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# Social Interactions Among Two Males in a Captive Group of Rough-Toothed Dolphins (*Steno bredanesis*)

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SOCIAL INTERACTIONS AMONG TWO MALES IN A CAPTIVE GROUP OF  
ROUGH-TOOTHED DOLPHINS (*STENO BREDANESIS*)

by

Pepper Reid Hanna

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

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## ABSTRACT

### SOCIAL INTERACTIONS AMONG TWO MALES IN A CAPTIVE GROUP OF ROUGH-TOOTHED DOLPHINS (*STENO BREDANESIS*)

by Pepper Reid Hanna

May 2016

There is relatively little known about the social behavior of rough-toothed dolphins (*Steno bredanensis*) particularly in comparison to information on the Atlantic bottlenose dolphin (*Tursiops truncatus*). The purpose of the current study is to describe the social behavior of two juvenile male rough-toothed dolphins housed at Gulf World Marine Park in Panama City Beach, Florida. Rates of affiliative social behaviors were greater between the two males within this group compared to the other pairs of dolphins. The males exhibited a high rate of association, calculated using the half-weight index. Following aggressive behavior within the overall group, the focal pair was more likely to respond by engaging in affiliative interactions. The other pairs of dolphins were more likely to respond to aggression in the environment with other aggressive interactions.

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## LIST OF ABBREVIATIONS

<i>COA</i>	Coefficient of Association
<i>HWI</i>	Half Weight Index

## CHAPTER I - INTRODUCTION

### Dolphin Populations

Many dolphin species live in dynamic social groups characterized by a fission-fusion society in which group membership is constantly shifting, often on a rapid basis (e.g., Smolker, Richards, Connor, & Pepper, 1992; Wells, Scott, & Irvine, 1987). This contributes to a group's hierarchical structure in which subgroups exist with the capacity to create smaller groups that subsequently split from the main group when ecological pressures demand smaller group size, allowing it to adjust to a changing environment (Wiszniewski, Allen, & Möller, 2009).

The types of associations males and females form are often distinct. Female dolphins have been demonstrated to form a relatively large network of loose associations and a smaller more closely associated group or "band" (Lusseau et al., 2003; Smolker et al., 1992; Wells, 1991). In both the Port Stephens, Australia population (Möller, Beheregaray, Allen, & Harcourt, 2006) and the Shark Bay, Australia population (Frere et al., 2010), female associations appear to be related to maternal kinship. Access to food sources and foraging strategies used by female dolphins can limit group living in female dolphins making sociability more variable among females. Females are thus more likely to be solitary than males (Connor, Wells, Mann, & Read, 2000). Several dolphin populations feature stable, long-term associations among male dolphins. These populations include: Shark Bay, Australia (Connor, Heithaus, & Barre, 2001; Connor, Smolker, & Richards, 1992), Sarasota, Florida (Wells, 1991), Port Stephens, Australia (Möller, Beheregaray, Harcourt, & Krützen, 2001), and Doubtful Sound, New Zealand (Lusseau, 2003). Male coalitions have been found in Atlantic spotted dolphins as well

(Herzing, 1996; Welsh & Herzing, 2008). Male – male interactions in each of these populations have different characteristics and possibly serve different purposes.

### Male Alliances

The differences in the extent to which males form alliances between populations can be explained by a variety of ecological, social, and genetic factors. Sexual dimorphism is used to explain the formation of alliances in Shark Bay (Connor et al., 2000). In the Sarasota population, males in alliances have been demonstrated to live longer, suggesting the alliances in this population could provide protection from predation (Wells, 1991). Populations with low predation risk, such as the Moray Firth population, do not form alliances (Eisfeld & Robinson, 2004). Population characteristics can also favor the formation of alliances. A large population density in which animals are forced to interact could increase the likelihood of alliance formation. In addition, a large ratio of males to females within a population could increase competition of males which could support the formation of alliances (Connor & Whitehead, 2005).

These alliances are characterized by similar behavior patterns across populations. Spatial proximity is the most common means of determining associations among group members in wild populations and has been demonstrated to be a significant factor in establishing and maintaining alliances (Smolker et al., 1992). Other affiliative behaviors have been reported among male alliances. These include synchronous behaviors such as swimming and displays such as leaps (Connor et al., 1992, Connor, Smolker, & Bedjer, 2006, Sakai, Morisaka, Kogi, Hishii, & Kohshima, 2010). Vocal synchrony has also been observed in alliances. Atlantic spotted dolphins synchronize their squawks during aggressive interactions (Herzing, 1996) and members of a male alliance have been

demonstrated to create a blended whistle not typical of that used by either individual prior to formation of the alliance (Smolker & Pepper, 1999). Synchronous behavior not only establishes associations among alliance members but also signals this association to other members of the group (Connor et al., 2006). The synchronous displays male alliances perform around females provide the best evidence for this hypothesis (Connor et al., 1992; Connor et al., 2000). Male alliance members may also exhibit other affiliative behaviors within the alliance, including gentle tactile contact or petting between members (Connor et al., 2000) and, particularly during periods of consortship, intense social contact, including body-to-body contact, sexual behavior, and chasing (Connor et al., 2006).

#### Rough-Toothed Dolphin Societies

Rough-toothed dolphins typically live in deep waters of tropical, subtropical, or warm-temperate seas (Addink & Smeenk, 2001). There is relatively little known about the social organization and development of rough-toothed dolphins, particularly in comparison to information on the bottlenose dolphin. The first long term studies of bottlenose dolphin populations began in the 1970s, with photo-identification projects beginning in the 1980s (Wells, 1991). The first photo-identification project on rough-toothed dolphins did not begin until 2000 (Mayr & Ritter, 2005). Long term associations are clearly a significant contributor to the social structure seen in bottlenose dolphin populations. These associations could only be discovered through long term observational studies. The information available on rough-toothed dolphins suggests this species exhibits a dynamic social environment similar to the bottlenose dolphin (Addink & Smeenk, 2001; Baird et al., 2008; Kuczaj & Yeater, 2007). Behavioral observations of

this species suggest these animals travel in small groups that often then secondarily associate into much larger groups (Addink & Smeenk, 2001; Kuczaj & Yeater, 2007; Pitman & Stinchcomb, 2002; Ritter, 2002). Evidence of ‘eavesdropping,’ in which members of the group will use echolocation echoes of a single individual to locate food suggests a tight, unified social structure (Götz, Verfuss, & Schnitzler, 2006). Further evidence for a complex social structure in rough-toothed dolphins is the observation of epimeletic behavior similar to that seen in other cetacean species (De Moura, Da Silva Rodrigues, & Siciliano, 2009; Ritter, 2007). It is essential to perform similar studies on rough-toothed dolphin populations in order to determine if similar associations exist in these populations.

#### Captive Studies

Early studies on social behavior of bottlenose dolphins in captivity revealed the development of a dominance structure within the captive group (McBride & Hebb, 1948; Tavolga, 1966). Males have been demonstrated to initiate both aggressive and sexual behaviors as a means of establishing and maintaining the dominance hierarchy within the group (Ostman, 1991; Scott, Mann, Watson-Capps, Sargeant, & Connor, 2005). In one of the first studies on captive dolphins, McBride and Hebb (1948) described homosexual behavior occurring repeatedly within a captive group. This behavior was observed when a larger male would swim ventral up underneath the smaller male and often attempt intromission. This supported the hypothesis that males were using sexual behavior with the other males as a means of establishing dominance. Samuels and Gifford (1997) found most dominance related aggressive behavior occurred between two males within the group.

Developmental similarities in social interactions in wild and captive dolphins have been observed. For instance, Tavalga (1966) found that within a captive group three juvenile males associated almost exclusively with one another. This group engaged in a variety of play behaviors as well as homosexual interactions with one another (Tavalga, 1966).

The characteristics contributing to the formation of alliances previously discussed are specifically focused on these alliances in the wild. Dolphins in the captivity do not face the same ecological pressures. The early emphasis on the dominance structure within a captive group has made it difficult to determine what factors promote affiliative behavior and relationships between males within a captive group. However, there has been one report of male – male interactions reported within a captive group. Waples and Gales (2002) reported strong associations between a pair of males in a captive group. Descriptions of the interaction and behavioral patterns of these animals are not found in the literature. Male alliance formation within a captive group suggests that there could be other forces that drive this type of bond among males that are shared by dolphins in captivity.

