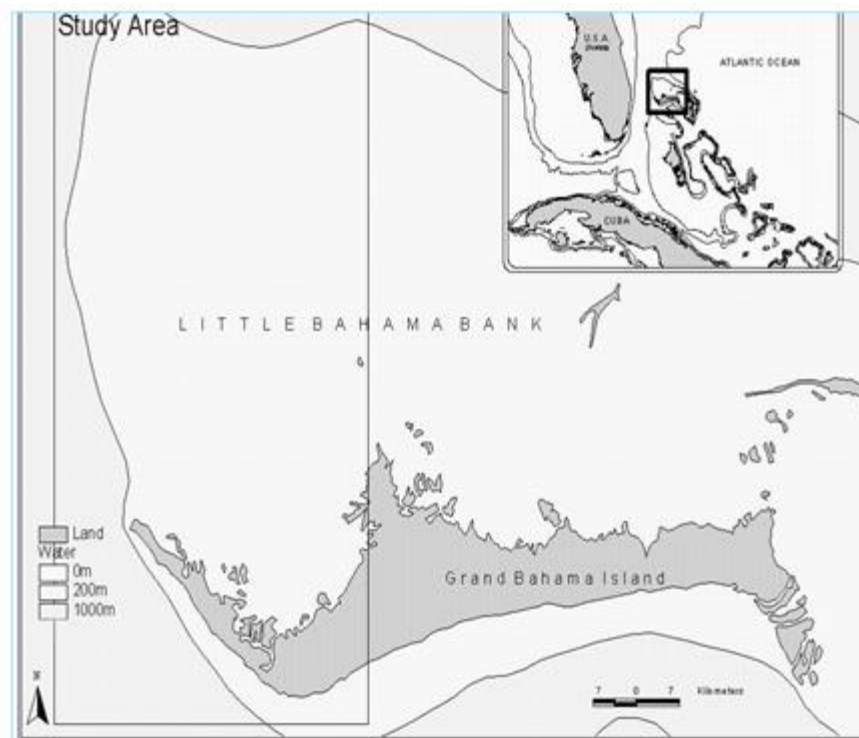


Figure 1. Study site. Little Bahama Bank and Grand Bahama Island in the Bahamas.

A resident community of Atlantic spotted dolphins (*Stenella frontalis*) has been studied since 1985 by the Wild Dolphin Project (WDP) and has identified over 200 individuals based on spot patterns and other body markings. Sex was determined when possible based on observation of the genital slit. Herzing (1997) classified Atlantic spotted dolphins into four age classes based on spot development with maturity. Age of each individual is estimated based on spot development, or known from tracking the

animal since birth. Neonates and calves ages 1 – 3 were termed *two-tone*, characterized by a lack of spots and a gray and white overall coloration. Juvenile dolphins, age 4 – 8, were considered *speckled*, young adults aged 9 – 15 years were *mottled*, and adults aged 16 and above were classified as *fused*. Most females reach sexual maturity during the mottled years (Herzing, 1997). It is unknown when male Atlantic spotted dolphins reach sexual maturity (Green et al., 2011). This study focused on spotted dolphins ranging in age from neonates to adults. On several occasions, age classes were combined to include juveniles (calves and juveniles) and adults (young and older adults).

Data Collection

Dolphin behavior was recorded with various underwater video cameras (including Sony XR 550, Sony CCDV9 8mm, or Yashica KXV1u 8mm) with an attached hydrophone. Dolphin behavioral data was collected using *ad lib*, behavioral event, and focal sampling methods (Altman, 1974). Underwater photographs were used to identify the dolphins present during the encounter, and video recordings were used to confirm those identities.

Data for this study were selected from the WDP long term database, which includes a photo identification catalog of individuals, written encounter details, video footage, and supplemental video logs.

Behavioral Definitions

Discipline was defined as an instance in which an older dolphin directed an actual or threatened stimulus to a younger dolphin in an attempt to immediately change the younger individual's behavior. Successful discipline resulted in the immediate and sustained change of the receiver's behavior. Discipline did not include instances where aggression was elevated or prolonged, nor did it culminate in copulation or related mating behaviors. The individual dolphin that performed the disciplinary act was identified as the "disciplinarian." The "receiver" was defined as the dolphin towards which the disciplinary act was directed.

"Precursor behavior" was defined as the receiver's activity within ten seconds before discipline occurred. All behaviors in this category were scored as behavioral events. "Outcome behavior" was defined as the activity of the receiver within ten seconds after the disciplinary event. All behaviors in this category were also scored as behavioral events. Finally, the overall "discipline sequence" was composed of the precursor behaviors of the receiver, the disciplinary event itself, and the outcome, or subsequent behaviors of the receiver. The operational definitions of all independent variables and behavioral categories are listed in Tables 1 and 2.

