Spring 5-2017

Identifying Behavioral Response Trends Following Aggression in Bottlenose Dolphins (*Tursiops truncatus*)

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Recommended Citation

Cheri, Breanna M., "Identifying Behavioral Response Trends Following Aggression in Bottlenose Dolphins (*Tursiops truncatus*)" (2017). *Honors Theses*. 537.
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The University of Southern Mississippi

Identifying Behavioral Response Trends Following Aggression in Bottlenose Dolphins (*Tursiops truncatus*)

by

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A Thesis
Submitted to the Honors College of
The University of Southern Mississippi
in Partial Fulfillment
of the Requirement for the Degree of
Bachelor of Science
in the Department of Biological Sciences

May 2017

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Abstract

In group-living species, an individual's response to aggression from another animal can reveal information about the complexities of their social relationships. The current study sought to categorize behavioral responses between conspecifics following direct aggression. Agonistic behavioral interactions were analyzed in a semi-captive group of bottlenose dolphins housed at the Roatan Institute for Marine Sciences, whose population dynamics mirror those observed in the wild. Interactions began at the onset of an aggressive behavior, and all concomitant behaviors between aggressor(s) and recipient(s) were coded chronologically for the length of each event. Results revealed five response types present following aggression: retaliation, reconciliation, avoidance, sexual, or no reaction. Response type varied based upon age-class, sex, and initiator/recipient role in the initial aggression. Specifically, subadults were more likely to be involved in retaliation than other age-classes. Calves were more likely to respond through reconciliation, avoidance, or had no reaction during conflicts, possibly due to mother-calf relationships (i.e., alloparenting, discipline, and protection). Additionally, males were more likely to retaliate, while females tended to avoid or reconcile with opponents, which is a reflection of the sex specific reproductive pressures observed in fission-fusion groups. Understanding behavioral pressures on demographic and social roles in aggressive interactions may aid management practices for both captive and wild populations.

Key Terms: *Tursiops truncatus*, aggression, reconciliation, conflict, avoidance, sociality, behavioral response

Dedication

Thank you to everyone who has supported me through my college career. With your love and encouragement I have completed another chapter in my life and will be embarking on my newest adventure as a Marine Biologist.

Acknowledgements

I would like to thank my thesis advisor, Dr. Stan Kuczaj, for accepting me into the Marine Mammal and Cognition Laboratory when I started here at USM. You pushed me to further my interest in the areas of marine mammal behavior and showed me what it would take to pursue my ambitions. I am gracious for all of the opportunities you gave me, for your help and understanding, and most of all for your kindness throughout my time in lab and while working on my thesis. Thank you from the bottom of my heart.

I would like to thank Erin Frick for the years you spent mentoring me. I could not have completed this thesis without your support. Through this entire rigorous process of research and coding, you were always there to lend me a hand. I cannot thank you enough for motivating me and keeping me going.

I would like to thank Kelsey Moreno for your assistance in making my research goals a reality. You were always nearby, never failing to offer your help and advice. I deeply appreciate everything you have done.

I would like to thank Dr. Eric Platt for teaching me how to begin the thesis writing process. I will never forget how enthusiastic you were about my research. Thank you for inspiring me.

Finally, thank you Dr. David Echevarria for stepping in to advise me while my thesis was in its final stages. I am very grateful for your support.

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Chapter 1: Introduction

Aggression is observed across many social species such as chimpanzees (*Pan troglodytes*; Koski, Kopps & Sterck, 2007), ravens (*Corvus corax*; Fraser & Bugnyar, 2011), African elephants (*Loxodonta africana*; Poole, 1989), and bottlenose dolphins (*Tursiops truncatus*; Sargeant, & Connor, 2005; Scott, Mann, Watson-Capps, Sargeant, & Connor, 2005). Aggression is typically categorized as hostile behaviors exhibited towards other conspecifics, potentially inflicting harm (e.g., Samuels & Gifford, 1997; Scott et al., 2005). Causes of aggression are not well understood, but records of these exchanges may lead to a more refined understanding of group living for social species. Due to their complex social structures and maintenance of a social hierarchy, bottlenose dolphins have served as a model species in recent decades to assess aggression and conflict resolution (e.g., Holobinko & Waring, 2009; Krutzen et al., 2003).

Evolutionarily, cetaceans have developed as social animals. Bottlenose dolphins in particular live in fission-fusion societies in which members of a group frequently split and intersperse (i.e., change composition) with other members of the same species (Conner, 2000). This provides the opportunity to socialize with and potentially learn from other conspecifics (Conner, 2000). The function of social behavior is context-specific (e.g., breeding, parental care (Tinbergen, 2012), alliance formation, competition (Conner, 2007)). Aspects of group-living such as dominance, inclusive fitness, reproductive competition, and different levels of kin and non-kin cooperation often lead to bouts of aggression between members (Marler, 1976; Widdig, Streich, Nurnberg, Croucher, Bercovitch, & Krawczak, 2006). Following aggression, opponents may experience anxiety, elevated stress levels, or an increased potential for further hostility (Koski et al., 2007).

Sex differences in gregarious species often play a large role in how frequently aggression is expressed by individuals. In bottlenose dolphins, males show heightened sexual aggression (Smuts, 1993). Intrasexual selection pressures (i.e., polygamy) have a direct influence on male dolphin dimorphism and dominance behaviors directed towards other males (Tolley et al., 1995). Female dominance is suggested to be more influenced by social bond formation with calves and subadults, evidenced by the stable relationships female dolphins' exhibit and maintain in adulthood (Stockley & Bro-Jorgensen, 2011). Scott et al. (2005) discussed how adult and juvenile male bottlenose dolphins are more likely to engage in raking behavior compared to females. Conversely, adult females are suggested to be highly tolerant, thus exhibiting decreased frequencies of aggressive behavior towards males or other females (Scott et al., 2005). Frick (2016) showed that personality traits may correlate with dominance for both the male and female hierarchies. Dominant males exhibited higher rates of agonistic behavior (i.e., assertive traits), but lower rates of sexual behavior. In the study population, sexual behaviors were nearly always between less dominant males, suggesting their need to build social bonds and decreased access to receptive females. Female dominance had no correlation to agonistic or sexual behaviors (Frick, 2016). Females may exhibit decreased amounts of female-female conflict due to stable associations (i.e., social bonds with other females) and lack of competition for mating opportunities (Samuels & Gifford, 1997; Scott, 2005). Males are the larger sex as adults, however, smaller juvenile males may begin to aggress towards larger females to begin establishing dominance before competing with dominant males (Samuels & Gifford, 1997). Thus relative social rank position for both sexes should play a role in the context of aggressive behavior and to what extent those behaviors will be expressed (e.g., advertising threat vs. contact aggression).

Aggressive behaviors in dolphins can vary in their severity. For example, dolphins are often observed to bite one another, at times escalating to directly ramming with the rostrum, which can be fatal to calves (Connor, 2000). A modified form of bite behavior is rake marking. Rake marks are faded scars resulting from a dolphin running its teeth across the skin of another leaving relatively deep tears (Scott et al., 2005). Overstrom (1983) made observations of captive bottlenose dolphins identifying a "warning" behavior in the form of slow pulse trains from one male to another. Jaw claps (i.e., mouth is suddenly snapped closed, typically creating a loud "pop" sound) served as an index for aggression in this population, as the occurrence of jaw claps preceded an escalation of aggressive responses (i.e., open mouth displays, burst pulse emission, and chase attacks). Open mouth displays constitute a "threat" which consists of one dolphin facing another dolphin head on with vertical up-down motions of the head, and may be accompanied by the expelling of bubbles. Open mouth displays are typically accompanied by chases (i.e., one or more dolphins rapidly pursue another; Dudzinski, 1996), mouthing (i.e., placement of the mouth over a part of the body of another without biting; Overstrom, 1983), and burst pulse emissions (i.e., broad band sounds directed at an opponent, Overstrom, 1983) which all can vary in frequency and severity (Overstrom, 1983). Conflict also resulted in bubble expulsion and tail slaps (i.e., one dolphins hits another with their fluke; Overstrom, 1983).

