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Briana Nicole Harvey
University of Southern Mississippi

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THE NATURE OF SOCIAL RELATIONSHIPS IN BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*): ASSOCIATIONS AND THE ROLE OF AFFILIATIVE, AGONISTIC, AND SOCIO-SEXUAL BEHAVIORS

by

Briana Nicole Harvey

A Thesis
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for the Degree of Master of Arts

Approved:

Dr. Stanley A. Kuczaj II, Committee Chair
Professor, Psychology

Dr. David Echevarria, Committee Member
Associate Professor, Psychology

Dr. Kathleen Dudzinski, Committee Member
Director, Dolphin Communication Project

Dr. Karen S. Coats
Dean of the Graduate School

May 2015

ABSTRACT

THE NATURE OF SOCIAL RELATIONSHIPS IN BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*): ASSOCIATIONS AND THE ROLE OF AFFILIATIVE, AGONISTIC, AND SOCIO-SEXUAL BEHAVIORS

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May 2015

Little is known about the specific behavioral exchanges that occur on a day-to-day basis between dyads of bottlenose dolphins (*Tursiops truncatus*). This thesis assesses proximity between dyads (~ 2 meters) and the proportion of time that is spent in either an affiliative, agonistic, or socio-sexual context within age/sex pairings of dolphins in order to better understand the nature of social relationships in this species. Observations of bottlenose dolphins housed at the Roatan Institute of Marine Sciences, collected in 2010, provided 10.5 hours of underwater footage for assessment of association coefficients and proportions of interactions. These data suggested similar patterns to previous studies on bottlenose dolphin association patterns and interactions. Mother-calf dyads were found to share the highest coefficients of association, followed by male-male, female-female, and male-female dyads. Four classes of association coefficients were defined for the population: low, medium, medium-high and high. Regardless of which class dyads fell into, affiliative behavior was the most prevalent context recorded, followed by agonistic, and then socio-sexual contexts. This same pattern was also found regardless of which age/sex categories the dyads were placed. This study is the first to quantitatively assess association patterns with affiliative, agonistic, and socio-sexual behaviors in this species concurrently and reveals that the social relationships of these dolphins are predominately affiliative in nature. Furthermore, the patterns of social relationships observed appear to be consistent with sex-specific reproductive strategies.

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CHAPTER I

INTRODUCTION

Among social species, individuals often spend more time associating or interacting with certain conspecifics than with others (Krause & Ruxton, 2002). When such social preferences occur, and are consistent over time, individuals are thought to share a social relationship (Whitehead, 1997). Assessing who spends time with whom, and how that time is spent, is necessary to understand the nature of social relationships. This has been achieved for several species such as meerkats (*Suricata suricatta*) (Drewe, Madden, & Pearce, 2009; Kutsukake & Clutton-Brock, 2010), dwarf mongooses (*Helogale undulata rufula*) (Rasa, 1987), ravens (*Corvus corax*) (Fraser & Bugnyar, 2010), giraffes (*Giraffa camelopardalis*) (Bashaw, Bloomsmith, Maple, & Bercovitch, 2007), and non-human primates (Goodall, 1986; Mitani, Watts, & Muller, 2002; Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987). Long-term behavioral studies of primates have led to a greater understanding of the social relationships between individuals. Male chimpanzees (*Pan troglodytes*) form long-lasting and stable bonds with other males, and the quality of these relationships may be affected by kinship and dominance status (Mitani, 2009). Similarly, in baboons (*Papio cynocephalus ursinus*), Silk, Alberts, and Altmann (2006) found that females form long-lasting bonds with other females that are close kin or of similar age.

In a recent study comparing chimpanzees and bottlenose dolphins (*Tursiops truncatus*), Pearson (2011) found male-male bonds to be the strongest, followed by female-female bonds, and lastly, male-female bonds for both species, though the mother-infant bond was the strongest in both species. Dependent young of both species rely on their mothers for the first three to six years of life. During this time, females associate almost exclusively with their infant or other females (Pearson, 2011).