The disciplinarian was either a mother or alloparent. The mother was defined as the biological parent of an offspring, and was determined by visible pregnancies in females followed by resightings of female with a nursing calf (Herzing, 1997). All mothers were mottled (young adults) or fused (adult), as reproductive maturity occurred during the mottled age class. An alloparent was defined as a speckled (juvenile), mottled, or fused male or female dolphin that directed disciplinary behavior toward another dolphin that was not its known biological offspring. The receiver was defined as an immature dolphin, either a calf (two-tone age class) or juvenile (speckled age class). Discipline between adults was not measured in the current study. Only discipline directed from an older dolphin to younger dolphin was analyzed, which included discipline between a juvenile and a calf because females may practice parenting skills such as discipline in their juvenile years.

A discipline ethogram was developed by modifying of the existing WDP ethogram (Herzing, 1995), and consisted of behavioral events performed by both the disciplinarian and the receiver (Table 2). Discipline behavior was defined using three behavioral categories: 1) Pursuit, 2) Contact, and 3) Display. Behavioral events performed by the receiver before and after discipline were included in the ethogram under each behavioral category, as were modifiers used to further describe the behavioral events observed (Table 2). The outcome of each discipline sequence was defined as how or if the behavior of the receiver

changed after the discipline behavior ended. Outcome was scored as one of the following: 1) Behavior of the receiver stayed the same, 2) Behavior of the receiver stayed the same but energy level increased or decreased 3) Behavior of the receiver changed with an *increased* energy state, 4) Behavior of the receiver changed with a *decreased* energy state, 5) Disciplinarian performed more discipline, or 6) Other. An outcome qualified as “other” if the behavior of the receiver did not fall into one of the previous categories. Energy level was considered because behaviors such as *swimming* were often involved in analysis (i.e. chase, inverted chase). Dolphins swim almost continuously; thus it was necessary to include a quantifiable measure, such as energy level, to examine the response of the receiver to a disciplinary act. Energy level was measured based on number of fluke beats in five seconds, and number of directional changes in five seconds. Discipline was considered successful if the behavior of the receiver changed (outcomes 3 & 4) or if energy level of the receiver changed (outcome 2). During analysis, more emphasis was placed on receivers’ behavioral changes rather than energy changes. Changes in behavior were measured with the specific direction in energy level (i.e., increase or decrease), whereas the type of energy level change was not specified when no behavioral change occurred in the receiver following discipline.

Table 1

Independent Variables: All Subjects Involved in Discipline Sequences Including Disciplinarians and Receivers

Independent Variable	Description
A. Disciplinarian ID	Identification of dolphin performing disciplinary behavior
Mother	
Non-mother	
B. Disciplinarian Sex	Sex of disciplinarian
Female	
Male	
C. Disciplinarian Age Class	Age classes based on Herzing (1997)
Speckled	
Mottled	
Fused	
D. Parity of Disciplinarian	Number of times female has given birth
Nulliparous	Female has never given birth
Primiparous	Female has given birth one time
Multiparous	Female has given birth more than once
K. Receiver Sex	Sex of receiver
Female	
Male	
L. Receiver age class	Age classes based on Herzing (1997)
Two-tone	
Speckled	
M. Kinship of Receiver	Genetic relationship between disciplinarian and receiver
Yes	
No	
Unknown	