There are many other behaviors from the dolphin behavioral repertoire that are discussed in the context of their relevance in certain agonistic contexts. Dudzinski (1996) described several of these behaviors including head and tail jerks, sharp vertical or lateral movements of the head and flukes. Other behaviors include head-to-head circling or pushing. Ongoing aggression between opponents may initiate a sequence of behaviors such as fighting (e.g., chasing, biting, and hitting another individual). Aggression may escalate with body slamming (e.g., slamming the body against another, charging (e.g., a direct, fast approach), or fluke hitting (e.g., hitting another dolphin with a quick, full-on vertical thrust of its flukes) (Dudzinski, 1996). Emissions of bubbles from the blowhole are also thought to occur in aggressive contexts or to add emphasis to vocalizations (Pryor, 1990). A common bubble display are bubble streams (e.g., a stream of several small bubbles and bubble bursts are a cloud of bubbles) (Dudzinski, 1996). Pryor (1990) also reported S-shaped body posture (i.e., S-posturing) among threatening displays, although less is known about how this particular behavior communicates agonistic signals.

Physical contact plays an essential role in dolphin aggression, but it is also believed to serve a function in affiliation. Dudzinski (1998) observed three associative behaviors, petting (i.e., movement between pectoral fins), rubbing (i.e., movement between one dolphin’s body and a portion of another’s body), and contact position (i.e., pectoral fin placed on the lateral surface of another without movement). Petting was speculated to function in reciprocal behavior or appeasement while rubbing was believed to strengthen bonds. Contact position appeared to involve some level of synchrony and could serve to advertise short-term associations. Paulos, Dudzinski, and Kuczaj (2008), also examined touch behaviors associated with three focal interactions, depart (i.e., one or more dolphins leave company of others), join (i.e., two or more dolphins come together) and contact (i.e., contact using any part of the body), between individual dolphins. The authors suggested that touch may serve a role in strengthening social bonds between individuals as well as other aspects of communication.

Species that exhibit a fission-fusion social structure such as the bottlenose dolphin cannot maintain their social structures if relationships are discontinued as a result of conflict (Aureli, Cords, & van Schaik, 2002; Aureli & Schaffner, 2007). Similarly, Aureli et al. (2002) suggested that animals would have a harder time predicting their opponent's response to a conflict if they exhibit low compatibility and low relationship security. Therefore, if bonds are weakened by aggressive encounters, the benefits that could be gained through association are reduced (de Waal, & Aureli, 1996). Thus, the re-strengthening of those bonds may require the initiation of reconciliatory behaviors (i.e., affiliative).

Reconciliation is when opponents engage in behaviors that resolve past conflict and establish positive relations (Aureli et al., 2002). Relationships encourage cooperation between conspecifics who benefit from shared interactions, as seen with the frequency that spotted hyena (*Crocuta crocuta*) reconcile with non-kin who share less secure relationships than kin, but whose cooperation is valuable to survivorship (Wahaj, Guse, & Holekamp, 2001). As it pertains to cetaceans, reconciliatory behaviors may exemplify the need to maintain strong pair bonds after aggressive encounters, as seen in a study where affiliative behavior in bottlenose dolphins (i.e., from the same population used in the current study) in 2010 were more prevalent than agonistic or socio-sexual behaviors

(Harvey, Dudzinski, & Kuczaj, 2017). Given they reside in a managed care facility with different constraints than the wild, the tendency towards affiliation between pairs of the same age and sex serves an important role in socialization and bond formation (Harvey et al., 2017). The degree to which members of any given species choose to affiliate with one another largely depends on the behavioral and physical costs the organism faces, and how worthwhile a continued or renewed relationship outweighs those costs (Koski et al., 2007). Costs among various species can range from energy expenditure, likelihood of injury, loss of access to resources, a lowering of social rank, and the chronic release of hormones related to stress (Goymann & Wingfield, 2004; Koski et al., 2007; Pellis, 1997). For example, Enghet al. (2006) found that stress levels increase in female chacma baboons (*Papio hamadryas ursinus*) when a close relative dies. After this stressful event, females exhibit increased attempts to form bonds with new individuals, especially their closest female relatives (Silk, Altmann, & Alberts, 2006), which effectively lowers stress levels (Engh et al. 2006).

While close kinships may compel individuals to reconcile, certain species have been observed to exhibit reconciliatory behaviors with unrelated conspecifics. Ravens have been observed to be capable of exhibiting relationship repair after conflict, despite opponents not having a close pair bond—which is indicative of the relationship having an adaptive value even with the presence of competition or clashing of interests (Fraser & Bugnyar, 2011). In captive chimpanzees, reconciliation between females may occur less often due to a decreased risk to their secure relationships as supported by the lack of elevated scratching rates (e.g., anxiety) prior to conflicts (Koski et al., 2007). After conflicts have taken place, opponents enter into a timeframe when they may express behaviors which may help reestablish their social connection to the opposing individual if seen as advantageous. For example, stumptailed macaques (*Macaca arctoides*) remain in close proximity with an opponent during a post conflict period suggested to initiate some form of reconciliatory behavior (Call, Aureli, & Waal, 1999).

In cetaceans, behaviors such as contact swimming and flipper-rubbing have been identified as means to reaffirm social bonds and increase latency between future aggressive acts (Conner, Mann, & Watson-Capps, 2006; Tamaki, Morisaka, & Taki, 2006). Pectoral fin contact (rubbing) has been determined to be a social behavior, possibly affiliative in nature, in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) and Atlantic spotted dolphins (*Stenella frontalis*; Dudzinski, Gregg, Ribic, & Kuczaj, 2009). Tamaki et al. (2006) examined if flipper-rubbing behavior in dolphins decreased the likelihood of future aggressive acts occurring between group members. There was a significant number of flipper-rubbing behaviors that fell within the post-aggression (post-AG) period between both the adult female dolphins and juvenile male dolphin (Tamaki et al., 2006). For each individual, there was a significant increase in the length of time between aggressive acts after an opponent initiated post-AG flipper-rubbing (Tamaki et al., 2006). These findings show that minimized occurrences of aggression are seen in captive dolphins after prior affiliative contact, which leads to further questioning of how these findings correlate with wild populations.

Holobinko and Waring (2009) showed that a small population of captive bottlenose dolphins exhibited a lower rate of reconciliation (e.g., the act of repairing weakened social bonds) following conflict (e.g., direct or indirect aggression between opponents) than expected when examining how sex and age influence post-conflict affiliative behavior. Their results showed that in most cases, instances of post-conflict reconciliation were decreased compared to other outcomes for conflict, which was contrary to previous findings (e.g., Weaver, 2003) where rates of affiliation were significantly high. Age was significantly related to an individual's frequency of engaging in conflict, but not reconciliation. The sex composition of the study group was not adequate to determine sex differences. However, there were low rates of conflict between a juvenile male and allomaternal female pair, which contradict results of conflict analysis in other studies (e.g., Schroeder, 1990; Wells, Scott, & Irvine, 1987). The authors suggest expanding analysis of post-conflict reconciliation to a larger population with more variable demographics (i.e., age-class and sex) in order to validate any behavioral hypotheses. They speculate that reconciliation may be a less necessary and frequent outcome to conflict in the wild due to relaxed physical constraints in those habitats, and that more variables than age and sex affect outcomes to aggression. Lastly, aggression and affiliation (i.e., reconciliation) are termed conclusions to animal motor patterns rather than behaviors themselves (as stated by S, Green in Holobinko & Warring, 2009). It is then required that agreement between researchers over the stability of context-specific motor patterns related to conflict must be made before assuming that reconciliation is taking place (Holobinko & Warring, 2009).