There have been very few captive groups of rough-toothed dolphins available for study. One study does suggest the formation of stable bonds in this species. This study examined impact of a change in group size upon the social dynamic of a captive group of rough toothed dolphins (Yeater, Miller, Caffery, & Kuczaj, 2013). The results indicated the introduction of animals to the group allowed for new bonds to form, but there was not a significant impact on the bonds established prior to the introduction. This suggests that

rough toothed dolphins can form relatively stable bonds and have preferential partners similar to what has been found in bottlenose dolphins.

### Current Study

The purpose of the current study is to describe the social behavior of two juvenile male rough-toothed dolphins in captivity. The captive environment provides a means of studying the social behavior of a species difficult to observe in the wild. While there are limitations to observing social behavior in captivity due to the reduced number of potential associates and the influences of the training staff, housing unit, and the facility itself on a captive group, long-term studies of wild and captive groups have demonstrated an overlap between information provided by each type of study (Dudzinski, 2010).

Comparison studies between wild and captive animals have demonstrated a similarity in social organization as well as use of specific behaviors between these different groups of dolphins (Dudzinski, 2010; Dudzinski, Gregg, Paulos, & Kuczaj, 2010). This means that information gathered from captive rough-toothed dolphins can provide important insight into their wild counterparts.

We expect that the two juvenile males within this group will have the strongest associations and show high rates of affiliative behaviors with each other. It is expected these behaviors will be similar to juvenile male dolphins in the wild during the formation of alliances.



## CHAPTER II – METHOD

### Subjects

Seven rough-toothed dolphins housed at Gulf World Marine Park in Panama City Beach, Florida served as the subjects for this study. Four were female (Vixen, Dancer, Doris, Largo) and three were male (Ivan, Astro, Noah). All seven dolphins had previously stranded and after rescue and rehabilitation were determined to be non-releasable by the National Marine Fisheries Service. These dolphins were housed either together in a single pool or in two separate pools during the study period.

### Procedure

Opportunistic observations collected between October 14, 2005 and October 3, 2009 resulting in 5326 minutes of video provided the data for this investigation. Video data was collected using a SONY DCR-HC96 Camcorder, a SONY DCR-HC65 Camcorder, or a SONY DCR-VX1000 Camcorder.

### Intercoder Reliability

To assess the reliability of behavioral measures, each observer coded 20% of the total video data. The tapes were divided into 30 s segments for reliability analysis. Both observers used the same Microsoft Excel database to record all occurrences of behaviors during the portion of tape, although each coder was blind to behaviors recorded by all other coders. Each segment was given a “Yes” or “No” as to whether the observers agreed on a behavioral event, the initiator of the event, and the body regions involved, occurring within that 30 s segment. The level of agreement between all observers was calculated using the Cohen’s kappa formula (Cohen, 1960) as follows:

$$\kappa = (p_o - p_e) / (1 - p_e)$$

Where:

Observed agreement,  $p_o = (a + d) / n$

Expected agreement,  $p_e = [(n_1/n) * (m_1/n)] + [(n_o/n) * (m_o/n)]$

## Analyses

### *Behavioral Measures*

Videos were coded to indicate the initiator and recipient (if applicable) of all behaviors by each dolphin or group of dolphins. Social behaviors were classified as either affiliative or aggressive. Operational definitions and classification of behaviors are provided in Table 1. The overall rates (occurrence of behavior per minute of video) of each behavior as well as the rates of each behavioral category were calculated based on dyad classification. Dyads were classified into four groups: (1) the Astro/Ivan pair, (2) Astro with any other dolphin, (3) Ivan with any other dolphin, and (4) all other pairs of dolphins. ANOVAs were used to analyze the differences in behavioral rates of dolphins and dolphin pair classification. Rates of overall behavior, categories of behavior, and specific behaviors were analyzed. The data were analyzed *in toto* as well as by year. During 2005 the dolphins were housed in two separate pools, therefore not all pairs of dolphins were observed for this period. When analyses were performed by year, only the years 2006 – 2009 were included. For the Astro/Ivan pair, additional analyses were conducted to determine the difference in rates of solo behaviors and behaviors the pair engaged in together.

The impact of stress on the interaction of dolphins within this group was determined by how the dolphins responded to aggression with the group. The frequency

of behavioral category (affiliative or aggressive) an animal engaged in immediately following an aggressive action within the group was calculated. In addition, we determined the type of response Astro and Ivan would most likely engage in after they were recipients of aggressive behaviors. Of these incidents, the percent in which they responded by interacting with each other, with any other dolphin, or remained solo was calculated.

Table 1

*Operational Definitions of Behaviors Analyzed*

<b>Behavior</b>	<b>Definition</b>	<b>Category</b>
<b>Pair Swim</b>	Two dolphins swim in synchrony within one body length	Affiliative
<b>Orient Dolphin</b>	One dolphin looks at another dolphin, must be for a minimum duration of two seconds and not in conjunction with another behavior	Affiliative
<b>Group Social Ball</b>	Two or more dolphins swim around each other and appear to be “wrestling” (often associated with play)	Affiliative
<b>Sexual Contact</b>	Sex related behaviors such as genital inspection or genital rubs; mating	Sexual
<b>Play with Dolphin</b>	Play directed at conspecifics that does not include any additional forms of enrichment	Affiliative
<b>Tactile</b>	One dolphin makes contact with or actively rubs another dolphin	Affiliative
<b>Chase</b>	Dolphin swims quickly and actively in persistent pursuit of another dolphin(s)	Aggressive
<b>Rake</b>	Dolphin opens its mouth and makes forceful contact with another dolphin by rubbing/sliding its jaws on another dolphin	Aggressive

Table 1 (continued).

<b>Hit</b>	<b>One dolphin contacts another dolphin in a quick and aggressive manner (usually with rostrum or fluke)</b>	<b>Aggressive</b>
<b>Mouth/Bite</b>	One dolphin opens and closes mouth quickly and with force around another dolphin anywhere on body	Aggressive
<b>Threat</b>	Open mouth directed at another dolphin, often abrupt, vertical head movement	Aggressive

*Measure of Association*

One thousand hours of video data were used to determine the associations between individual dolphins. Only periods in which all animals within the group had access to each other were used. A two minute instantaneous sampling procedure was used to determine groups, with a new group defined for each sample period (Altmann, 1974). Dolphins were considered within a group if they were within 2 m of another dolphin. A chaining procedure was used such that if Dolphin A was within 2 m of Dolphin B and Dolphin C all three would be considered a group even if Dolphin B and Dolphin C were greater than 2 m apart. The half-weight index (HWI) was used to define the coefficients of association for all dyads (Cairns & Schwager, 1987). This analysis was completed using SOCPROG (Whitehead, 2009).

$$HWI = \frac{x}{x + y_{AB} + \frac{1}{2}(y_A + y_B)}$$

Where:

x = observations in which dolphin A and B are recorded together

y<sub>A</sub> = observations in which only A is identified

$y_B$  = observations in which only B is identified

$y_{AB}$  = observations in which both A and B are identified but not associated

## CHAPTER III – RESULTS

### Intercoder Reliability

Agreement between coders was found to be 84.19%, and this corresponds to a kappa of 0.675 and is considered good agreement.

### Behavioral Analyses

For the statistical analyses described in the following pages, the Tukey post hoc test is reported for all comparisons in which there were no violations. Alternative post hoc analyses are used in situations in which there were violations to assumptions in the test.

#### *Solo and Paired Behaviors*

Astro and Ivan displayed a higher rate of solo behaviors than interactions with each other overall (Figure 1). However, there are differences in this pattern over time; see Figure 2. A shift occurred in 2008 in which they showed a higher rate of interaction with one another than solo behaviors, although this difference was only significant for Ivan (*Welch's*  $F(1, 152.84) = 4.782, p = 0.03$ ). In 2009, Ivan engaged in slightly more behaviors with Astro than alone, although this difference was not significant.