Table 2

Behavioral Events: Operational Definitions and Behavioral Ethogram

Category	Description
Pursuit	Behaviors in which one dolphin or a group of dolphins follow another
Chase	One dolphins, or a group of dolphins chasing each other in fast, medium, or slow chases
Inverted Chase	Following dolphin is inverted while chasing another
Contact	Behavior in which physical contact is made between dolphins involved
Hold Down	Dolphin or group of dolphins hold down another on the bottom
Charge	Two or more dolphins charge, head to head, sometimes making contact
Tail Slap	A tail slap that makes contact with another dolphin's body
Tail Swipe	One dolphin swipes the face/body if another dolphin
Rostrum Bop	One dolphin hits another with its rostrum
Rostrum Joust	Dolphins dueling with rostrums
Pec to	One dolphin is rubbing pectoral fin to corresponding body part of second dolphin
Pec/Head/Genitals/Flank/Belly/Fluke	
Pec body swim	One dolphin sustains contact with another pec fin touching mid body of other while swimming
Nursing	Infant receives milk from mother; mother or calf initiates
Tail bite	One dolphin bites another's tail, usually in chase
Bite	One dolphin bites or rakes another
Passive Float	Dolphin floats passively while others nudge it or roll it
Contact Swim	One dolphin swims with pec fin to body with another
Group Cluster	Two or more dolphins form a tight, within body contact unit and synchronize swim, breathing, and vocalizing
Rostrum Push	One dolphin contacts or pushes another with rostrum
Display	Behaviors in which one dolphin directs a body orientation to another dolphin without physical contact
Jaw snap	Dolphin opens and shuts jaw rapidly, directed toward another dolphins
S-posture	Dolphin is arched so that rostrum is up, body is down and flukes are up
Head to Head	Dolphins take head to head position; motion or stationary position
Inverted Head to Head	One or more dolphin orient in a head to head position, body posture inverted
Open Mouth	One or more dolphin open their mouth toward another
Reunite	One dolphin rejoins another after a departure away
Pout	Dolphin hangs in relaxed arch at surface, facing away from others
Group Dash	Two or more dolphins accelerate rapidly underwater
Erratic Swim	Dolphin is swimming through water erratically, usually in circles and contained in small area
Play	
Group Tussle	Dolphins in general body tumble
Aerial Behavior	
Breach Side/Belly	Dolphin leaps out of the water and lands on side/belly
Tail Slap	Dolphin hits surface of water with ventral fluke
Inverted Tail Slap	Dolphin hits surface of water with dorsal fluke while inverted on surface or under surface
Exit/Re-enter	Dolphin exits and reenters same spot while being chased out of the water
Vocalizations	
Excitement Vocalizations	Burst pulse vocalization with overlapping signature whistle
Signature Whistle	Frequency modulated whistle
Genital Buzz	High repetition-rate clicks
Squawk	Broad band burst pulse vocalization
Proximity during pursuit	Proximity of disciplinarian during chase or inverted chase
Near	Less than two adult body lengths
Far	More than two adult body lengths
Other dolphins present during discipline	Other dolphins present during discipline and may or may not participate in discipline behavior

Note. Mutually exclusive behaviors performed by disciplinarians and receivers during, before, and after discipline.

Analyzing Discipline Behavior

Videos were selected from the WDP's long term database between 1991 through 2009. Video clips were analyzed using the discipline ethogram. The ethogram was uploaded into Observer XT 7.0 to observe and analyze the video clips of discipline. All behavioral activity observed in a discipline sequence was recorded as a mutually exclusive behavioral event which allowed the frequency of occurrence of that specific behavior to be measured (Martin & Bateson, 2007). The behavioral activity of the receiver before and after the disciplinary act were scored as behavioral events (discrete occurrences), and allowed the recorder to view any changes in the receiver's behavior that occurred relative to the disciplinary act. The beginning of the specific disciplinary behavioral activity performed by the disciplinarian was scored as a behavioral event, as was the cessation of the disciplinary act. Although behavior was not scored as a state, the durations of behavioral activities such as chases and hold-downs were manually derived by measuring the time between the behavioral event scored at the start of the disciplinary behavior, and the behavioral event scored at the end of the disciplinary event. Figure 2 is a visual representation of the discipline sequence including precursor, disciplinary, and outcome behavior.

All videos were scored by the first author, and 25% of the videos ($n = 6$) were scored by the second, trained observer to test for inter-observer reliability. There was a significant correlation between the all observations by the first and second observers (all $r^2 \geq 0.92$).

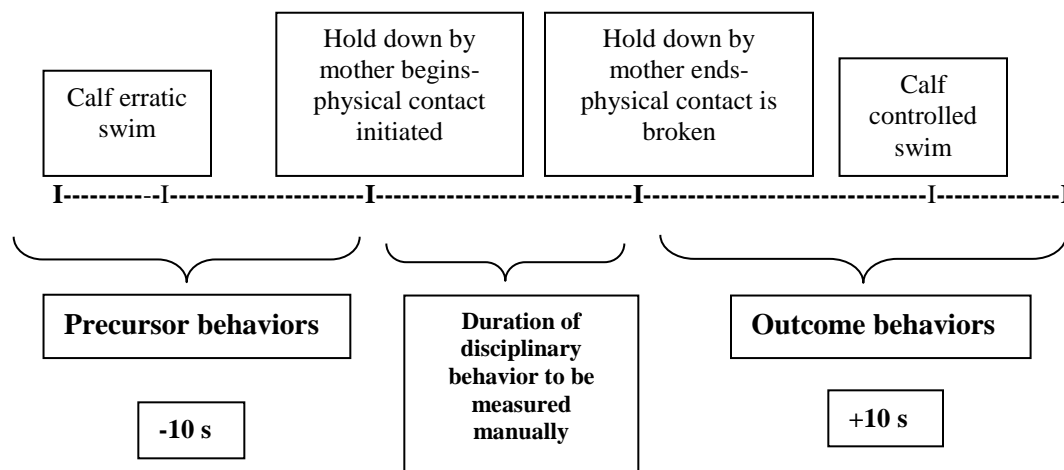


Figure 2. Disciplinary sequence. Analysis of disciplinary behavior with precursor and outcome behavior using behavioral events.