A study performed on wild Assamese macaques (*Macaca assamensis*) sought to collect information on displays of positive and negative interaction relating to aggression, affiliation, and submission (Cooper, Bernstein, & Hemelrijk, 2005). The importance of distinguishing these behaviors is that it allows for notating association patterns between individuals and what reactions they will likely exhibit during continued or later interactions. While submission signifies avoidance of an aggressive party it may also be a sign of recognizing hierarchal rank, whereas, affiliation (e.g., playing contact, arousal, etc.) may illustrate the desire to cooperate. Direction of aggression is also an important factor to consider, as it dictates who initiated a conflict and if the aggressee retaliated (Koski et al., 2007).

Retaliation is a physical counterattack by an aggresse or a returned warning meant to intimidate. These acts are not well documented across the field of animal behavior and cognition, but it is suggested that retaliation behaviors take place in communities of social animals. Pellis (1997) explained that whether or not an animal will choose to strike out against an opponent may depend on the situation and the desired message the two opponent's attempt to convey through their behaviors. Therefore, an aggressor's behavior and body morphology may influence the choice to retaliate. If retaliation does occur, whether or not it is meant to warn or suppress the aggressor may largely depend on the intensity of the counter attack and the body parts that are targeted (Pellis, 1997). The intent of retaliation, the particular members of a group that exhibit this behavior, and how the attack is directed are important factors in understanding when retaliation is likely to take place.

The Current Study

The goal of the present study is to determine what different reactions to aggression (i.e., social conflict) in bottlenose dolphins are occurring. This study coded the consecutive response behaviors that followed aggression between opposing dolphins from the time the event started to 15 seconds after the opponents ceased interacting. Events were defined by the broader category of response (e.g., retaliation, reconciliation, avoidance, sexual, no reaction) and ANOVA and Chi-square comparisons were made within age-classes, sexes, and roles as initiator or recipient. Based on previous literature, it is likely that variables such as age, sex, rank, and kin-status will affect responses to aggression. Specifically, it was hypothesized that adults will retaliate more often when confronted with conflict than younger individuals, where adults will be more inclined to reconcile and calves will be the most likely to avoid aggression. It is expected that males will be more likely to initiate and be involved in aggressive interactions, and exhibit a retaliatory response more often than females. Conversely, females will have a lower frequency of aggressive responses and will reconcile more often. Initiators of conflict-retaliation events will more often be males and recipients of conflict-reconciliation events will more often be females. These hypotheses are believed to support the sex differences in bottlenose dolphins previously found in the literature.

Chapter 2: Methods

Subjects and Facility

The study population of semi-captive bottlenose dolphins was housed at The Roatán Institute for Marine Science (RIMS) at St. Anthony's Key Roatán Honduras (Figure 1). The dolphins reside in an enclosed sea pen approximately 8,000m^2, with a depth range from the shoreline to approximately 7m. The population during 2013 consisted of 30 bottlenose dolphins (both males and females) of varying age-class (i.e., calf – dependent and nursing, Sub adult – independent but not sexually mature, adult – reproductive (Eskelinen, Winship, & Borger-Turner, 2015)).

Figure 1. RIMS facility. Photograph by Enrick H. Bush.

Data Collection

Dr. Stan Kuczaj and graduate students from the Marine Mammal Behavior and Cognition lab (University of Southern Mississippi) collected underwater video and audio data using a Nauticam M16 with Amphibico hydrophone adapter, which allowed for simultaneous audio and video data. Video footage was recorded opportunistically during

2013, between 5:30am-4:00pm. Videos ranged from a few seconds to several minutes long, totaling 788 minutes of data for analysis. The data was collected using focal-animal all-occurrence sampling (Altmann, 1974). Focal follows began when an animal came into view and terminated when the animal disappeared from view (Dudzinski et al., 2009).

Data Analysis

Behavior coding of a variety of known aggressive behaviors in dolphins (Appendix A) was used identify all occurrences of aggressive interactions (i.e., events). For each of these events, the initiator and the recipient identified and all behaviors following aggression were coded for both the initiator(s) and recipient(s). Behaviors from each broader context group of, retaliation (e.g., aggressive behaviors that are redirected towards the aggressor, reconciliation (e.g., post-conflict affiliative behaviors), avoidance (e.g., attempt to move away from an aggressor), sexual (e.g., mounting or copulation attempt), and no reaction, were coded for each aggressive event (for operational definitions of all behaviors, see Appendix A). Behaviors were coded chronologically from the first instance of aggression to the last behavior exhibited between the group. Sampling periods were noted for each encounter between opponents providing the general length of each encounter. If the dolphins swim out of view then only the initial actions can be observed unless they swim back into view. To address this, 15 seconds will be added to the end of each aggressive encounter. The end of these 15 seconds is considered the coding end time in which no interaction has continued. If opponents swim back into view—before the defined end time—then the encounter is a continuation of when it began.

Each aggressive event was categorized for the overall response to aggression based upon the ending behavior of that event. For example, if subject A is the recipient of an aggressive behavior (i.e., conflict) from subject C, and the majority of the behaviors that ended the interaction consisted of mounting (i.e., sexual), the interaction was categorized as conflict-sexual. Other possible categories for each event include conflict-retaliation, conflict-reconciliation, conflict-avoidance, conflict-sexual, conflict-no reaction. These broad categories were used to make comparisons between the ages and sex of the individuals.

The initiator of an encounter was defined as the first individual observed to exhibit aggression. The recipient was defined as the individual that the aggressive behavior was directed toward. Multiple initiators or recipients may appear in a single encounter. All initiators and recipients were identified using physical attributes visible on their dorsal fins, flukes, and body. These include nicks, notches, and scars (Wursig & Wursig, 1977) as well as differences in pigmentation. Temporary visual characteristics such as rake marks and scratches are tracked and monitored during the seasons to assist in identification. In some events multiple individuals aggressed towards one or more recipients. These encounters were coded as ‘group aggression’ if individual dolphins could not be identified. Group aggression was not included in analysis. Only aggressive encounters in which both identities can be confirmed for dolphins will be included in statistical analysis.

All statistical analyses were run through SPPS software. Analysis of variance (ANOVA) tests ran comparisons of frequencies between response type and age class across all dolphins involved in that type of interaction, their likelihood of being the initiator, and likelihood of being the recipient of overall differences. Chi-square tests were run to compare frequencies between females and males in each of the broader categories (i.e., conflict-retaliation, conflict-avoidance, etc.,) across all dolphins involved in that type of interaction, their likelihood of being the initiator, and likelihood of being the recipient of overall differences. For significant omnibus tests, standardized residuals greater than ± 2 were used to determine significant groups (Sharpe, 2015).