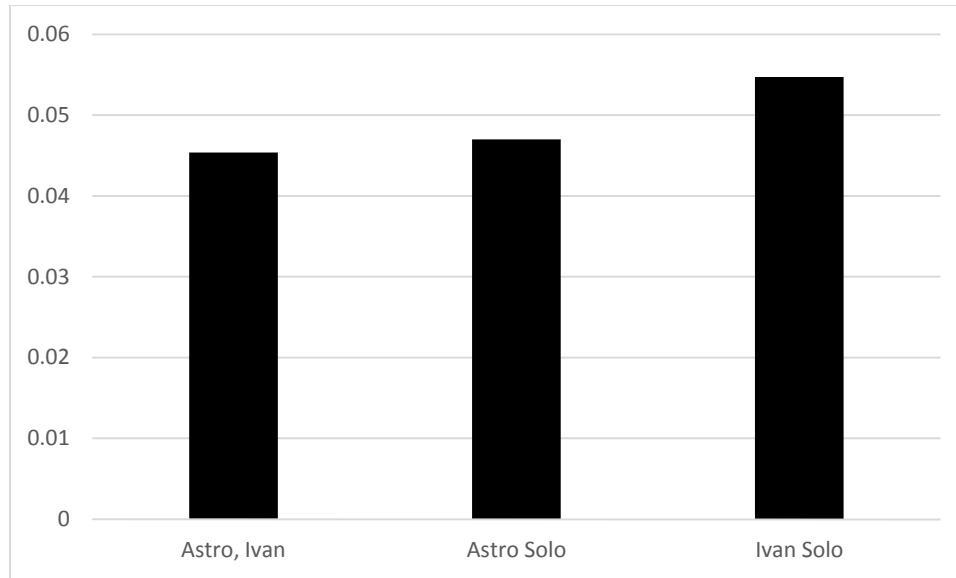


Figure 1. Mean rates of solo vs. pair behaviors

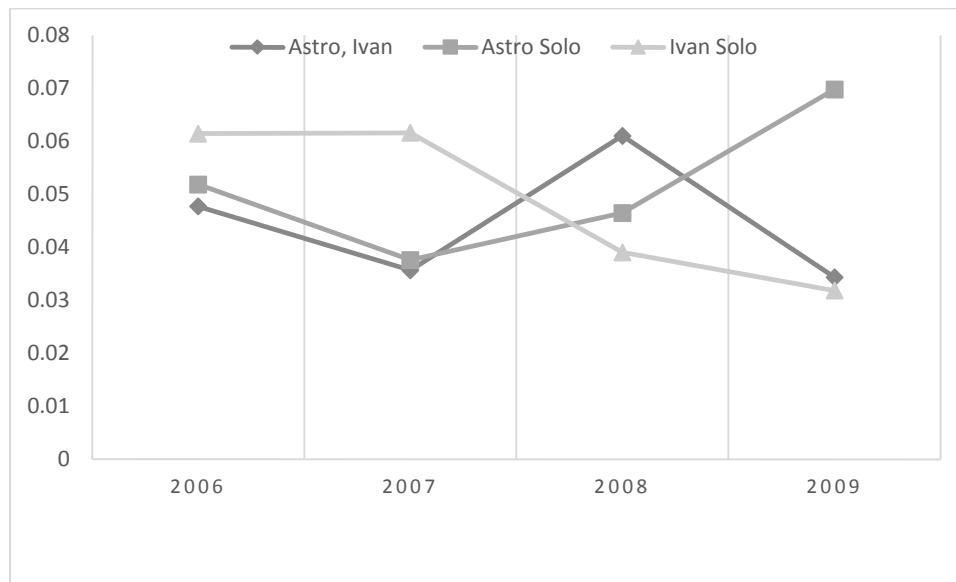


Figure 2. Rates of solo and pair behaviors over time

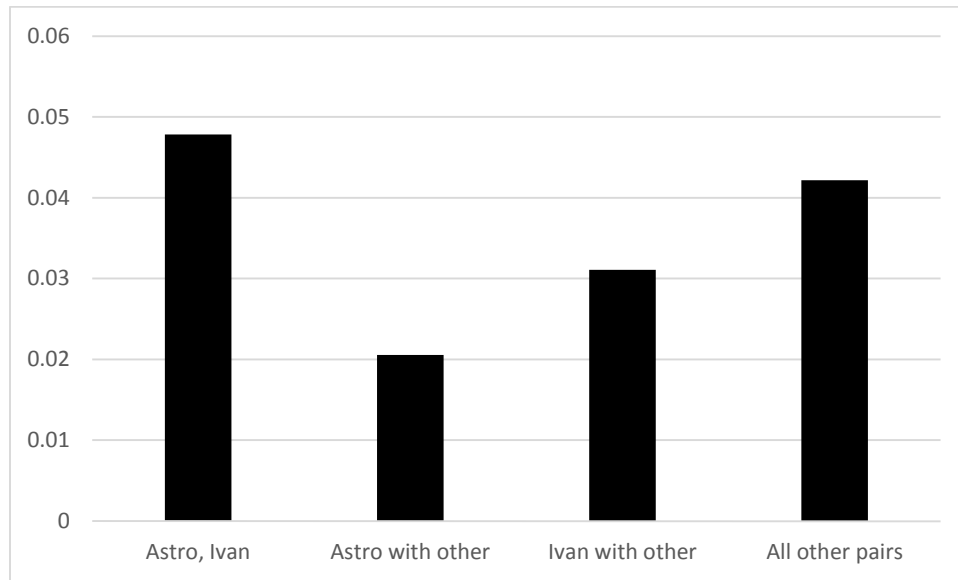
*Overall Paired Behavioral Rate*

There was a significant difference in the overall rate of pair behaviors based on dyad classification (Figure 3) ( $Welch's F(3, 829.44) = 29.647, p < 0.001$ ). See Figure 3.

Astro and Ivan engaged in more behaviors with each other than either did with any of the

other dolphins (Astro: Games-Howell,  $p < 0.001$ ; Ivan: Games-Howell,  $p = 0.002$ ).

Astro maintained this preference for each year of the study (2006: Games-Howell,  $p = 0.003$ , 2007: Games-Howell,  $p < 0.001$ , 2008: Games-Howell,  $p < 0.001$ , 2009: Games-Howell,  $p = 0.010$ ). For Ivan, the years in which he interacted significantly more with Astro than any other dolphin were 2007 and 2009 (Games-Howell,  $p < 0.001$ , Games-Howell,  $p = 0.014$ ). In 2008, Ivan engaged in a higher rate of behaviors with Astro than with any other dolphin, this difference was not significant. Figure 4 depicts the changes in rates between pairs over the study years.



*Figure 3.* Mean overall rate of pair behaviors



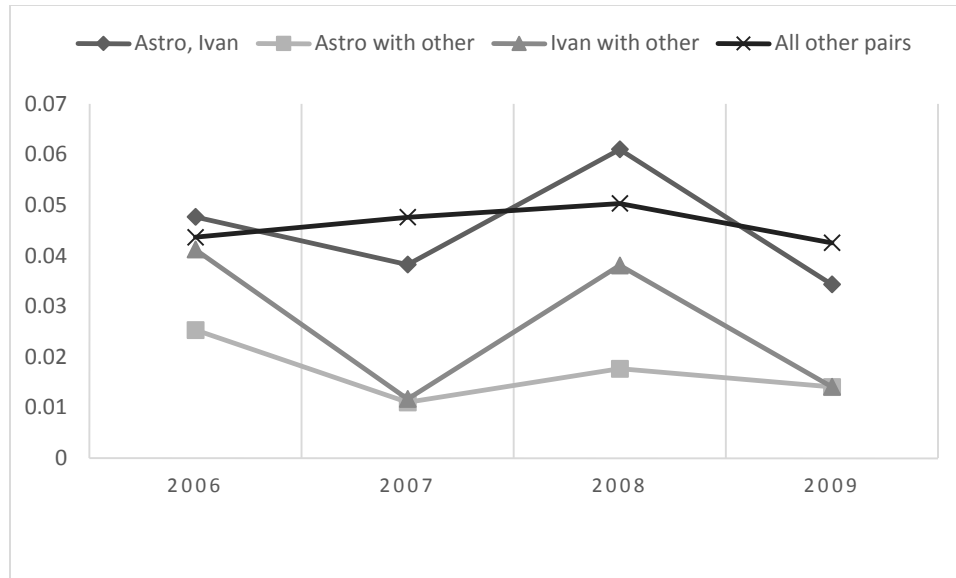


Figure 4. Rate of pair behaviors over time

#### *Affiliative and Aggressive Behaviors*

Astro and Ivan engaged in significantly more behaviors together than all the other pairs of dolphins (*Welch's*  $F(1, 198.27) = 10.551, p = 0.001$ ). The rate of affiliative behaviors within a pair was different based on pair membership (Figure 6) (*Welch's*  $F(3, 239.44) = 9.804, p < 0.001$ ). Astro engaged in more affiliative behaviors with Ivan than he did with any other dolphin (Games-Howell,  $p = 0.007$ ). Ivan did not engage in a different rate of affiliative behaviors with Astro compared to other dolphins within the group. When ANOVAs were performed by year, 2007 was the only year in which either Astro or Ivan engaged in significantly more affiliative interactions within the pair than either did with other dolphins. During this year, both Astro and Ivan engaged in more affiliative interactions within the pair (Games – Howell,  $p < 0.001$ ). See Figure 6 for a summary of changes in rates of affiliative interaction across year.