Description of Disciplinarians

All disciplinarians. Of the 31 videos scored for discipline, 24 met the criteria set for this project and were used in analysis. In the 24 complete discipline sequences analyzed, 48% of disciplinary sequences were performed by mothers, and 48% by alloparents (male and female) (Table 3). When age class was merged to compare adults (mottled and fused) vs. juveniles (speckled) for mother and alloparent disciplinarians, there were significantly more adult disciplinarians than juvenile disciplinarians ($p < 0.05$) (Table 4).

Table 3

Subjects Involved in Discipline

Disciplinarians	Two-Tone	Speckled	Mottled	Fused
Mothers				
Female	N/A	0	7	4
Males	N/A	N/A	N/A	N/A
Alloparents				
Female	N/A	0	1	4
Male	N/A	4	0	3
Unknown	N/A	1	0	0
Receivers				
Female	8	2	N/A	N/A
Male	12	1	N/A	N/A
Unknown	0	0	N/A	N/A

Note. Includes mother and alloparent disciplinarians, and receivers of discipline.

Table 4

Comparison of Mother and Alloparent Disciplinarians

Group	<i>N</i>	<i>p</i>
Age Class		
Juvenile*Adult	24	0.04
Speckled*Mottled*Fused	24	0.01
Mottled*Speckled	16	0.004
Mottled*Fused	19	0.06
Fused*Speckled	16	0.24
Parity		
Primiparous*Multiparous	16	1

Note. Results from Fisher exact test in which age class and parity were compared for significance. Bold indicates a significant difference ($p < 0.05$)

*-groups being compared

Description of receivers of discipline. In 23 discipline sequences analyzed in which sex of receiver was known, mothers and alloparents disciplined two-tones significantly more than speckled individuals ($\chi^2 = 12.61$, $df = 1$, $p < 0.05$). In regards to sex of the receiver, there was no significant difference found in how mothers and alloparents disciplined males versus females ($p > 0.05$)

Behaviors used in discipline

A behavioral event from the *pursuit* behavioral category (including chase or inverted chase) was observed in 17 of the 24 complete discipline sequences analyzed (Table 5). Inverted chases were observed frequently as well as regular chases discipline. Behavioral events from the *display* and *contact* categories were observed in equal proportions (Table 5).

Table 5

Behaviors Used in Discipline

Behavior	Frequency of Occurrence
<i>Pursuit</i>	17
Chase	6
Inverted Case	11
<i>Display</i>	4
Open Mouth	3
Tail Slap	1
<i>Contact</i>	3
Tail Swipe	2
Hold Down	1

Analysis of Pursuit Behavior

Behavioral events in the pursuit behavioral category (chase or inverted chase) were observed in 17 discipline sequences. The mean duration of pursuit was 10.01 ($SD = 6.19$) seconds. There was no significant difference between the pursuit durations means of mother and alloparent disciplinarians ($t(15) = 1.85$, $p > 0.05$), (Table 6).

Twelve of the seventeen pursuit behavioral events were classified as an inverted chase. The mean inverted chase duration for all disciplinarians was 8.31 seconds ($SD = 4.20$). Figure 3 depicts the average duration of inverted chase for alloparents and mothers. There was no significant difference between the mean durations of mother and alloparent inverted chases used in discipline ($t(10) = 1.05$, $p > 0.05$) (Table 6).

Table 6

Pursuit Means Statistical Analysis

Group	N	t	df	p
All Pursuit				
Mothers*Alloparents	17	-1.84	15	0.08
Mothers Only				
Mottled*Fused	8	0.237	6	0.82
Multiparous*Primiparous	8	NA	NA	NA
Alloparents Only				
Male*Female	8	0.622	6	0.56
Juvenile*Adult	9	1.961	7	0.09
Inverted Chase All				
Mothers*Alloparents	11	-1.05	10	0.32
Inverted Chase Mothers Only				
Mottled*Fused	8	-0.57	6	0.59
Multiparous*Primiparous	8	NA	NA	NA
Successful*Unsuccessful	14	-1.76	12	0.1

Note. Results from independent measures t test in which pursuit means were compared.