Chapter 3: Results

Age-Class Comparisons

Retaliation

There was a significant effect of age-class on which individuals were involved in conflict-retaliation interactions ($F(2, 27) = 7.755$, $p = 0.002$; Figure 2). Post hoc tests using the Bonferroni correction revealed that subadults ($p = 0.002$) were significantly more likely to be involved in conflict-retaliation exchanges than adults. There was no significant difference between calves and subadults or adults and calves ($p > 0.05$). There also was a significant effect on if individuals of a certain age-class were the initiators of a conflict-retaliation event ($F(2, 27) = 6.772$, $p = 0.004$), or the recipients ($F(2, 27) = 4.774$, $p = 0.07$; Figure 2) in that subadults were significantly more likely to be the initiators ($p = 0.004$) and the recipients ($p = 0.019$) of a conflict-retaliation interaction compared to adults. There was no significant relationship found between subadults and calves and adults and calves for the initiator or recipient of conflict-retaliation interactions.

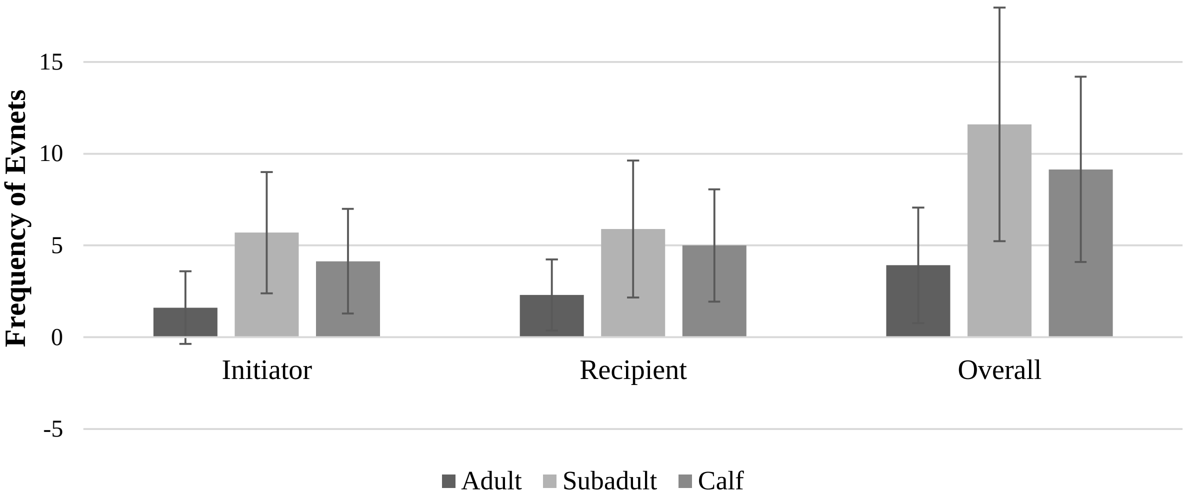

Figure 2. Mean values for retaliation between age-classes. Error bars indicate standard deviation.

Reconciliation

There was a significant effect of age-class on which individuals were involved in conflict-reconciliation interactions (*F*(2, 27) = 5.041, $p = 0.014$; Figure 3). Post hoc tests using the Bonferroni correction revealed that calves ($p = 0.012$) were significantly more likely to be involved in conflict-reconciliation exchanges than adults. There was no significant difference between calves and subadults or adults and subadults ($p > 0.05$). There was no significant effect on whether individuals of a certain age-classes were the initiators or recipients of a conflict-reconciliation event.

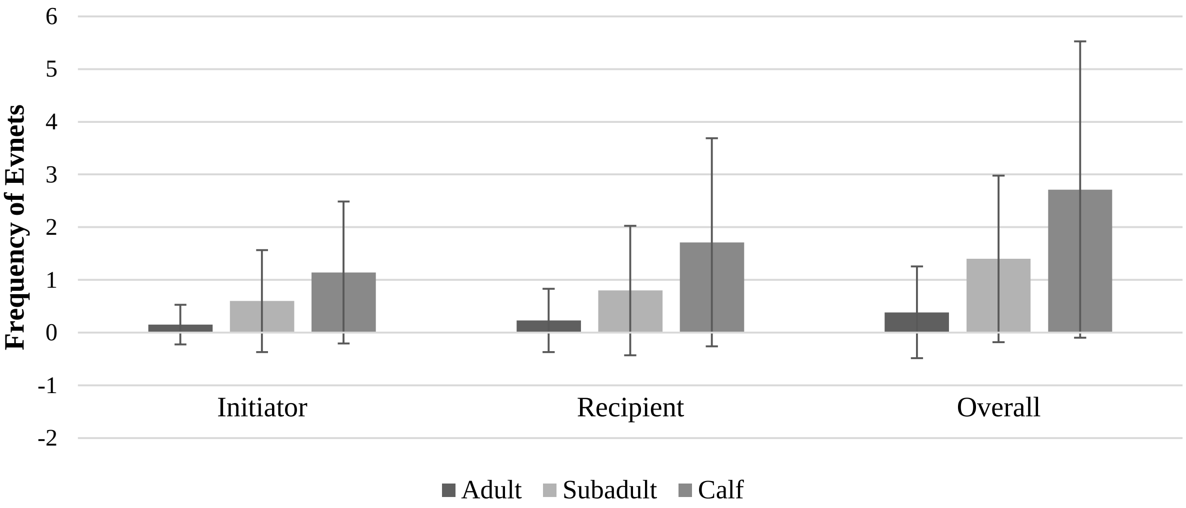

Figure 3. Mean values for reconciliation between age-classes. Error bars indicate standard deviation.

Avoidance

There was a significant effect of age-class on which individuals were involved in conflict-avoidance interactions (*F*(2, 27) = 8.724, $p = 0.001$; Figure 4). Post hoc tests using the Bonferroni correction revealed that calves were significantly more likely to be involved in conflict-avoidance exchanges than adults ($p = 0.001$) and subadults ($p = 0.044$). There was no significant difference between subadults and adults ($p > 0.05$). There also was a significant effect on if individuals of a certain age-class were the recipients of a conflict-avoidance event (*F*(2, 27) = 6.772, $p = 0.004$; Figure 4), in that calves were significantly more likely to be the recipients of a conflict-avoidance interaction compared to adults ($p = 0.000$) and subadults ($p = 0.004$). There was no significant relationship found between subadults and adults for the recipient of conflict-avoidance interactions. There was also no significant relationship between age-classes for the initiator of conflict-avoidance interactions.

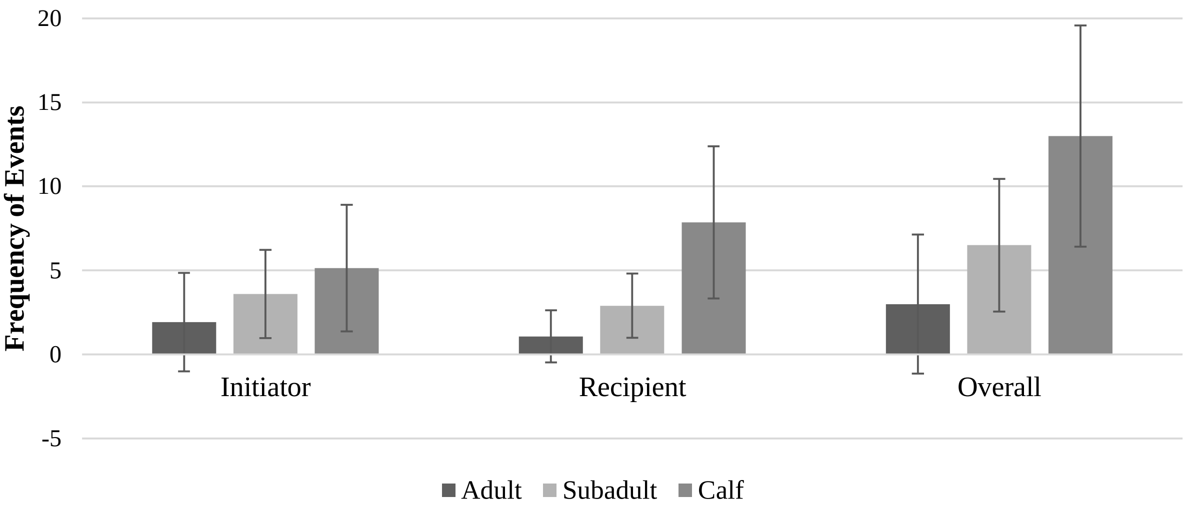

Figure 4. Mean values for avoidance between age-classes. Error bars indicate standard deviation.