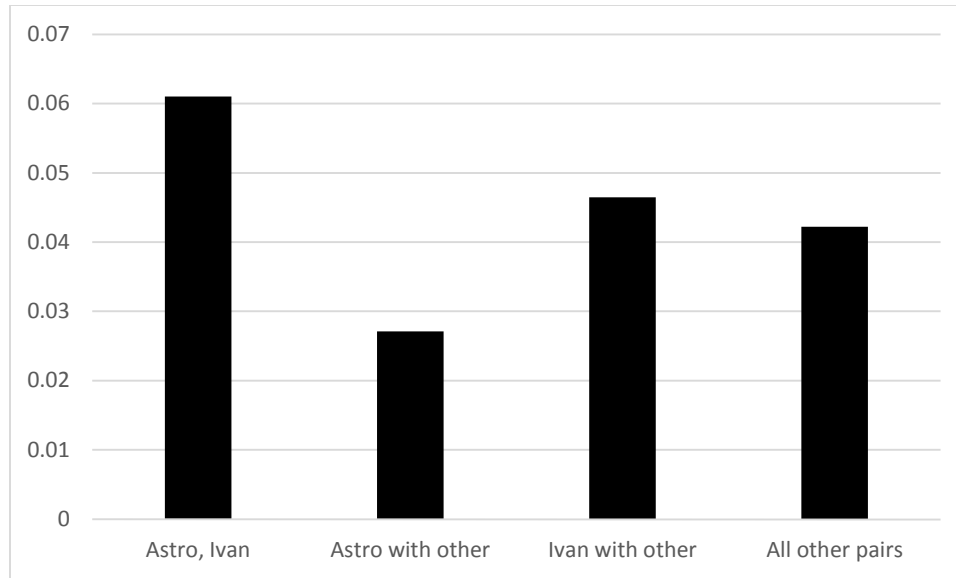


Figure 5. Mean rate of affiliative interactions

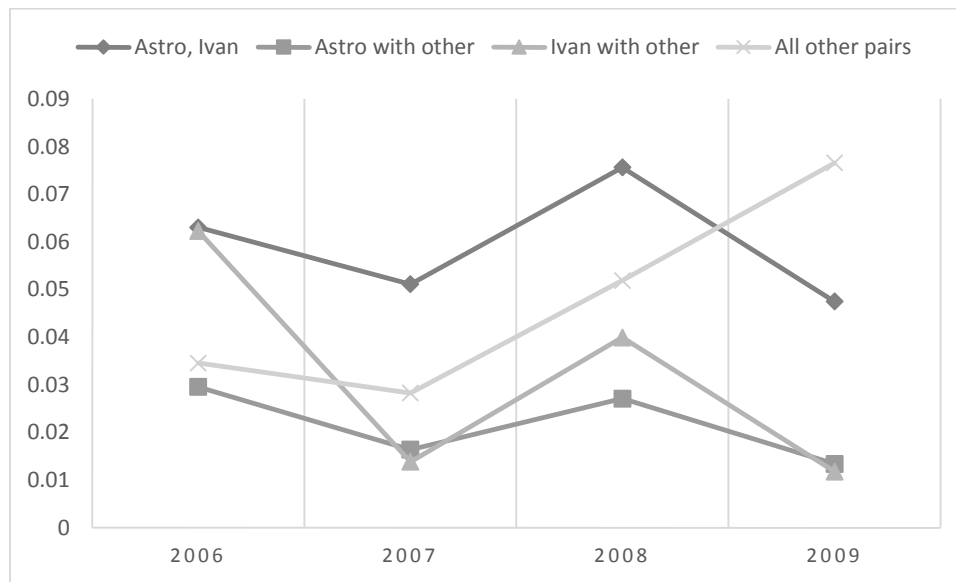
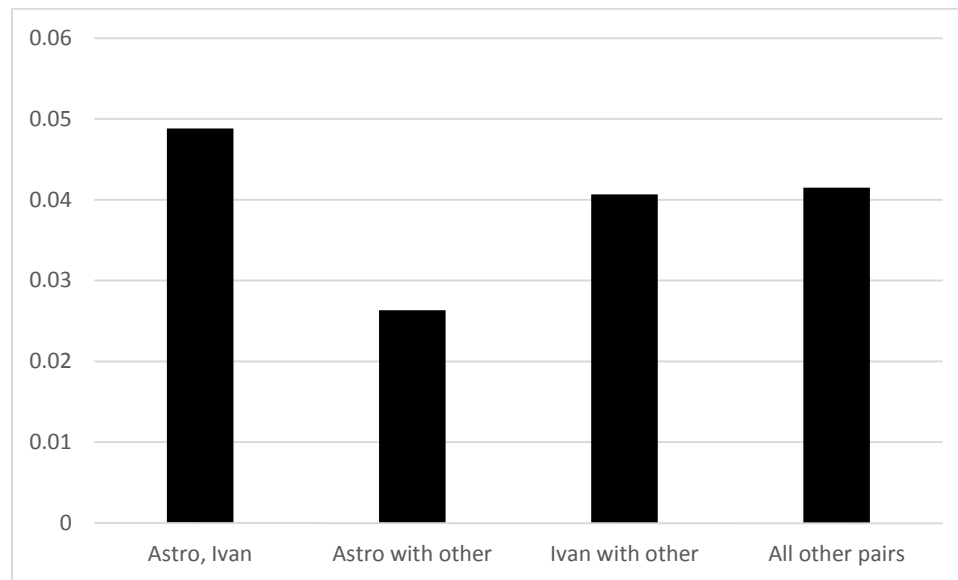


Figure 6. Mean rate of affiliative interactions over time

The two affiliative behaviors observed most frequently were tactile and pair swims. Astro engaged in more tactile (Games-Howell,  $p = 0.007$ ) and pair swim behaviors (Tukey,  $p = 0.002$ ) with Ivan than with any other dolphin (Figure 7). Tactile behaviors followed the same trend as the combined affiliative behaviors. In 2007, both

Astro and Ivan engaged in significantly more tactile behaviors within the pair than either did with other dolphins (Games-Howell, Astro:  $p = 0.004$ , Ivan:  $p = 0.002$ ). Figure 8 provides a summary of changes in the rates of tactile behaviors across the study period. Analyzing pair swims by year found similar results (see Figures 9 and 10). Astro also engaged in more pair swim behaviors (Tukey,  $p = 0.002$ ) with Ivan than with any other dolphin. 2007 was the only year in which these dolphins engaged in significantly more pair swims together than with other dolphins (Games-Howell, Astro:  $p = 0.026$ , Ivan:  $p = 0.019$ ).