Bottlenose dolphins often inhabit shallow coastal waters, which facilitates ongoing long-term studies. Individuals can be identified using reliably recognizable characteristics on their dorsal fins, such as nicks, notches, and scars (Würsig & Würsig, 1977). Association coefficients are often used to represent the amount of time individuals spend together (Ginsberg & Young, 1992), and have been used to describe social bonds and structure in bottlenose dolphins (Bräger, Würsig, Acevedo, & Henningsen, 1994; Connor, Wells, Mann, & Read, 2000; Lusseau et al., 2003; Smolker, Richards, Connor, & Pepper, 1992; Wells, Scott, & Irvine, 1987). Strong association coefficients between individuals are assumed to reflect affiliative interactions and relationships (Bräger et al., 1994; Connor et al., 2000). Additionally, studies have quantitatively assessed other affiliative (Connor, Mann, & Watson-Capps, 2006; Dudzinski, Gregg, Paulos, & Kuczaj, 2010; Sakai, Morisaka, Kogi, Hishii, & Kohshima, 2010), agonistic (Holobinko & Waring, 2010; Scott, Mann, Watson-Capps, Sargeant, & Connor, 2005; Weaver, 2003), and socio-sexual (Mann, 2006) behavior in attempts to describe the patterns and functions of these behaviors. Nevertheless, no studies have attempted to concurrently assess the affiliative, socio-sexual, and agonistic behaviors that bottlenose dolphins display. By examining these three behavioral contexts together, we can see how dolphins manage their social relationships on a day-to-day basis.

Background Information

Dolphins in the genus *Tursiops sp*. are among the most studied members of the Delphinidae family that live in fluid fission-fusion societies (Mann, 2000). The larger groups are of variable size and composition, while smaller subgroups that dolphins split into typically reflect stable associations based on sex and age classes for some populations of bottlenose dolphins (Smolker et al., 1992; Wells et al., 1987). A fission-fusion organization has also been used to describe other social species including humans (Marlowe, 2005), and some non-human primates such as chimpanzees (Mitani et al., 2002) and spider monkeys (*Ateles geoffroyi*) (Chapman, Chapman, & Wrangham, 1995).

Association via Proximity

Spatial proximity, or nearness in space, is commonly used as a method to determine the proportion of time two individuals are associated, which can be used to measure coefficients of association (COA) (Ginsberg & Young, 1992; Whitehead, 2008). COAs can range in value from 0 (individuals never found in the same group) to 1.00 (individuals always sighted together). Field studies typically define associations as individuals sighted from the surface within the same group. One of the criterion to assign group membership is the distance between animals, which widely varies between studies and may range from 10 meters up to 100 meters apart (Gibson & Mann, 2008b; Irvine & Wells, 1972; Lusseau et al., 2003; Mann & Smuts, 1999; Möller, Beheregaray, Allen, & Harcourt, 2006; Quintana-Rizzo & Wells, 2001; Shane, Wells, & Würsig, 1986; Smolker et al., 1992; Wells et al., 1987).

In situations where good visibility enables underwater observations, it is possible to examine spatial proximity at a much finer scale. Definitions based on spatial proximity are often used for the calculation of association measures because they are ecologically meaningful. Maintaining close spatial proximity is believed to represent social affiliation between individuals because being close places them in a position to interact with each other (Bräger, 1999; Connor et al., 2000). Consequently, an individual in close spatial proximity could also either harm or protect another individual, which may be significant in terms of survival (Connor et al., 2000; Mann, 2000). Therefore, according to Mann (2000), it is useful to focus on associations that occur within a body length of the species being studied because it may reflect their vulnerability to predators or harm by conspecifics. Even an animal just passing by another within a body length is in a position to engage in an interaction with that animal.

Studies have revealed both similarities and differences in group composition and stability of associations between bottlenose dolphins [Gulf de Guayaquil, Ecuador (Félix, 1997), Doubtful Sound, New Zealand (Lusseau et al., 2003), Cedar Keys, Florida (Quintana-Rizzo & Wells, 2001), The Bahamas (Rogers, Brunnick, Herzing, & Baldwin, 2004), Shark Bay, Australia (Smolker et al., 1992), and Sarasota, Florida (Wells et al., 1987)]. Male bottlenose dolphins have been reported to share both high (e.g., HWI= .65; Lusseau et al., 2003; e.g., HWI= .75; Wells et al., 1987) and low coefficients of association with other males (e.g., HWI = .24; Quintana-Rizzo & Wells, 2001; e.g., HWI = .17; Rogers et al., 2004). Males in Sarasota, Florida, may either be solitary or associate in pairs that have been observed to remain stable for up to 20 years (Wells, 2003). It has been suggested; however, that lone males may simply be in a transition phase and that pair bonds are the predominant strategy for males in Sarasota, Florida (Owen, Wells, & Hofmann, 2002). In Shark Bay, Australia, males form first-order alliances consisting of a dyad or triad of males, each sharing COAs between .70 and 1.00 that cooperate to obtain access to females (Connor, Smolker, & Richards, 1992b). Males cooperate by herding females, a behavior that likely allows males to increase their reproductive success through an increase in copulations. Furthermore, these male-male alliances have been reported to last up to 17 years in Shark Bay (Krutzen et al., 2003).