Sexual

There was no significant effect of age-class on which individuals were involved in conflict-sexual interactions or if they were the actors or recipients.

No Reaction

There was a significant effect of age-class on which individuals were involved in conflict-no reaction interactions ($F(2, 27) = 6.747$, $p = 0.004$; Figure 5). Post hoc tests using the Bonferroni correction revealed that calves ($p = 0.003$) were significantly more likely to be involved in conflict-no reaction exchanges than adults. There was no significant difference between calves and subadults or adults and subadults ($p > 0.05$). There also was a significant effect on if individuals of a certain age-class were the recipients of a conflict-no reaction event ($F(2, 27) = 9.424$, $p = 0.001$; Figure 5), in that calves were significantly more likely to be the recipients of a conflict-no reaction interaction compared to adults (*p* = 0.001) or subadults (*p* = 0.007). There was no significant relationship found between adults and subadults for the recipient of conflict-no reaction interactions. There was no significant relationship found between age-classes for the initiator of conflict-no reaction interactions.

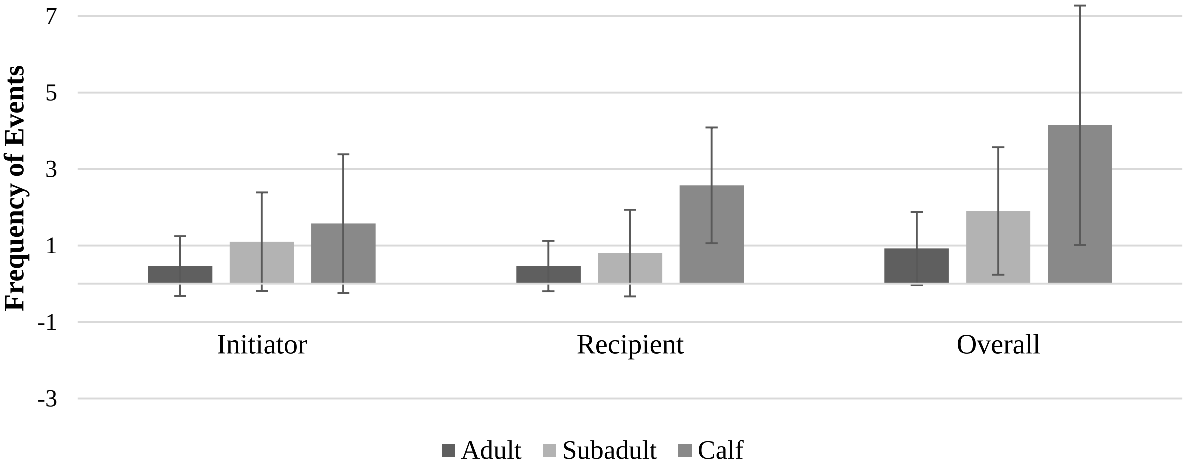

Figure 5. Mean values for no reaction between age-classes. Error bars indicate standard deviation.

Sex Differences

Overall

There was a significant difference in the frequency of the type of outcome following aggression males or females engaged in X^2 (4, *N* = 548) = 14.58, *p* = 0.006; Figure 6). Males were significantly more likely to engage in conflict-retaliation interactions (Std. Residual = 3.40) compared to females. Females were significantly more likely to engage in interactions conflict-avoidance (Std. Residual = 2.30) compared to males. There was no significant differences between sexes for frequencies of interaction types conflict-reconciliation (Std. Residual = ± 1.9) conflict-sexual (Std. Residual= ± 0.80) and conflict-no reaction (Std. Residual = ± 0.70).

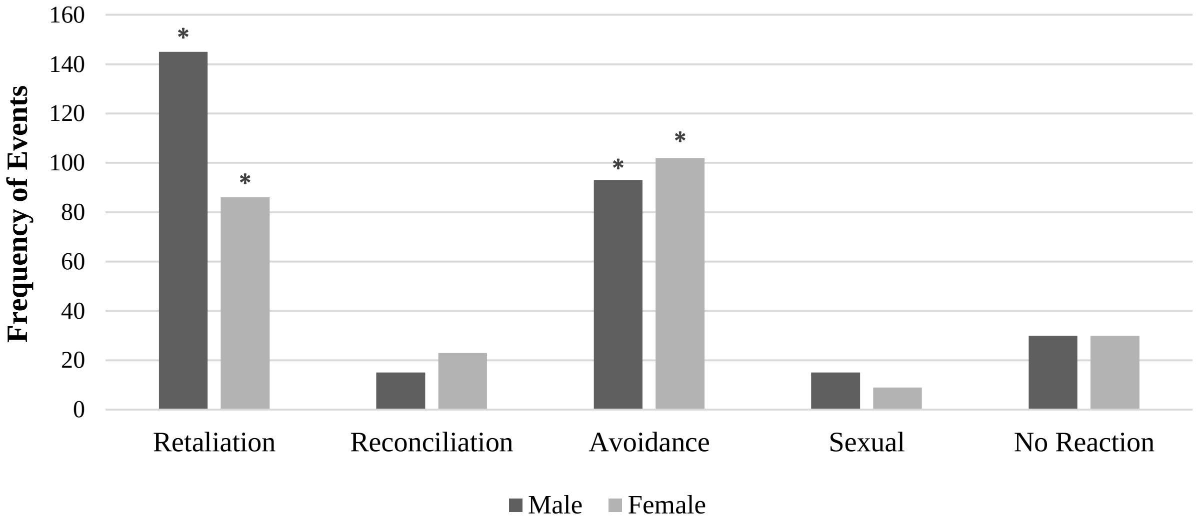

Figure 6. Overall sex differences in each category of behavior. Asterisks (*) indicate a significant difference.

Initiator

There was a significant difference in the frequency of the type of outcome following aggression in which males or females were the initiator in X^2 (4, N = 250) = 12.89, p = 0.012; Figure 7). Males were significantly more likely to initiate conflict-retaliation interactions (Std. Residual = 2.70) compared to females. Conversely, females were significantly more likely to initiate conflict-reconciliation interactions (Std. Residual = 2.90) compared to males. There was no significant differences between sexes for whether males or females were the initiator for conflict-avoidance (Std. Residual = ± 0.60), conflict-sexual (Std. Residual= ± 0.10), and conflict-no reaction (Std. Residual = ± 0.30).