*Figure 7.* Overall mean rate of tactile behaviors

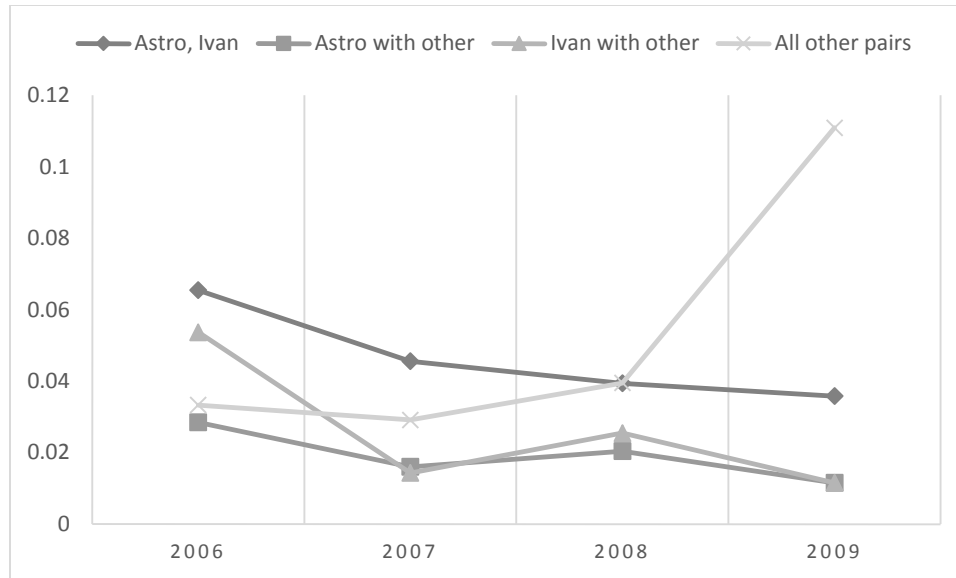


Figure 8. Mean rates of tactile behaviors over time

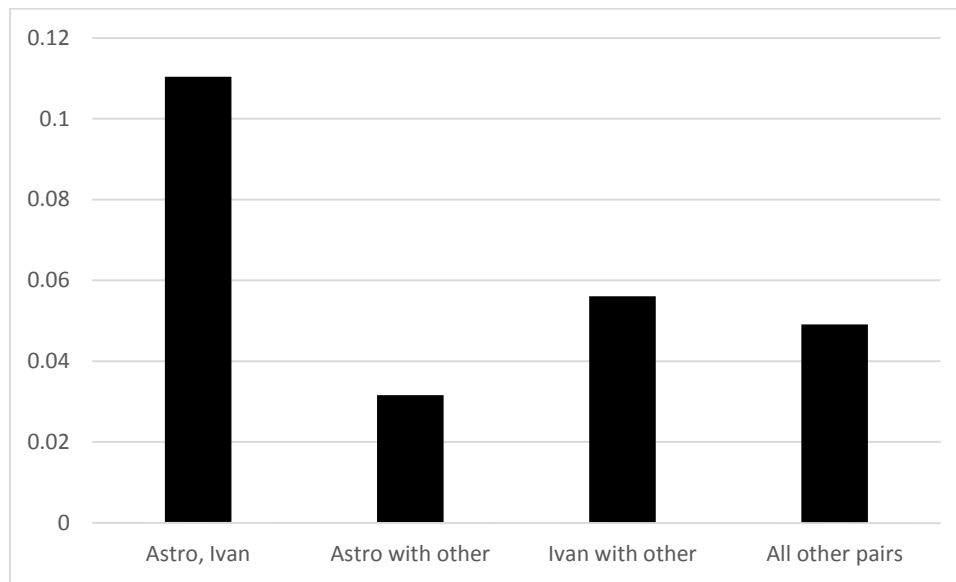
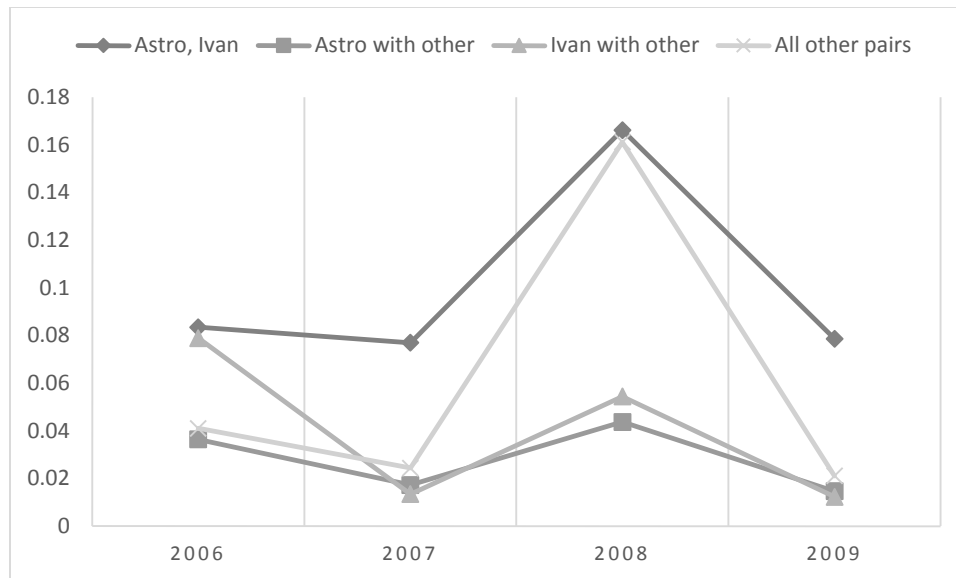
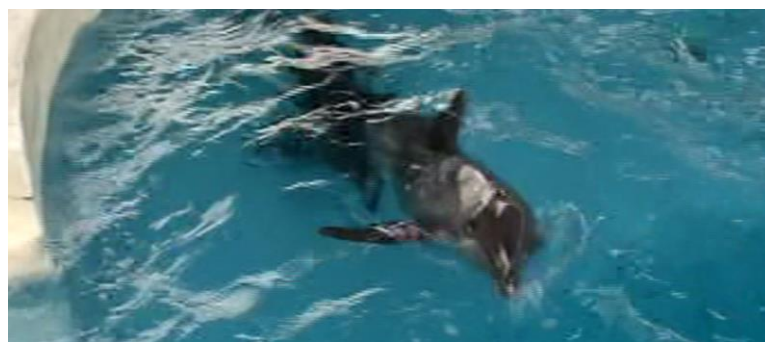


Figure 9. Overall mean rate of pair swims



*Figure 10.* Mean rate of pair swims over time

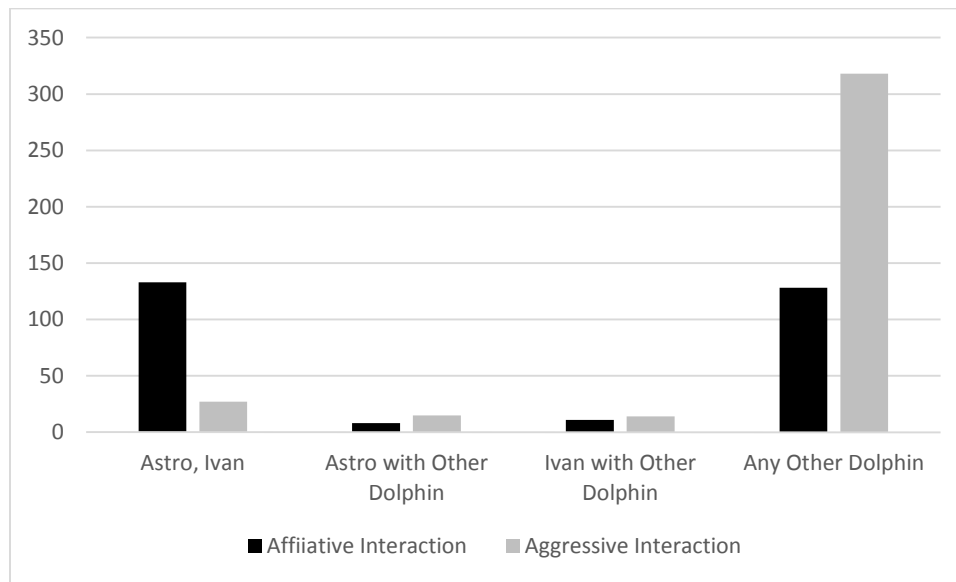
Interestingly, although Astro engaged in more behaviors exclusively with Ivan than Ivan did with Astro, Ivan initiated these affiliative interactions significantly more often (Welch (1, 64) = 5.466,  $p = 0.023$ ). In addition, Astro/Ivan pair swims were characterized by a swim pattern in which Ivan followed Astro (Figure 11). Rates of aggressive behaviors were low for the entire group, and there were not any significant differences based on the pair involved.



*Figure 11.* Astro/Ivan typically swim pattern with Ivan following Astro

### *Response to Aggressive Behaviors*

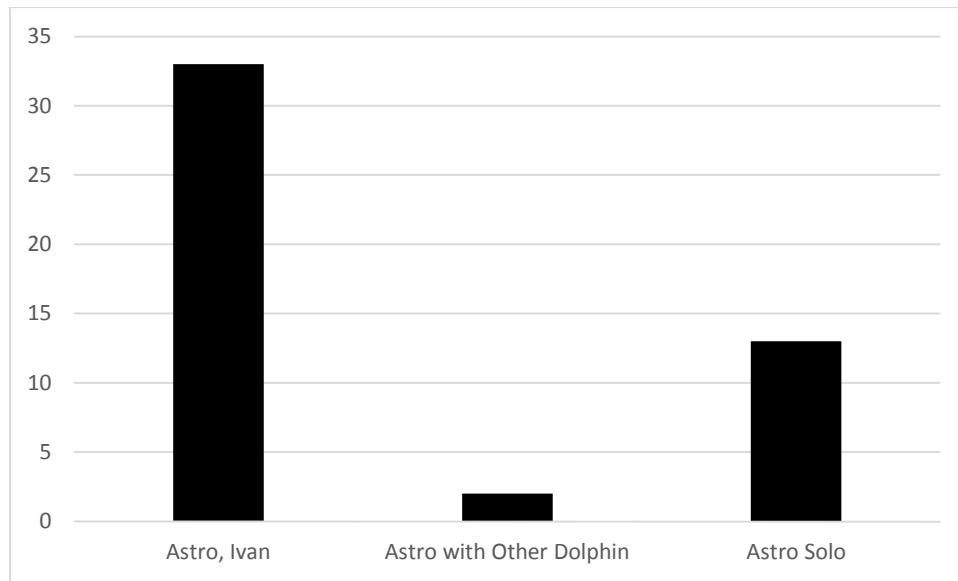
Astro and Ivan responded differently to aggressive behaviors within the group than did the other dolphins (see Figure 12). When any dolphin in the group engaged in aggressive behaviors, Astro and Ivan responded more often by interacting with each other with affiliative behaviors ( $N = 133$ ) than aggressive behaviors ( $N = 27$ ) and rarely interacted with other members of the group following these actions. The other dolphins within the group were more likely to engage in aggressive behaviors ( $N = 318$ ) following aggressive behaviors by other members of the group. They were also less likely to engage in affiliative behaviors following these behaviors ( $N = 128$ ).