Associations between females have also been reported as having both high coefficients of association (e.g., HWI = .83; Félix, 1997; e.g., HWI = .80; Wells et al., 1987), and low ones (e.g., HWI = .10; Quintana-Rizzo & Wells, 2001). Some females form loose social networks with other females of varying age and kinship that have been observed to last up to five years (Möller et al., 2006; Smolker et al., 1992; Wells, 2003). It appears these female-female associations may largely be dependent upon the shared need for vigilance and protection from predators or male harassment (Connor et al., 2000). Nursery groups, consisting of females and calves, have also been reported in both Sarasota Bay and Shark Bay (Gibson & Mann, 2008a; Wells, 2003; Wells et al., 1987) but not in the Doubtful Sound (Lusseau et al., 2003). It has been suggested that nursery groups exist so calves may develop important social skills through early interaction with conspecifics (Gibson & Mann, 2008a). Some females, however, appear to remain solitary (Connor et al., 2000; Wells et al., 1987).

Male-female associations occur less frequently than same-sex associations in both Shark Bay and Sarasota Bay (Smolker et al., 1992; Wells et al., 1987). Associations between males and females at both study sites were strongly influenced by female reproductive status. Although COAs between adult males and females were not strong, males and females were observed in mixed sex groups about 50% of the time in Shark Bay (Smolker et al., 1992), and about 31% of the time in Sarasota Bay (Wells et al., 1987). In contrast, strong associations between the sexes were found in Doubtful Sound, New Zealand (e.g., HWI = .57; Lusseau et al., 2003). These strong associations between sexes are assumed to be due to isolation from other communities as a consequence of ecological factors that make dispersal unlikely, thus leading to an increase in group stability as a means to increase inclusive fitness for the population (Lusseau et al., 2003).

Social Behavior and Interactions

Observable social interactions between individuals often reflect a pattern where the occurrence and outcome of one interaction affects subsequent ones (Hinde, 1976). The interactions observed in dolphins are typically grouped into three types of social behavior: affiliative, agonistic, and socio-sexual. Affiliation is expressed by close proximity (~ 2 meters), synchronous behavior, and physical contact (Connor et al., 2000). Synchrony occurs when two or more individuals perform the same behavior in unison (Connor, Smolker, & Bejder, 2006). Proximity and synchrony have been described in the mother-calf relationship (Mann & Smuts, 1999; Wells et al., 1987), between bonded males, and between females in Shark Bay (Connor, Mann, et al., 2006). In Japan, Sakai et al. (2010) reported that synchronous breathing occurred most frequently between mother-calf pairs, and that adults and sub-adults also frequently engaged in synchronous breathing with members of the same sex and age class. Additionally, male-female adult pairs were occasionally observed breathing in synchrony (Sakai et al., 2010); however, the authors did report that the distance between these dyads was greater when compared to other same sex dyads and mother calf pairs who maintained closer proximity within a meter. Although Sakai et al. (2010) did not discuss why this might have occurred, Wells (2003) described a similar behavior in Sarasota that was characterized as mate guarding; males were described as following behind females within several meters during times when females were in estrus. In a study of synchronous behavior in male dyads, Connor, Smolker, et al. (2006) suggested that males might engage in synchronous breathing with other males as a means to maintain sight of each other and engage in allied underwater activities. It would make sense then that a male guarding a female would want to maintain sight of her at all times and be prepared to defend against any approaching males or give chase in the event that she fled.