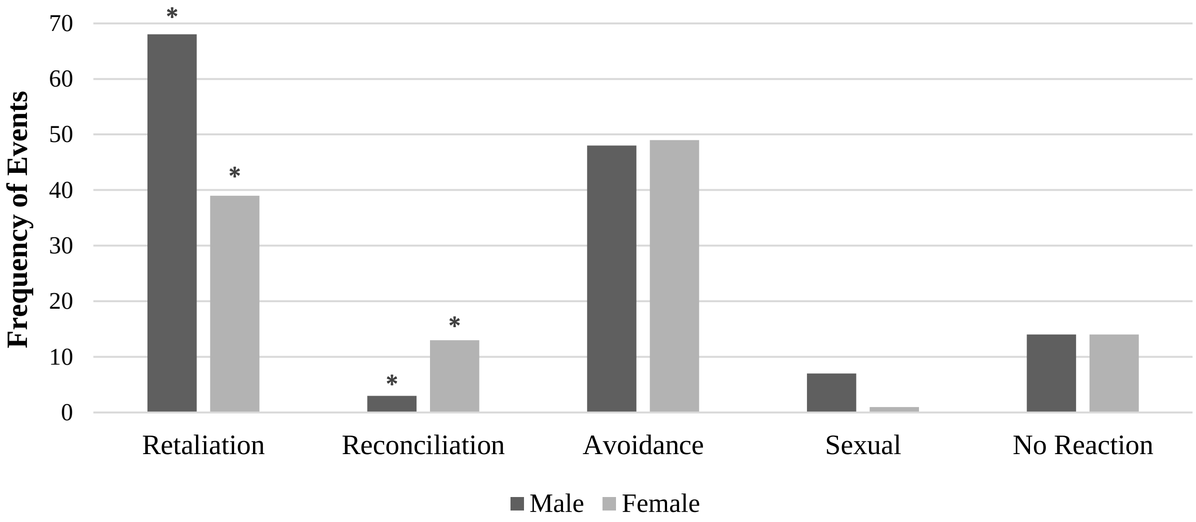

Figure 7. Initiator sex differences in each category of behavior. Asterisks (*) indicate a significant difference.

Recipient

There was no significant omnibus effect in the frequency of the type of outcome following aggression in which males or females were the recipient in X^2 (4, N = 293) = 6.22, p = 0.184; Figure 8). However, comparisons of the adjusted residuals indicated that males were more likely to be recipients in conflict-retaliation interactions (Std. Residual = 2.3) whereas females were more likely to be a recipient of conflict-avoidance interactions (Std. Residual = 2.0). There was no marked differences between sexes for whether males or females were the recipient of conflict-no reaction (Std. Residual = ± 0.50), conflict-sexual (Std. Residual= ± 0.40), and conflict-reconciliation (Std. Residual = ± 0.20).

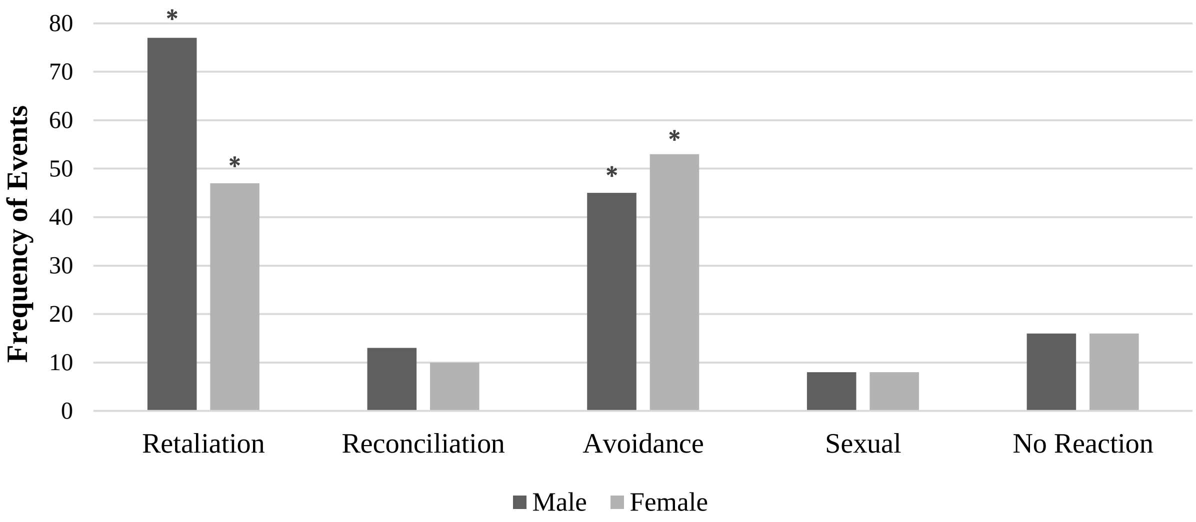

Figure 8. Recipient sex differences in each category of behavior. Asterisks (*) indicate a significant difference.

Chapter 4: Discussion

Significant patterns of agonistic behavior for each of the compared fields was present across this focal population. The hypotheses that stated adults would be involved in more cases of conflict-retaliation and conflict-reconciliation were not supported by the data. Subadults were significantly more likely to be involved in conflict-retaliation than adults, which was also the case when subadults were the initiators and recipients in conflicts. Additionally, calves were involved in significantly more conflict-reconciliation events that adults. The hypothesis on avoidance in calves was supported in that calves were significantly more involved in conflict-avoidance events than both adults and subadults. Calves were more likely to avoid conflict when they were the recipients of aggression by both adults and subadults.

Males were more likely than females to be involved in conflict-retaliation and were similarly more involved as the initiators and recipients in retaliation. Females were more often the initiators of reconciliation compared to males. Females more frequently avoided conflict than males, which was also the case when females were the recipients of aggression. These results do support the hypotheses on sex differences and initiator/recipient differences, except that females were initiators of events that led to reconciliation more often than they were recipients. There was no significance between age-class or sex in conflict-sexual events. Calves, however, were significantly more likely to be involved in conflict-no reaction events than adults, and calves were more likely to be the recipients in conflict-no reaction events than both adults and subadults. There were no significant findings between sexes in the case of conflict-no reaction events. Each of these findings can be discussed by what is known about dominance and sociality in bottlenose dolphins.

Retaliation

In responses of retaliation, subadults were more likely to exhibit retaliatory behaviors than adults. This was the same outcome when subadults were the initiators or recipients. This may indicate for subadults that they are more likely to challenge and react when confronted with conflict or possible agitation. Subadults are not necessarily high ranking in the dominance hierarchy. Their attempts at initiating retaliation could be preliminary actions meant to help them attain a certain rank as they age or defend their current position from challengers (Veit & Bojanowski, 1996). Their challenges would be directed towards individuals who have dominance over them or who are similar in rank, but pose a threat (Benus, Bohus, Koolhaas, & Oortmerssen, 1991). This is supported in how middle ranked individuals (i.e., primarily subadults) exhibit slightly higher assertive personality trait scores than adults (Frick, 2016).

Scott et al. (2005) reported a high frequency of aggression in juvenile dolphins, with no significant difference in tooth rake marks between sexes. They suggest that the prevalence of markings in juvenile and subadult males is a result of practice behaviors (e.g., bouts and copulation attempts) between each other, while females likely receive most of their markings from subadult and adult males during periods of cycling. Females were not thought to contribute extensive rake marking in other females (Scott et al. 2005). This supports the notion that males tend to retaliate more frequently than females in post-conflict exchanges. However, more research should be done on female-female aggression and the costs of retaliation in order to better understand how aggression in females changes over time.

Males were more likely to be involved in and serve as initiators and recipients in conflict-retaliation events than females. As dominance plays a role in aggression, males may be expected to show aggression as they engage in more acts of dominance than females. Males may have short-term, stable associations that are subject to more fluctuation over time (Samuels & Gifford, 1997; Yamamoto et al., 2015). Conner, Smolker, and Richards (1992) called these associations "alliances," in which two to three males formed strong associations that functioned to aggressively herd females. These alliances enable all males to increase their opportunities to mate with females and guard them from other males, which if successful will result in either male fathering more offspring. In some cases partner changes occurred within the next day following the termination of a herding event and at other times second-order alliances form in which two first-order alliances (i.e., two or three males herding males) combine in order to secure females from a different alliance (Conner et al., 1992). Alliances may last for years before being discontinued, however, this is largely dependent on the type of alliance, as shown in superalliances (i.e., a very large second order alliance) where stability between males is non-existent, but offers an advantage over smaller stable alliances (Connor, Heithaus, & Barre, 1999). These cumulative findings suggest males are more inclined to be aggressive toward females and other males as it serves to increase their reproductive fitness. This current study's findings are consistent with how females show low frequencies of aggression towards other adults. Their dominance is largely ageordered and more stable over their lifetime (Samuels & Gifford, 1997). This is largely due to the formation of long term, relationships among female kin (Wells et al., 1987).