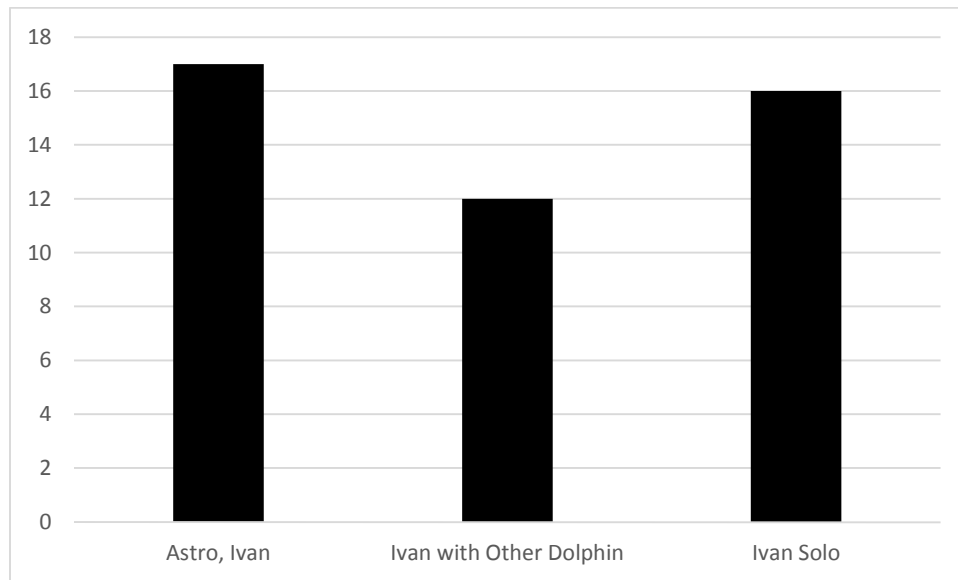
*Figure 12.* Frequency of affiliative and aggressive behaviors following aggression within overall group

When Astro was the recipient of an aggressive action from another dolphin within the group, his subsequent behavior was most often an interaction with Ivan. He was least likely to interact with another dolphin (see Figure 13). Ivan also engaged in more interactions with Astro and solo behaviors than interactions with other dolphins after he

was the recipient of an aggressive act, however these differences were not as pronounced as Astro's (Figure 14).



*Figure 13.* Astro's response to experiencing aggression



*Figure 14.* Ivan's response to experiencing aggression

## Measures of Association

The HWI for Astro and Ivan for the entire study period was 0.97 (See Table 2).

This indicates a strong association among this pair. There were changes in the strength of the association over time. The strongest association for this pair was found in 2006 (HWI = 0.94, Table 3). This decreased to 0.81 in 2007 and 0.79 in 2008 (See Tables 4 and 5).

Although there was some decline in the strength of these associations over time, these associations remained high throughout the study period. Associations were not calculated for 2009 since there was only a single day of observation.

Table 2

*Summary of Associations 2006 – 2008*

	<b>Strongest Associate (HWI)</b>	<b>Weakest Associate (HWI)</b>
<b>Astro</b>	Ivan (0.97)	Dancer (0.16)
<b>Dancer</b>	Doris/Noah (0.17)	Largo (0.09)
<b>Doris</b>	Noah (0.84)	Dancer (0.17)
<b>Ivan</b>	Astro (0.97)	Dancer (0.12)
<b>Largo</b>	Ivan (0.79)	Dancer (0.09)
<b>Noah</b>	Doris (0.84)	Vixen (0.11)
<b>Vixen</b>	Ivan (0.47)	Noah (0.11)

Table 3

*Summary of Associations 2006*

	<b>Strongest Associate (HWI)</b>	<b>Weakest Associate (HWI)</b>
<b>Astro</b>	Ivan (0.94)	Noah (0.09)



Table 3 (continued).

<b>Doris</b>	<b>Astro (0.29)</b>	<b>Ivan (0.12)</b>
<b>Ivan</b>	Astro (0.94)	Noah (0.04)
<b>Largo</b>	Ivan (0.58)	Noah (0.04)
<b>Noah</b>	Doris (0.28)	Ivan/Largo (0.04)
<b>Vixen</b>	<b>Doris (0.27)</b>	<b>Noah (0.14)</b>

Table 4

*Summary of Associations 2007*

	<b>Strongest Associate (HWI)</b>	<b>Weakest Associate (HWI)</b>
<b>Astro</b>	Ivan (0.81)	Doris (0.09)
<b>Doris</b>	Noah (0.72)	Ivan (0.00)
<b>Ivan</b>	Astro (0.81)	Doris (0.00)
<b>Largo</b>	Ivan (0.47)	Noah (0.09)
<b>Noah</b>	Doris (0.72)	Ivan/Vixen (0.00)
<b>Vixen</b>	Largo (0.45)	Noah (0.00)

Table 5

*Summary of Associations 2008*

	<b>Strongest Associate (HWI)</b>	<b>Weakest Associate (HWI)</b>
<b>Astro</b>	Ivan (0.79)	Doris/Noah (0.13)
<b>Dancer</b>	Doris/Noah (0.21)	Largo (0.10)
<b>Doris</b>	Noah (0.86)	Vixen (0.00)

Table 5 (continued).

<b>Ivan</b>	<b>Astro (0.79)</b>	<b>Dancer/Noah (0.13)</b>
<b>Largo</b>	Astro (0.61)	Dancer (0.10)
<b>Noah</b>	Doris (0.86)	Astro/Ivan (0.13)
<b>Vixen</b>	Ivan (0.25)	Doris/Noah (0.00)

## CHAPTER IV - DISCUSSION

The results of this study indicate that the two juvenile males in this study developed a strong affiliation over the course of the study period and that this bond was distinct from the interactions of other pairs within the group. Astro and Ivan engaged in affiliative behaviors significantly more often together than did the other pairs of dolphins. This cannot be attributed to more affiliative interactions in general. There was a decline for both Astro and Ivan in affiliative interactions when these involved other dolphins. This trend was more pronounced for Astro. The results are less clear for Ivan. Although Ivan engaged in more affiliative behaviors with Astro than with other dolphins, this result was not significant. For each study year the pair engaged in more affiliative behaviors together than with other dolphins in the group, but this difference achieved significance only in the 2007 period. Astro and Ivan were introduced in September of 2006, suggesting that 2007 marked a critical point in the formation of their affiliative bond. This suggests that these affiliative behaviors are important in the establishment of a new bond between animals. The affiliative behaviors that occurred with greatest frequency were tactile and pair swims. These behaviors were analyzed separately to determine if there were any differences in the use of tactile behaviors and pair swims across the study period as this bond formed. Both of these behaviors followed a similar pattern, with 2007 being the year in which the differences in rates of these behaviors in the Astro/Ivan pair were significantly greater than their interactions with other dolphins. The use of tactile behaviors and pair swims behavior by these dolphins in establishing this bond is similar to behavioral patterns described in alliances in the wild (Connor et al., 1992, 2000, 2006, Sakai et al., 2010). Further evidence of the importance of the early stages of

bond formation come from the results on the association patterns. The COA was highest in the months immediately following the introduction of these animals. These values declined slightly in the subsequent years although they did retain a strong association throughout the study period. The comparison of Astro and Ivan solo behaviors to their interaction rate also suggests that their alliance had reached maturity in 2008. It was in this year that they displayed a higher rate of interactions than solo behaviors.