Another potential explanation of synchronous behavior is that it signals cooperation or may ease tension between two individuals in close proximity (Connor, Smolker, et al., 2006). Dyads in close proximity may also engage in physical contact, such as when one individual rests its pectoral fin against the side of another that can sometimes involve more active movement such as petting or rubbing (Dudzinski et al., 2010; Dudzinski, Gregg, Ribic, & Kuczaj, 2009; Mann & Smuts, 1998; Mann & Smuts, 1999; Sakai, Hishii, Takeda, & Kohshima, 2006; Samuels, Sevenich, Gifford, Sullivan, & Sustman, 1989; Tamaki, Morisaka, & Taki, 2006; Tavolga & Essapian, 1957). Both male and female dolphins engage in these contact behaviors (Connor et al., 2000; Mann & Smuts, 1999; Tavolga & Essapian, 1957), which are believed to be important in developing and maintaining social bonds (Connor, Mann, et al., 2006). In fact, petting and rubbing have been observed frequently between bonded individuals in Shark Bay (Mann & Smuts, 1998; Mann & Smuts, 1999). It has been suggested that these behaviors are analogous to grooming in primates (Dudzinski, 1998; Norris, Würsig, Wells, & Würsig, 1994; Sakai et al., 2006), which serves a social function to maintain relationships (Lehmann, Korstjens, & Dunbar, 2007).

Agonistic behavior includes both aggressive and submissive behaviors. Aggression is characterized by threats and physical contact that may cause harm

(Samuels & Gifford, 1997). Threats include the open mouth display, jaw claps, charges, and a head-to-head or 90° swift approach at a conspecific (Dudzinski, 1996; Holobinko & Waring, 2010; Weaver, 2003). Aggressive physical contact may include tail swats, hits, bites, tooth raking, pushes, or body slams (Connor et al., 2000; Samuels & Gifford, 1997; Weaver, 2003). Aggression is often a product of intrasexual competition between males and intersexual conflict such as sexual coercion (Scott et al., 2005). Increased intersexual aggression has been reported in association with seasonal mating peaks (Caldwell & Caldwell, 1977; Essapian, 1963; McBride & Kritzler, 1951; Samuels & Gifford, 1997), along with a significant increase in new tooth-rake marks on cycling females (Scott et al., 2005). Scott et al. (2005) assessed aggression in wild odontocetes in Shark Bay using tooth-rake marks and focal follows on females with calves. The authors found a large proportion (83.1%) of dolphins had tooth-rake marks. Males had more rakes than females, while cycling females tended to have more rakes than non-cycling females. The focal follows revealed almost no aggression from adult females, the only occurrences involved aggression to their calves. Additionally, females were the receivers of aggressive acts from primarily adult and juvenile males. Finally, male calves showed higher rates of aggression than female calves (Scott et al., 2005). In a study of agonistic behavior, Samuels and Gifford (1997) found that rates of agonism were significantly higher within male-male dyads, followed by male-female dyads. Aggression rates between female-female dyads were consistently low. In contrast, Weaver (2003) found slightly higher rates of conflict between female-female dyads, with no significant difference between male-male or male-female dyads. However, the higher rates of conflict observed between female-female dyads in her study were primarily due to aggression to a calf occurring over repeated weaning and allonursing disputes (Weaver, 2003). Holobinko and Waring (2010) were unable to make conclusions about the effects of sex on rates of conflict due to sample size, but were able to determine that age class was a significant determinant of aggression, with juveniles engaging in more conflict than adults. Although not statistically analyzed, Samuels and Gifford (1997) and Weaver (2003) also noted a prevalence of agonistic interactions in juveniles; however, neither of these studies offered any discussion as to why juveniles might show higher aggression than other age classes. In most mammalian societies, juveniles engage in more play and mock fighting than other age groups (Byers, 1984; Gibson & Mann, 2008a; Meaney, Stewart, & Beatty, 1985). In fact, play behavior is prevalent in immature dolphins (Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006). One theory of juvenile play is that it provides juvenile dolphins practice for skills needed for survival and reproduction (Gibson & Mann, 2008b).

Socio-sexual behavior includes mounting, genital inspection, genital nudging, and attempted or actual copulations (Connor et al., 2000). These behaviors have been documented for every possible dolphin age-sex class combination (Mann & Smuts, 1999; Östman 1991; Tavolga & Essapian, 1957). Calves and juveniles engage in the highest rates of socio-sexual behavior, including activity with same-sex individuals (Mann, 2006). These behaviors may allow young animals to gain experience for future mating opportunities, promote bonds with other individuals, and may be a result of increased hormonal activity during development or a combination of these factors (Mann, 2006). Frequent same-sex activity between males has been reported (McBride, 1940; McBride & Hebb, 1948; Östman, 1991; Tavolga & Essapian, 1957). In Shark Bay, females have been reported to occasionally mount other females (Connor et al., 2000; Mann, 2006). In a study of dolphin dominance hierarchies, Östman (1991) proposed that socio-sexual behavior occurring between two males might be used to assert dominance. A more common theory is that socio-sexual behaviors (excluding intromission between a male and female) may function to mediate social relationships as suggested for other primate and cetacean species (Connor et al., 2000).