*groups being compared

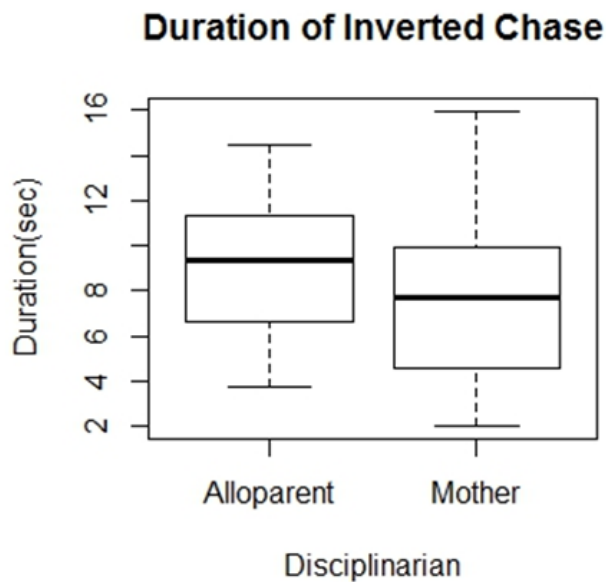


Figure 3. Mean duration of inverted chase. Includes mean duration of inverted chase for mother and alloprenant disciplinarians ($N = 12$).

Success in Discipline

For analysis, success was subcategorized into the following subcategories: 1) Success of all disciplinarians, 2) Success of behaviors used in discipline, 3) Success of mothers versus alloparents, and 4) The success of mothers as a group and success alloparents as a group. Success in discipline was determined in 24 discipline sequences. Fifty-four percent of disciplinary attempts were successful. There was no significant difference in the success between each behavioral category ($p > 0.05$) (Table 7). Mothers were successful in sixty-two percent of discipline and alloparents were successful in forty-five percent of discipline. However, there was no significant difference in the success of mothers versus alloparents in discipline ($p > 0.05$) (Table 7). Age class, sex, and parity were not found to be significant predictors of success in discipline ($p > 0.05$) (Table 7)).

Table 7

Disciplinarians Success Statistical Analysis

Group	N	p value
All disciplinarians		
Mothers*Alloparents	24	0.682
Age Class (Speckled*Mottled*Fused)	24	0.73
Age Class (Juvenile*Adult)	25	1
Parity (Primiparous*Multiparous)	18	1
Sex (Male*Female)	24	0.65
Behaviors (Contact*Pursuit*Display)	24	0.45

*groups being compared

Discussion

Description of Participants

Disciplinarians. In the spotted dolphin community on Little Bahama Bank, adults were significantly more likely to perform discipline than juveniles. Disciplinarians were equally likely to be mothers and alloparents, and both female and male dolphins were observed to perform discipline. Despite a dearth of animal behavior research that describes who performs discipline in dolphin communities, there are similarities between the spotted dolphins on Little Bahama Bank and other marine mammals in terms of what members of a community participate in parental and alloparental behavior (Herzing 1996; Hill 2003, 2009; McCowan & Reiss, 1995).

One of the main findings of this study was that adults are more likely to perform discipline than juveniles. However, the majority of dolphins sampled in this study were adults, as about half of the dolphins studied were mothers. Atlantic spotted dolphins do not reach sexual maturity until their young adult years (mottled age class), and would obviously not be able to give birth before becoming adults (Herzing, 1997). Juvenile disciplinarians were also included in the sample, but were not observed performing discipline as often as adults. Although juvenile females have been observed providing discipline to calves in the field (D. Herzing, personal communication), they were not represented in this research due to lack of video examples that met criteria for analysis. Only male juveniles were observed disciplining calves in this study, and may account for the low proportion of juveniles that performed discipline relative to adults. The possibility that juveniles, specifically females, were underrepresented in this study is high considering juvenile females have been reported to be more attracted to young and more likely to perform parental care towards young than males in human and non-human primate species, as well as in cetacean species (Cords, Sheehan, & Ekernas, 2010; Herman, Measday, & Wallen, 2003;

Maestripieri & Pelka, 2002; Mann & Smuts, 1998; Waite, Maestripieri, & Gerald, 2007). Nonetheless, discipline is often considered a component of parental care, suggesting reproductively active adults are more likely to be reported performing discipline. In social species such as dolphins, with age often comes acquisition of survival skills and knowledge of social roles, which may be related to imparting parenting/disciplinary behavior towards younger animals in their social group.