The descriptions of alliances in the wild have focused on ecological benefits of these bonds, including access to reproductive females, protection from predators, distribution of food, and population density (Connor et al., 2000; Connor & Whitehead, 2005; Einfeld & Robinson, 2004; Wells, 1991). As members of a captive group, Astro and Ivan do not face these same ecological pressures. This suggests that other forces are involved in selecting for this type of bond formation. The behavior of these animals in response to aggression within the group provides important information into how this type of bond is beneficial to captive animals. Aggression by any dolphin in the group can create a stressful environment within the pool, and the behaviors of animals following such an event provide information on how that animal responds to stress. Following an aggressive act by any dolphin within the pool, Astro was most likely to respond by interacting with Ivan and these interactions were most often affiliative. Astro rarely interacted with other dolphins immediately following aggression. It is possible that affiliative interactions with Ivan provided Astro with a way of minimizing stress due to aggression in the pool. There are also differences in how Astro and Ivan respond to being the recipient of aggression. The behavior of both of these dolphins after experiencing an act of aggression was most likely an affiliative interaction within the

pair. They occasionally engaged in aggressive behaviors independently, but rarely engaged in aggressive interactions with each other following these incidents. This was in contrast to other members of the group, who were more likely to engage in aggressive behaviors than affiliative interactions following an act of aggression. This difference suggests a benefit to animals that have formed an affiliative bond in that this bond provides a means of coping with the fluctuating environment within a group.

Even though this association provided an important benefit to Astro and Ivan, there were individual differences between these dolphins. Astro engaged in more affiliative behaviors exclusively within the pair than did Ivan. However, Ivan was more likely to be the initiator of these affiliative interactions. Ivan also followed Astro during pair swims and either joined or left, thereby controlling the duration of these events. This supports a previous study which found that Ivan established a higher dominance rank in the group than Astro (Yeater et al., 2013). By directing the interactions with Astro, Ivan maintained this positioned dominance within the pair.

Astro and Ivan were both juveniles during the time period of this study. This provides a potential explanation for the formation of their affiliative bond. Studies of bottlenose dolphins indicate that male juveniles begin to associate in groups of similar age and begin forming strong associations with each other that tend to persist (Gero, Bejder, Whitehead, Mann, & Connor, 2005; Smolker et al., 1992; Wells et al., 1987). The other male within the group was an adult, and the other juvenile was a female. Therefore, the only juvenile males within the group were Astro and Ivan, which can explain the preferred association exhibited by these animals.

These findings have implications for the welfare of animals housed in captivity and in establishing an enriching environment. Environmental enrichment is used to improve the welfare of captive animals by decreasing stereotypic behavior and increasing natural behaviors of a species (Kuczaj et al. 2002; Shyne, 2006). Astro and Ivan engaged in more behaviors together than individually as this bond developed, limiting their performance of stereotypical behaviors. This finding suggests that the opportunity to form strong affiliative bonds can have important benefits in creating an enriching environment for rough-toothed dolphins. This is supported by previous work that found access to conspecifics to be enriching (e.g., Lambeth & Bloomsmith, 1992).

The formation of an alliance between two juvenile males suggests a similarity between the social behaviors of rough-toothed dolphins and bottlenose dolphins. This study indicates a social benefit for alliance formation. The captive setting of this study provides an opportunity to see if similar behaviors emerge under different conditions than that of the wild. These studies are important because they improve our understanding of these animals in captivity and allow for better management for their welfare in this environment. In addition, this study can provide important information about the social structure of this species that is difficult to observe in the wild. Future research may focus on how an alliance functions in the reduction of stress. It would also be beneficial to determine any personality differences in the dolphins that would contribute to individual differences observed within an alliance. Examining how this type of affiliative association changes from the juvenile period into adulthood will provide information about the social development of this species.

## REFERENCES

- Addink, M. J., & Smeenk, C. (2001). Opportunistic feeding behaviour of rough-toothed dolphins, *Steno bredanensis*, off Mauritania. *Zoologica Verh Leiden*, 334, 38-48.
- Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, 49, 227-267.
- Baird, R. W., Webster, D. L., Mahaffy, S. D., McSweeney, D. J., Schorr, G. S., & Ligon, A. D. (2008). Site fidelity and association patterns in a deep-water dolphin: Rough-toothed dolphins ( *Steno bredanensis* ) in the Hawaiian Archipelago. *Marine Mammal Science*, 24(3), 535–553. doi:10.1111/j.1748-7692.2008.00201.x
- Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, 35, 1454-1469.
- Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, 20, 37-46.
- Connor, R.C. (1995). The benefits of mutualism: A conceptual framework. *Biological Reviews*, 70, 427 – 457.
- Connor, R. C., & Curry, R. L. (1995). Helping non-relatives: A role for deceit? *Animal Behaviour*, 49, 389–393. doi:10.1006/anbe.1995.0051
- Connor, R. C., Heithaus, M. R., & Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin “super-alliance”. *Proceedings. Biological sciences / The Royal Society*, 268, 263–267.  
doi:10.1098/rspb.2000.1357
- Connor, R.C. & Norris, K.S.. (1982). Are Dolphins Reciprocal Altruists? *The American Naturalist*, 119, 358 - 374. doi:10.1086/283915

- Connor, R., Smolker, R., & Bejder, L. (2006). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal Behaviour*, 72(6), 1371–1378. doi:10.1016/j.anbehav.2006.03.014
- Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences of the United States of America*, 89, 987-990.
- Connor, R. C., Wells, R. S., Mann, J., & Read, A. J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91-126). Chicago, IL: University of Chicago Press.
- Connor, R., & Whitehead, H. (2005). Alliances II. Rates of encounter during resource utilization: a general model of intrasexual alliance formation in fission–fusion societies. *Animal Behaviour*, 69(1), 127–132. doi:10.1016/j.anbehav.2004.02.022
- De Moura, J. F., Da Silva Rodrigues, É., & Siciliano, S. (2009). Epimeletic behaviour in rough-toothed dolphins (*Steno bredanensis*) on the east coast of Rio de Janeiro State, Brazil. *Marine Biodiversity Records*, 2, e12.  
doi:10.1017/S1755267208000122
- Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals*, 24(3), 129–142.
- Dudzinski, K. M. (2010). Overlap between Information Gained from Complementary and Comparative Studies of Captive and Wild Dolphins. *International Journal of Comparative Psychology*, 23(2), 566–586. doi:10.1016/j.jebdp.2005.04.004



- Dudzinski, K.M., Gregg, J.D., Paolos, R.D., & Kuczaj, S.A. (2010). Pectoral fin contact behavior: Functional uses by captive and wild dolphins. *Behavioral Processes*, 84, 559 – 567.
- Dudzinski, K. M., Gregg, J. D., Ribic, C. A., & Kuczaj, S. A. (2009). A comparison of pectoral fin contact between two different wild dolphin populations. *Behavioral Processes*, 80, 182-190.
- Eisfeld, S. M., & Robinson, K. P. (2004). The Sociality of Bottlenose Dolphins in the Outer Southern Moray Firth, NE Scotland: Implications for Current Management Proposals? *European Research on Cetaceans*, 18.
- Frère, C. H., Krützen, M., Mann, J., Watson-Capps, J. J., Tsai, Y. J., Patterson, E. M., Connor, R., et al. (2010). Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. *Animal Behaviour*, 80(3), 481–486. doi:10.1016/j.anbehav.2010.06.007
- Gero, S., Bejder, L., Whitehead, H., Mann, J., & Connor, R. C. (2005). Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops* spp, 1573, 1566–1573. doi:10.1139/Z05-155
- Gibson, Q. A., & Mann, J. (2008a). Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. *Animal Behaviour*, 76(2), 375–387. doi:10.1016/j.anbehav.2008.01.021
- Gibson, Q. A., & Mann, J. (2008b). The size, composition and function of wild bottlenose dolphin (*Tursiops* sp.) mother–calf groups in Shark Bay, Australia. *Animal Behaviour*. doi:10.1016/j.anbehav.2008.01.022