Reconciliation

In events of reconciliation, calves were overall more likely to be a part of conflict-reconciliation events than adults. Relationship repair may serve a critical role in mother-calf pairs, as strong social bonds are important to the calves' survival. Particularly for mother-calf pairs, adult females may discipline calves to extinguish undesirable behavior. Discipline is a punishment (e.g., hold down, genital buzz, rostrum bop; Weinpress & Herzing, 2015) typically used by caregivers (i.e., mother or alloparent) on younger individuals to reduce the individual from repeating an unfavorable behavior that puts the individual or others at risk (Weinpress, 2013). Observations of a group of Atlantic spotted dolphins (*Stenella frontalis*) showed that mothers or alloparents would often discipline calves following highly successful pursuit behaviors which together served to decrease the likelihood of risky behavior by the calf (e.g., swimming away from the mother; Weinpress, 2013; Weinpress & Herzing, 2015). Age-class and sex of the disciplinarian did not appear to affect the type or success rate of the discipline (Weinpress, 2013; Weinpress & Herzing, 2015), which may indicate that many forms of discipline performed by adults or younger alloparents reduce undesirable behaviors from the calf. It may be to the calf's benefit to then reconcile as a means to reduce the likelihood of further discipline. An affiliative response following aggression from discipline (e.g., petting, rubbing) may reinforce social bonds between mothers and calves after discipline action is taken. However, the results of the current study did not separately examine events considered discipline versus other aggression between adults and calves (i.e., an adult male may aggress on a calf if the individual is encroaching its territory or annoying them; Frick, 2016) suggesting that other factors may contribute to this finding.

Females were more likely to be initiators in conflict-reconciliation events than males. Female-female reconciliation is important in maintaining stable relationships that would aid in reproductive success (Yamamoto et al., 2015; Yamamoto, Ishibashi, Yoshida, & Amano, 2016). Maintaining social bonds between females reflects the reciprocity observed in matrilineal lines, which is supported in this study's findings due to the close kinship of the study group. In contrast, bonding between non-kin pairs show that juvenile and adult males preform pectoral fin contact behavior more often with other males that are around the same age, which is suggested to function in maintaining pair bonds, in this case alliances, which have the potential to last for many years (Dudzinski & Ribic, 2017). Behaviors between sexes are complex and share additional correlations between dominance and age. Harvey et al. (2017) found that same sex dyads had higher coefficients of association (COA) than mixed sex dyads, especially with males spending more time together whether paired as adults, juveniles, or both. Male-female dyads spent more time engaging in agonistic interactions on average, whereas female-female agonistic interactions were infrequent. Affiliation was the most observed behavior within any age-sex dyads (Harvey et al, 2017), supporting how affiliative behaviors serve an important function and require frequent use in calves and between strong paired individuals, such as females.

Avoidance

For conflict-avoidance events, calves were overall more likely to exhibit these behaviors than adults and subadults. As recipients, calves were also more likely to avoid aggression than adults and subadults. Fight or flight strategies dictate that if self-defense is not an option when avoiding attack, quickly fleeing is an adaptive survival alternative (Ford & Reeves, 2008). Mothers defend their calves, but if there is considerable distance between a caregiver and a calf, it would be at risk for injury or fatality. As the youngest individuals in the population, the act of avoidance by calves offers more protection at a vulnerable age, especially when confronted by much older individuals. However, calves are not always successful in evading conflict. Infanticide (i.e., the killing of young offspring by conspecifics) can be implemented from kin or non-kin, regardless of sex. Hrdy (1979) discusses that many species exhibit five classes (i.e., incentives) that direct aggression towards young conspecifics: exploitation (i.e., consumption), parental manipulation (i.e., ensuring survivorship of another offspring), social pathology (i.e., behaviors which decrease individual and inclusive fitness), resource competition (i.e., competition for physical resources), and sexual selection (i.e., competition between one sex for reproductive investment by the other sex). It is most probable that cetacean infanticide falls exclusively into the last two classes (i.e., resource competition and sexual selection). The first report of infanticide in cetaceans occurred in in the 1990s when evidence from necropsies supported the likelihood of adult bottlenose dolphins harassing infants (e.g., tooth rake scarring and forceful, direct contact) and subsequently killing several calves (Patterson, Reid, Wilson, Grellier, Ross, & Thompson, 1998). Similar findings were reported in nine bottlenose dolphins calves stranded off the coast of Virginia in 1996 and 1997 suffering multiple injuries such as fractures, lesions and severe blunt-force trauma. These injuries are highly correlated with instances of infanticide and suggest violent behavior by conspecifics (Dunn, Barco, Pabst, & McLellan, 2002).

Females were more likely to avoid conflict and be the recipients in conflict-avoidance events than males. No observations of male coalitions were made in this study, however females may be especially inclined to avoid aggression by larger males. Scott et al. (2005) observed that juvenile females may be caught in aggressive encounter due to their inexperience in avoiding such encounters. Females would likely attempt to avoid costly encounters that raise their chances of injury. Frick (2016) showed that in some contexts females displayed personality traits suggestive of more caution before approach and less tendency towards initiating conflict than males. It was observed that sex and dominance do not strictly dictate how bold an individual may act (Frick, 2016). However, traits along the bold-shy dimension behavior may serve as an advantage in selective social learning in that a timid individual may be more likely to mimic a bold individual (Kuczaj, Yeater, & Highfill, 2012). Bold individuals (i.e., assertive, extraverted) tend to have a higher social status (Frick, 2016). Mimicking the behavior of higher ranking individuals may improve the rank of lower status individuals (Frick, 2016; Kuczaj, Yeater, & Highfill, 2012), but boldness will not necessarily be a trait consistently exhibited in dominant individuals across different contexts (Kuczaj, Highfill, & Byerly, 2012). In the context of play, females who grow up with tendencies towards boldness or shyness may show varying levels of success in avoiding or confronting conflict (Frick, 2016).

Sexual

There were no significant differences between age-class or sex in the outcome of sexual behavior. Copulation attempts with females were rarely observed on the video data for this study. All conflict-sexual events for the current study ended with male socio-sexual behavior, with female homosexual behaviors were not observed and attempts at mating were extremely low. Mann (2006) found that male homosexual bouts are longer lasting than female homosexual bouts or heterosexual bouts, suggesting the importance of male-male socio-sexual behavior on development. In immature males, this behavior may help facilitate bonds and allow for practicing courtship behaviors. These interactions are often seen in playful contexts and most often between calves, so the likelihood that these behaviors are used in reconciliation is low. Dominance relationships may begin to form with these behaviors, observed through the symmetry of these socio-sexual exchanges in that frequent role exchange of actor and recipient suggests an equal dominance ranking where as a skewed role exchange (i.e., one male is always the actor and the other the recipient) suggests the actor is the more dominant individual (Mann, 2006). To that effect, it is hypothesized that these socio-sexual behaviors may communicate dominance information without the need for aggression, supporting the lack of findings related to sexual behaviors following aggression. It may be likely that sexual behaviors may mitigate the need for aggression (Frick, 2016), but this area of research warrants further study.