Examining the sex of disciplinarians revealed that both males and females performed discipline in the spotted dolphin community. This suggests that although male spotted dolphins have not been reported to show paternal behavior, they may still gain fitness benefits by investing in the young of their community. The high energetic cost of reproduction may elicit parental behavior in females (Clutton-Brock, 1991). Males however, may have a different motivation for disciplining a young dolphin. Their motivation may be more related to the fitness costs and benefits balanced in social living. Males, and alloparents in general, may increase their fitness by influencing the behavior of conspecifics in their social group, as they would when disciplining another dolphin. Studies on punishment in humans and primates have suggested that punishment evolved as a way to encourage cooperation and reduce selfish behavior in social groups (Boyd, Gintis, & Bowles, 2010; Gardner & West, 2004; Jensen, 2010; Riedl, Jensen, Call, & Tomasello, 2012; Seymour, Singer, & Dolan, 2007). A review of punishment in animal groups (Clutton-Brock & Parker, 1995) suggested that punishment from a dominant animal to a subordinate can increase the dominant animal's fitness. A dominant animal can use punishment to reduce unwanted behaviors by subordinate group members that would otherwise decrease the fitness of the dominant individual (Clutton-Brock & Parker, 1995). Researchers have suggested that the cost of punishment to the dominant individual is low considering the benefit that it would gain in terms of its own fitness (Boyd et al., 2010; Clutton-Brock & Parker, 1995; Gardner & West, 2004). The punisher is generally able to punish at little cost, since the receiver is already a subdominant individual. These concepts of punishment are very similar to the definition of discipline that was developed for this study. In this study, the dominant animal is the older, more experienced mother, male or alloparent, and the subordinate animal is the young calf or juvenile disciplined. A spotted dolphin calf is smaller in size than juveniles and adults, and the risk of retaliation is low from an inexperienced calf or juvenile. The dominant punisher could then benefit from the disciplinary energy expenditure by reducing the frequency of occurrence of the unwanted behavior, and increase its own fitness. A variety of individuals providing discipline in the spotted dolphin community, as well as the correlation between punishment and cooperative behavior in a social group, suggest that disciplining another group member may not just be a benefit a mother, but also to the social groups as a whole.

Receivers

In the spotted dolphin community of Little Bahama Bank, calves received significantly more discipline than juveniles. There are several reasons why this likely occurred. Spotted dolphin calves are age three and under (Herzing, 1997), and are dependent on their mothers for survival and integration into their social group. This is the case for many social mammals including other dolphin species and primates (Maestripieri, 2011; Mann, Stanton, Patterson, Bienenstock, & Singh, 2012; Rendell & Whitehead, 2001). Calves are also reported to spend the majority of their time with their mothers for the first three years of life (Herzing & Brunnick, 1997), until subsequent offspring are born. Many dolphin studies, including those on this spotted dolphin community, have indicated that mother/calf interaction and maternal care are highest in the first few months to year of an offspring's life (Hill et al., 2007; Mann & Smuts, 1998, 1999; Miles & Herzing, 2003). Thus parental care behaviors, including discipline, may be performed with higher frequency in the early years of a spotted dolphin calf's life, as opposed to their juvenile years. Furthermore, dolphin calves have the least life experience of any age class and are thus more likely to

engage in behaviors maladaptive to their survival. By the time they become juveniles, previous years of discipline may result in a lower occurrence of behaviors that reduce their chances for survival.

Alloparents may have disciplined calves more than juveniles because they were associating with other mothers. Herzing and Brunnick (1997) reported that females are most likely to associate with other females of similar reproductive status; for example, females with young calves are likely to be in the company of other females with young calves. These groups of mothers may discipline their own calves, and those of their close associates. In social living animals such as dolphins, the behavior of each individual may affect the fitness of others in the group (Clutton-Brock & Parker, 1995; Lusseau, 2007). Misbehaving calves would not only affect their own survival, but that of their mother and the social unit as a whole. Groups of mothers and calves would benefit from ensuring each calf in a social group behaved in an appropriate manner.

Behavioral Descriptions and Analyses

Behaviors used in discipline-all disciplinarians. The behaviors used in discipline included pursuit behaviors, contact behaviors, and display behaviors. Though not statistically significant, a notable trend was observed; the majority of disciplinary behaviors were pursuit behaviors, while display and contact behavior were used less often.

Pursuit behaviors were frequently observed during disciplinary behavior, and were successful more than half the time (59% success). All chases by mothers and alloparents were relatively short; every pursuit measured lasted less than thirty seconds. Considering the mechanics of a disciplinary chase, the fleeing receiver would have to change their behavior immediately in order to avoid another dolphin “catching” them. If the unwanted behavior was altered at the onset of pursuit, there would be no further need by the disciplinarian to continue to expend energy in the chase. Pursuit is an energetically expensive behavior, and a longer chase would require the use of more energy than a short chase. If a disciplinarian implemented a short, efficient chase, they may be able to change the behavior of the receiver without expending excess energy that they would otherwise allocate to other behaviors.