Current Study

This study examined a population of captive bottlenose dolphins (*Tursiops truncatus*) that reside at the Roatan Institute of Marine Science (RIMS) located at Anthony's Key Resort in Roatan, Honduras. The study population ranged in age from neonate to 30+ years, and included both captive born and wild caught individuals. According to Dudzinski et al. (2010), the sex and age demographics of this study group closely resemble those of coastal wild bottlenose dolphin populations found in Shark Bay, Australia (Connor, Smolker, et al., 2006), and around Mikura Island, Japan (Kogi, Hishii, Imamura, Iwatani, & Dudzinski, 2004). This setting provided an excellent opportunity to record underwater observations of interactions between identified individuals. To provide information on the nature of social relationships in these bottlenose dolphins, proximity measures and proportions of affiliative, agonistic, and socio-sexual behaviors were assessed using 10.5 hours of underwater video recordings collected in 2010, as part of an ongoing, long-term study by the Dolphin Communication Project. The purpose of this study was to determine who was spending time together and generally how that time was being spent. The study addressed the following questions: (a) Which sex and age classes are more likely to associate with each other? (b) Do these association coefficients affect the proportion of sampling periods spent in affiliative, agonistic, and socio-sexual behaviors? (c) Does sex and age affect the proportion of sampling periods spent in affiliative, agonistic, and socio-sexual behaviors?

CHAPTER II

METHODS

Subjects and Study Site

The Roatan Institute for Marine Science (RIMS) is located on the NW side of Roatan Island, which is the center of three bay islands located 43.5 km north of the Honduras coast. The dolphins at this site are kept in an enclosed sea pen adjacent to Bailey's Key (Figure 1). The enclosure has a total surface are of approximately 8,000 m^2 and ranges in depth from the shoreline to about 7 m. The sea floor consists of coral, sand, and sea-grass beds.

Figure 1. Baileys Key as part of Anthony's Key Resort, Roatan, Honduras, with dolphin sea pens visible. (Photo credit, Anthony's Key Resort. Retrieved January 15, 2011, from: http://www.anthonyskey.com/dolphins/dolphin-programs.htm)

During the study period (January 2010), the population consisted of 12 males and 12 females. Age distribution was: four calves, six juveniles, three sub-adults, and 11 adults. Age classes were provided by Dudzinski and associates at RIMS and were based on year born (K. Dudzinski, personal communication, March 2013).

Data Collection

Underwater video data were collected by the Dolphin Communication Project (DCP) using a mobile video/acoustic system that allowed for synchronous video and stereo audio recordings (Dudzinski, Clark, & Würsig, 1995). The data were collected using focal–animal, all-occurrence sampling (Altmann, 1974). Focal follows began when an animal came into view and terminated when the animal went out of view (Dudzinski et al., 2009; Dudzinski et al., 2010). Video data were collected in 30 or 60-minute observational sessions.

Identification sketches for each dolphin in the 2010 video data were provided for recognition and confirmation of individual dolphins (K. Dudzinski, personal communication, March 2013). The sketches contained details such as rake marks, scars and other marks for each dolphin. Each videotaped session was also logged with respect to dolphin identification per second of video (K. Dudzinski, personal communication, March 2010): these video logs provided reliable confirmation for each confirmed dolphin ID within each videotaped session.

Eleven hours, five minutes of underwater footage was available for assessment, providing 221 sampling periods. Each session was divided into three-minute segments termed sampling periods, to yield data independence; a method used previously in studies on pectoral fin contact (Dudzinski et al., 2010; 2012). Of these original 221 sampling periods, nine were excluded from analysis because they did not meet the three-minute sampling period criterion. Thus, 212 sampling periods were assessed, with either 10 or 20 sampling periods per videotaped session.

For each three-minute segment, each individual dyad was recorded once as associating if they passed within an adult body-length (~2 meters) of each other during a segment. The first behavior each observed dyad engaged in, if any, for each segment was also recorded and categorized into one of three behavioral contexts: affiliative, agonistic, or socio-sexual. Additionally, the date, time of occurrence, initiator, and receiver in each interaction along with the identification of each individual and their age and sex were recorded.