- Götz, T., Verfuss, U. K., & Schnitzler, H.-U. (2006). Eavesdropping' in wild rough-toothed dolphins (*Steno bredanensis*)? *Biology Letters*, 2(1), 5–7.
- Herzing, D. L. (1996). Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*. *Aquatic Mammals*, 22(2), 61–79.
- Kuczaj, S.A. II, Lacinak, T., Otto, F., Trone, M., Solangi, M., & Ramos, J. (2002). Keeping environmental enrichment enriching. *International Journal of Comparative Psychology*, 15, 127–137.
- Kuczaj, S.A., Lacinak, C.T., & Turner, T. N. (1998). Environmental enrichment for marine mammals at Sea World. In D.J. Shepherdson, J.D. Mellen, & M. Hutchins. (Eds.), *Second nature* (pp. 314-328). Washington DC: Smithsonian Institution Press.
- Kuczaj II, S. A., & Yeater, D. B. (2007). Observations of rough-toothed dolphins (*Steno bredanensis*) off the coast of Utila, Honduras. *Journal of the Marine Biological Association of the UK*, 87(01), 141. doi:10.1017/S0025315407054999
- Lambeth, S. P., & Bloomsmith, M. A. (1992). Mirrors as enrichment for captive chimpanzees (*Pan troglodytes*). *Laboratory Animal Science*, 42(3), 261 – 266.
- Lusseau, D. (2003). The emergent properties of a dolphin social network. *Proceedings of the Royal Society B Biological Sciences*, 270(Suppl 2), S186–S188.
- Lusseau, D. (2007). Why Are Male Social Relationships Complex in the Doubtful Sound Bottlenose Dolphin Population? (S. Brosnan, Ed.) *PLoS ONE*, 2(4), 8.
- Lusseau, D., Schneider, K., Boisseau, O. J., Haase, P., Sloaten, E., & Dawson, S. M. (2003). The bottlenose dolphin community of Doubtful Sound features a large

- proportion of long-lasting associations. *Behavioral Ecology and Sociobiology*, 54(4), 396–405. doi:10.1007/s00265-003-0651-y
- Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, 136, 529-566.
- Mann, J. (1997). Individual Differences in Bottlenose Dolphin Infants. *Family Systems*, 4, 35–49.
- Mayr, I., & Ritter, F. (2005). Photo-identification of rough-toothed dolphins (*Steno bredanensis*) off La Gomera (Canary Islands) with new insights into social organisation. *19th Annual European Cetacean Society Meeting; La Rochelle, France. 2-7th April* (pp. 1–3).
- McBride, A.F. & Hebb, D.O. (1948). Behavior of the captive bottle-nose dolphin, *Tursiops truncatus*. *Journal of Comparative Physiological Psychology*, 41, 111-123.
- Möller, L. M., Beheregaray, L. B., Allen, S. J., & Harcourt, R. G. (2006). Association patterns and kinship in female Indo-pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Behavioral Ecology & Sociobiology*, 61, 109 – 117.
- Möller, L. M., Beheregaray, L. B., Harcourt, R. G., & Krützen, M. (2001). Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proceedings of the Royal Society of London Series B Biological Sciences*, 268, 1941–1947. doi:10.1098/rspb.2001.1756

- Norris, K.S. (1991). Looking at wild dolphin schools. In K. Pryor & K.S. Norris, (Eds). *Dolphin societies: Discoveries and puzzles*. Berkeley, CA: University of California Press
- Norris, K.S., Wursig, B., Wells, R.S., & Wursig, M. (1994). *The Hawaiian spinner dolphin*. Berkeley, CA: University of California Press.
- Ostman, J. (1991). Changes in aggressive and sexual behavior between two male bottlenose dolphins (*Tursiops truncatus*) in a captive colony. In Pryor, K. & Norris, K.S. (Eds.) *Dolphin societies: Discoveries and puzzles* (pp. 305–317). Berkeley, CA: University of California Press.
- Parsons, K. M., Durban, J. W., Claridge, D. E., Balcomb, K. C., Noble, L. R., & Thompson, P. M. (2003). Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Animal Behaviour*, 66(1), 185–194. doi:10.1006/anbe.2003.2186
- Pitman, R. L., & Stinchcomb, C. (2002). Rough-Toothed Dolphins (*Steno bredanensis*) as Predators of Mahimahi (*Coryphaena hippurus*). *Pacific Science*, 56(4), 447–450. doi:10.1353/psc.2002.0043
- Quintana-Rizzo, E., & Wells, R. S. (2001). Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: Insights into social organization. *Canadian Journal of Zoology*, 79(3), 447–456. doi:10.1139/cjz-79-3-447
- Ritter, F. (2002). Behavioural observations of rough-toothed dolphins (*Steno bredanensis*) off La Gomera, Canary Islands (1995-2000) with special reference to their interactions with humans. *Aquatic Mammals*, 28, 46–59.

- Ritter, F. (2007). Behavioral responses of rough-toothed dolphins to a dead newborn calf. *Marine Mammal Science*, 23(2), 429–433. doi:10.1111/j.1748-7692.2007.00107.x
- Rogers, C. A., Brunnick, B. J., Herzing, D. L., & Baldwin, J. D. (2004). The social structure of bottlenose dolphins, *Tursiops truncatus*, in the Bahamas. *Marine Mammal Science*, 20(4), 688-708.
- Sakai, M., Morisaka, T., Kogi, K., Hishii, T., & Kohshima, S. (2010). Fine-scale analysis of synchronous breathing in wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Behavioural Processes*, 83(1), 48–53.
- Sakai, M., Hishii, T., Takeda, S., & Kohshima, S. (2006). Laterality of flipper rubbing behaviour in wild bottlenose dolphins (*Tursiops aduncus*): Caused by asymmetry of eye use? *Behavioral Brain Research*, 170, 204–210.
- Samuels, A., & Gifford, T. (1997). A quantitative assessment of dominance relations among bottlenose dolphins. *Marine Mammal Science*, 13, 70-99.
- Sayigh, L., Tyack, P., Wells, R., Solow, A., Scott, M., & Irvine, A. (1999). Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal Behaviour*, 57(1), 41–50. doi:10.1006/anbe.1998.0961
- Scott, E., Mann, J., Watson-Capps, J.J., Sargeant, B.L., & Connor, R.C. (2005) Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour*, 142, 21-44.
- Scott, M.D., Wells, R.S., & Irvine, A.B. (1990). A long-term study of bottlenose dolphins on the west coast of Florida. In S. Leatherwood & R.R. Reeves (Eds.) *The Bottlenose Dolphin* (pp. 235-244). San Diego, CA: Academic Press, Inc.

- Shyne, A. (2006). Meta-analytic review of the effects of enrichment on stereotypic behavior in zoo mammals. *Zoo Biology*, 25, 317 – 337.
- Smolker, R., & Pepper, J. W. (1999). Whistle convergence among allied male bottlenose dolphins (Delphinidae, *Tursiops* sp.). *Ethology*, 105(7), 595–617.  
doi:10.1046/j.1439-0310.1999.00441.x
- Smolker, R. A., Richards, A. F., Connor, R. C., & Pepper, J. W. (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, 123, 38-69.
- Smuts, B., & Smuts, R. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior*, 22, 1–63. doi:10.1016/S0065-3454(08)604040
- Tamaki, N., Morisaka, T., & Taki, M. (2006). Does body contact contribute towards repairing relationships? The association between flipper-rubbing and aggressive behavior in captive bottlenose dolphins. *Behavioural Processes*, 73(2), 209–215.
- Tavolga, M. C. (1966). Behavior of the bottlenose dolphin (*Tursiops truncatus*): Social interaction in a captive colony. In K. S. Norris (Ed.) *Whales, dolphins and porpoises*. Berkeley, CA: University of California Press.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46, 35 - 57. doi:10.1086/406755
- Waples, K. A., & Gales, N. J. (2002). Evaluating and minimizing social stress in the care of captive bottlenose dolphins (*Tursiops aduncus*). *Zoo Biology*, 21, 5-26.
- Wells, R. S. (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In K. Pryor & K. S. Norris (Eds.) *Dolphin*

- Societies: Discoveries and Puzzles* (pp. 199–225). Berkeley, CA: University of California Press.
- Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. G. Genoway (Ed.), *Current mammalogy*, Vol. 1. (pp. 247 – 305). New York, NY: Plenum Press.
- Welsh, L., & Herzing, D. (2008). Preferential association among kin exhibited in a population of Atlantic spotted dolphins (*Stenella frontalis*). *International Journal of Comparative Psychology*, *21*, 1–11.
- Whitehead, H. (2009). *SOCPROG: Programs for analyzing social Structure*. Version 2.4. Halifax, Nova Scotia, Canada: Dalhousie University.
- Wiszniewski, J., Allen, S. J., & Möller, L. M. (2009). Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. *Animal Behaviour*, *77*(6), 1449–1457. doi:10.1016/j.anbehav.2009.02.025
- Yeater, D., Miller, L.E., Caffery, K.A., & Kuczaj, S.A. (2013). Effects of an increase in group size on the social behavior of a group of rough-toothed dolphins (*Steno bredanensis*). *Aquatic Mammals*, *39*, 344–355.