Many of pursuit behaviors observed in this study were inverted chases, in which the disciplinarian inverted their body throughout the entirety of the pursuit. It is unclear as to why disciplinarians inverted their bodies during many chases, or what additional benefit inverted chasing had compared to chasing in the upright position. The spotted dolphins in the Bahamas are the only cetacean community in which inverted chasing has been reported during discipline (Herzing, 1996). Inverted swimming has been identified in several dolphin species in a variety of behavioral contexts including foraging, play, and aggression (Ballance, 1992; Bearzi & Politi, 1999; Geise, Gomes, & Cerqueira, 1999; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Herzing, 1996), as well as in the spotted dolphin community in the Bahamas during courtship and aggression (Herzing, 1996). It is possible that being inverted is advantageous regardless of behavioral context in terms of sensory perception through vision and/or echolocation. Dolphins have ventral and rostral binocular vision (“Functional Systems,” 2008) and may gain a better view of their fleeing target if they invert their bodies and look upwards utilizing their stereoscopic vision. Odontocete echolocation has also been described in detail, and it has been shown that dolphins emit their most focused beam of echolocation at a five degree upward angle from their head (Au, 1997; Herzing & dos Santos, 2004). Inverting their bodies may allow them to angle this focused beam of echolocation more directly toward their fleeing target. Herzing (1996) also reported that spotted dolphin mothers “buzzed” their calf’s genitals with echolocation during inverted discipline chases; inversion of the body may again allow them to direct their strongest beam of echolocation towards the genitals of the receiving calf. This genital buzzing has also been suggested to produce a painful physical sensation to the

receiver in this highly sensitive area, which could add to the potency of the discipline being inflicted on the receiver (Herzing, 1996; Herzing & dos Santos, 2004).

Display behaviors were observed in a smaller proportion relative to pursuit behaviors. There are several reasons why this may have occurred. Compared to both contact and pursuit behaviors, display behaviors (such as an open mouth) did not require proximity to the receiver nor physical contact from the disciplinarian. The lack of proximity necessary during display behaviors may make it more challenging to change the unwanted behavior of the receiver. In addition, the success rate of behaviors from the display category was less than half (25%), which could discourage the use of display in future discipline.

Contact behaviors such as tail swipes and hold downs were observed relatively less often than both pursuit and display in discipline. This result is unexpected considering contact behaviors had the highest relative success rate of all disciplinary behavioral categories (67%). Contact behaviors could be an effective yet dangerous disciplinary tactic, resulting in infrequent use by disciplinarians. Contact behaviors are often observed in aggression in dolphins (Connor, Smolker, & Richards, 1992; Cusick, 2012; Herzing & Johnson, 1997; Scott, Mann, Watson-Capps, Sargeant, & Connor, 2004), and behaviors such as body slamming and biting have been known to cause bodily harm or even death to receivers (Dunn, Barco, Pabst, & McLellan, 2002; Scott et al., 2004). However, these behaviors are most often reported between adults (Connor et al., 1992; Scott et al., 2004) or in cases of infanticide (Dunn et al., 2002; Patterson et al., 1998). Although contact behaviors could be effective in changing a receiver's behavior, frequent use of contact discipline could result in the injury or death of a small calf or juvenile, a risk that would not be outweighed by changing their behavior. No disciplinarian, mother or alloparent, would benefit from injuring or killing their own offspring or kin, and this may explain the infrequent use of contact behaviors during discipline in the spotted dolphin community.

Behaviors used in discipline-disciplinarians subsets. One of the main goals of this study was to determine what factors influenced the use of different behaviors by individuals when disciplining. The results of this suggest that little difference exists between disciplinarians based on age class, sex, parity, or relationship to the receivers (mother vs. alloparent). Many alloparent studies have suggested that allopresents are practicing parenting skills when babysitting, so it is likely they would implement similar behaviors observed to be used by mothers (Buchan, Alberts, Silk, & Altmann, 2003; Forster & Cords, 2005; Riedman, 1982; Maestripieri, 1999; Mann & Smuts, 1998; Stone, Mathieu, Griffin, & Bales, 2010; Strier, 2007). Furthermore, studies on male parental behavior have indicated that the parenting behaviors used by males are also similar to those used by mothers and female allopresents (Schradin & Pillay, 2003; Schradin, Reeder, Mendoza, & Anzenberger, 2003). It should be noted, however, that data in this study spanned thirteen years, and some dolphins were observed performing discipline in the earlier years of this study, and again in later years. This could have influenced the results because some dolphins performed the same behaviors over many years of raising their own calves and providing alloparental care towards the calves of others. This could be representative of a consistent maternal style, which has been observed in studies on primates and cetaceans, and may be true for female spotted dolphins while implementing discipline (Fairbanks, 1996; Francis, Young, Meaney, & Insel, 2002; Hill et al., 2007; Maestripieri, 2011).