No Reaction

There were no significant differences between sexes for the conflict-no reaction events. An equal distribution existed between sexes in this category, which may suggest that neither sex shows a tendency towards disregarding conflict. The absence of reaction may actually be a random occurrence which depends on the context of the situation. These data can largely be attributed to aggression going unnoticed and therefore resulting in no response.

Calves were more likely not to exhibit any reaction to conflict than adults. As the recipients, calves were also more likely not to exhibit a reaction compared to adults and subadults. On several occasions individuals were observed to aggress towards calves outside of their viewing area or with a mother or possible alloparent in close proximity. These reasons, along with the unknown intent of the initiator, likely contribute to a calf’s disregard for certain conflicts. Two calves, Champ and Polly had the most involvement in conflict-no reaction events. Champ’s mother, Maury has a high coefficient of association (0.37) with male Paya (Harvey, 2015), which suggests that Paya may be the father. Maury was less active in caring for Champ and was assisted with alloparental needs by Mrs. Beasley. While Maury is ranked in the middle of the hierarchy for the females, Mrs. Beasley and Paya are both considered at the top (i.e., highest) social rank position within the hierarchy (Frick, 2016). Having dominant parents or being in the presence of a dominant caregiver may decrease the chances of other individuals engaging aggressively with a calf. Polly’s mother, Mika, is not highly dominant, but her offspring tend to have higher scores for personality traits considered bold, such as playful or exploratory and seeking contact with swimmers in the enclosure. Having a characteristically “bold” personality may predispose calves to being less concerned with potential conflict from members of their familial group (Frick, 2016).

Overall Conclusions

These findings support that subadults are involved in high levels of aggression relative to other age-classes as they attempt to advance in rank. Males are considered to be more aggressive over their lifetimes due to their drive to pass on their genes to offspring. Females will be less involved in retaliation due to higher costs and low benefits, but aggression is more often seen when trying to avoid attempted copulation, discipline, and when encountering unrelated females in certain contexts. Calves were shown to reconcile more often than adults which may serve as adaptive following discipline or conflict in order to decrease the amount of discomfort or harm inflicted on them. The higher frequency of females initiating reconciliation was likely a consequence of the desire to maintain close female bonds and the absence of similar close bonds between the males of the study group. Calves were more often involved in avoidance and the recipients of conflict-avoidance than adults and subadults which also relates to the need to remain a less likely target of threats by older individuals. Females were also more involved in avoidance overall and the recipients of conflict-avoidance. This is likely a result of avoiding harassing behaviors by adult or subadult males, but could also be that they are uninterested in interacting with less dominant and aggressive females.

Although females may have been involved during a bout that ended in sexual behavior, there were nearly no cases of male-female copulation. The bulk of sexual behaviors took place between males, which may serve as a communication of dominance information without contact aggression. Calves were overall more frequently involved in conflict-no reaction events and were less likely to react as the recipient to an initiator than adults or subadults. This is likely a result of calves not being left unattended by a caregiver who can offer them protection. This may leave calves with less of a fear response when encountered with potentially aggressive, but familiar individuals. There were no significant differences in conflict-no reaction events between sexes. The tendency not to react to conflict is largely context dependent and this may cause it to occur randomly between sexes. There may be higher frequencies of reaction to conflict in the wild due to the higher probability of encountering unfamiliar individuals.

Limitations

One of the limitations of this study included the uneven distribution between age classes (i.e., adults (13), subadults (10), calf (7)). A larger study pool with a more equal distribution would be needed to determine if the conclusions regarding age-class are comparable to other groups/populations. Another limitation was how events were terminated shortly after dolphins swam out of view. Unless a pair swam back into view and could be identified as the same participants before the event was marked as ending, it was impossible to determine what the final outcome of the event would have been. Knowing what behaviors followed their disappearance would have revealed more about the final outcomes of their interactions. This may be corrected with novel recording methods, but there exists no current method to ensure all behaviors are tracked if outside of a small enclosure.

Future Directions

This study did not assess encounters between individuals explicitly, however this is a topic of interest for a future study. Comparing the results of this study to a larger population over time would allow for determining trends in aggressive behavior throughout development. Looking at the trends in behavior between individuals may reveal behavioral tendencies unique to certain individuals in addition to determining if impulses to behave a certain way are evident between certain pairs. This may be useful in assessing personality differences and how different personalities and behavioral tendencies play a role in cetacean fission-fusion societies.

Looking at close-kin relationships and the frequency of reconciliation between siblings also warrants future study. This would lend support to whether or not sibling bonds are as essential to fitness as alliances, especially when analyzing the differences between same sex or separate sex siblings. It would be more ideal if given the ability to assess this over many years in order to determine the amount of inclusive fitness existing between younger and older siblings. Finally, this study's findings should be compared with age-class and sex differences in aggressive behavior for wild populations and between species. This would provide a more holistic understanding of how comparable species of cetaceans are from one another in how they react to aggression.

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Appendex A

Table 1. Behavioral definitions for aggressive interactions between dolphins.

Category	Behavior	Definition
Aggression and Retaliation		
	Bite	dolphin bites or rakes teeth on another dolphin' or behaves with intent to bite/rake
	Body Slam	one dolphin slams its body into another
	Bubble Bursts	cloud of bubbles produced through blowhole
	Bubble Streams	several small bubbles produced in a stream
	Charge	fast-speed, direct approach to another dolphin
	Chase	one or more dolphins swiftly following other dolphin(s)
	Fluke Hit	one dolphin hits another with its flukes
	Group Aggression	aggressive bout happening simultaneously between more than 2 dolphins
	Head Jerks	single quick deliberate movement of head
	Head to Head Circling	two dolphins positioned head to head, circling one another
	Jaw Clap	dolphin opens & closes jaws' causing a sharp, discomforting vocalization directed forward
	Melon-melon Hits	head to head collision between two dolphins
	Mouthing	dolphin has its mouth around a conspecific's body but is not biting down
	Posturing	assuming an 'S' shape (head 'up', anterior ventral surface 'down', peduncle 'up', and flukes 'down')
	Push up/down	one dolphin pushes another one up/down (usually with rostrum)
	Ram	one dolphin hits another's body with its body at fast pace that propels them through the water column
	Rostrum Hit	one dolphin hits another dolphin with rostrum
	Tail Jerk	sharp tail movement vertically or laterally
	Threat Display	open mouth displayed in a provoking or warning manner
Reconciliation		
	Contact Swimming	synchronous swimming while maintaining contact of one body part to another constantly
	Nudging	one dolphin pushes rostrum on another dolphin's body
	Pec Rub	one dolphin contacts another dolphin with its pectoral fin and either or both dolphins actively move the touching body parts back and forth
	Petting	pectoral fin-to-pectoral fin rubbing where active movement between pectoral fins of two dolphins is observed
	Rubbing	the active movement between one dolphin's body and another dolphin's body*
	Synchronous Swimming	two or more dolphins moving (swimming, etc.) in a similar fashion and at the same rate with respect to each other; position is staggered or parallel
	Tactile	one dolphin moves pec fin along another's body w/ no active movement
Avoidance		
	Flee	abrupt, rapid, and immediate departure to >1 m in response to action of another
	Flinch	cringe, cower, or recoil in response to action of another. Typically in the form of an abrupt movement of one or more body parts away from the other
	Submit	allowing aggression without retaliatory reaction. Typically orienting body towards or facing aggressor while remaining still or moving part of body slowly away

*Body refers to the melon, trunk, and peduncle.