Success in Discipline

Varying disciplinary outcomes could be evidence for different animals and behaviors yielding more success than others. However, the results of this study suggested there were few differences in who performed discipline apart from age of the disciplinarian. Furthermore, this analysis found an almost equal amount of successful and unsuccessful disciplinary encounters. Despite the fact that adults were

significantly more likely to perform discipline than juveniles, there was no evidence of adults achieving more success than juveniles. Other factors such as sex and parity did not appear to influence success in discipline either. These results may be due to small sample sizes, and more significant trends may have emerged if more samples of discipline were available. However, lack of significance could also be attributed to the nature of variables included in this study. For example, a factor such as parity may be a poor predictor of the success in discipline. Parity is based on how many times an individual has given birth; not necessarily how many successful offspring they have raised to independence. It is difficult to predict that multiparous females would have more success in parenting and discipline solely because they have had multiple offspring. A multiparous female may have given birth multiple times because their calves died, thus giving them more opportunities to reproduce. A primiparous female may have only given birth once, but may have more parenting experience by raising one successful calf or via alloparenting. Research on how parity affects parenting behavior is inconclusive. Although several studies have suggested differences in parenting behavior are related to parity (Hill, 2009; Lang, Boness, Bowen, & Iverson, 2011; Maestriperi et al., 2009), others have shown that individual differences in maternal style are consistent over time and offspring (Champagne, Francis, Mar, & Meaney, 2003; Hill et al., 2007).

The lack of difference in success rates may be also due to the fact that most individuals that performed discipline did so in a similar manner, and thus achieved similar rates of success and failure. All disciplinarians implemented all three behavioral categories of discipline; pursuit, contact, and display. Despite a lack of significance, there was evidence from the results of this study that pursuit and contact behaviors did yield more success in general than did display behaviors. Pursuit behaviors were widely used during discipline, and though not significantly different, the average duration of successful pursuits was shorter than that of unsuccessful pursuits. This may be due to the cost of *being* chased. Fleeing an incoming disciplinarian is energetically expensive, and may quickly motivate a receiver to stop their unwanted behavior and not perform it again. Short chases may also be related to the threat of discipline that a chase implies. In some cooperatively breeding animals, dominant individuals maintain cooperation and order in their society through the threat of costly punishment to an uncooperative individual (Jensen, 2010; Wong, Buston, Munday, & Jones, 2007). Subdominant individuals in the population may choose to limit the frequency of unpopular behaviors to avoid being attacked or exiled from their social group or denied other social and reproductive benefits (Balshine-Earn, Neat, Reid, & Taborsky, 1997; Johnstone & Cant, 1999; Wong et al., 2007). Similarly, humans are considered a highly cooperative species and much of human societal law and order is based on the threat of costly punishment for the breaking of laws; including fines, jail time, and other legal action (Boyd et al., 2010; Seymour et al., 2007; Sigmund, 2007).

Conclusion

This study found that on Little Bahama Bank in the Bahamas, adult spotted dolphins, including mothers and alloparents, primarily discipline calves. Various behaviors are used in discipline, most notably a pursuit behavior such as an inverted chase. Pursuit behaviors yielded a relatively high success rate, and chases ended within seconds from their start. Within disciplinarians, factors such as age class, sex, and parity did not appear to influence how discipline was imparted nor its success rate.

The operational definition of discipline defined for spotted dolphins in this study may be applied to the behavior of parents, alloparents, and other social associates of the receivers of discipline. Future research may utilize this definition as it can be applied to other social animal communities in which disciplinary behavior is observed. Future research should also focus on defining the similarities and differences between punishment and discipline. Punishment has been examined in many animal species, though little comparison or distinction is made between it and discipline. Studies on punishment tend to

include interactions between all individuals of a population, whereas discipline is generally considered in literature as occurring between parents and offspring. Detailed comparisons of punishment and disciplinary behavior would allow for a better understanding of the roles each play in social animal interactions.

Future research on discipline specifically should focus on exploring other aspects of discipline including what behaviors provoke disciplinary action, and how disciplinary styles affect survival of the offspring. This would allow for a more complete picture of the function of discipline in animal societies and how it is related to the fitness costs and benefits of living in a social group. Obtaining a large enough sample size to run powerful statistical tests is a common challenge in many animal behavior studies, and studies with larger sample sizes could strengthen the trends reported here. This project examined a small aspect of dolphin behavior that has never been explicitly analyzed, and the continued study of discipline will reveal insight into the nature of social behavior and cultural trends among group-living animals.

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