Definitions

For this study, two individuals were considered as associating if they passed within a body-length of each other at least once for every sample period. This places the individuals in a position to engage in a behavioral interaction. Behavioral interactions were adapted from Dudzinski (1996) and are defined in Appendix A. The behavioral interactions were further categorized into either an affiliative, agonistic, or socio-sexual behavioral context as presented in the background information and based on previous literature (Connor et al., 2000; Holobinko & Waring, 2010; Mann, 2006; Samuels & Gifford, 1997) (Appendix A).

Data Analysis

Interactions that included at least one individual that could not be identified, primarily because they were either too distant or only partially appeared within the video frame, were excluded from analysis. All identified dyads were analyzed using association indices to assess the number of sampling periods each dyad was observed together within an adult body-length of each other. Then, to assess what these individuals were doing when associating, the proportion of sampling periods in which individuals engaged as either affiliative, agonistic, or socio-sexual categorized behavior was calculated using only the first observed interaction per sampling period.

Association indices were calculated for each individual dyad using the half weight association coefficient (Cairns & Schwager, 1987), where X represents the number of sampling periods individuals a and b were sighted within one adult body length of each other, and N_a and N_b are the total number of times that either individual was sighted in a sampling period (either together, separately, or only one individual was observed). The half weight index (HWI) is the most commonly used index in behavioral studies (Cairns & Schwager, 1987). To test for inter-observer reliability, a second individual coded approximately 20% of the data from randomly selected video sessions. Using Pearson's Correlation Coefficient, 90% reliability was attained.

The proportion of sampling periods each dyad spent in each behavioral context was calculated by dividing the total number of sampling periods each dyad engaged in each behavioral context by the total number of sampling periods the dyad was observed together. Inter-observer reliability for the coding of interactions was also obtained using 20% of the video data and 92% reliability was achieved using Pearson's Correlation Coefficient.

The association indices and proportions of behavioral contexts individual dyads engaged in were then averaged together into different age and sex categories (Table 1).

Table 1

Dyads by Age and Sex Category

	Male	Female
Adult	6	8
Juvenile	4	2
Calf	2	2
Totals (*N* = 24)	12	12

When interactions between sex and age were assessed, the dyads were further characterized into one of 21 different possible age and sex combination categories (Table 2).

Table 2

Number of Dyads by Age-Sex Category Combined

Age-Sex Categories	Frequency
Adult Male-Adult Female	48
Adult Female-Juvenile Male	34
Adult Female-Adult Female	28
Adult Male-Juvenile Male	24
Adult Female-Juvenile Female	16
Adult Female-Calf Female	16
Adult Female-Calf Male	16

Table 2 (continued).

Age-Sex Categories	Frequency
Adult Male-Adult Male	15
Adult Male-Calf Male	12
Adult Male-Calf Female	12
Adult Male-Juvenile Female	10
Juvenile Male-Calf Male	8
Juvenile Male-Juvenile Female	8
Juvenile Male-Calf Female	8
Juvenile Male-Juvenile Male	6
Juvenile Female-Calf Female	4
Calf Male-Calf Female	4
Juvenile Female-Calf Male	4
Calf Male-Calf Male	1
Juvenile Female-Juvenile Female	1
Calf Female-Calf Female	1
Total	276

The category for sub adult-sub adult dyads was small (*N* = 3), limiting statistical analysis. Therefore, a Chi square analysis was used to determine if there were any statistical differences between age classes when using all four age classes (adults, sub-adults, juveniles, and calves) versus using three age categories (adult, juvenile, and calf). It was determined there was no statistical difference and sub adults were collapsed into the adult category. An analysis of variance (ANOVA) was preferred as it can detect differences between classes and examine the interactions between two independent variables (e.g., how sex and age together affect behavior). Additionally, mother-calf dyads were not analyzed separately due to small sample size ($N = 4$).

An ANOVA was conducted to determine if coefficients of association (COA) were affected by age and sex preferences among dyads. This was done by using the individual dyads that had been categorized into specific age and sex class categories (Table 1). Pillai's trace was used instead of Wilks' Lambda because it is more robust to unequal sample sizes (Tabachnick & Fidell, 2007).

Based on descriptive analysis, it was determined that there were four distinct categories of association for the population: low (0-.15), medium (.16-.35), medium-high (.36-.55), and high (.56-1.00) (Figure 2).

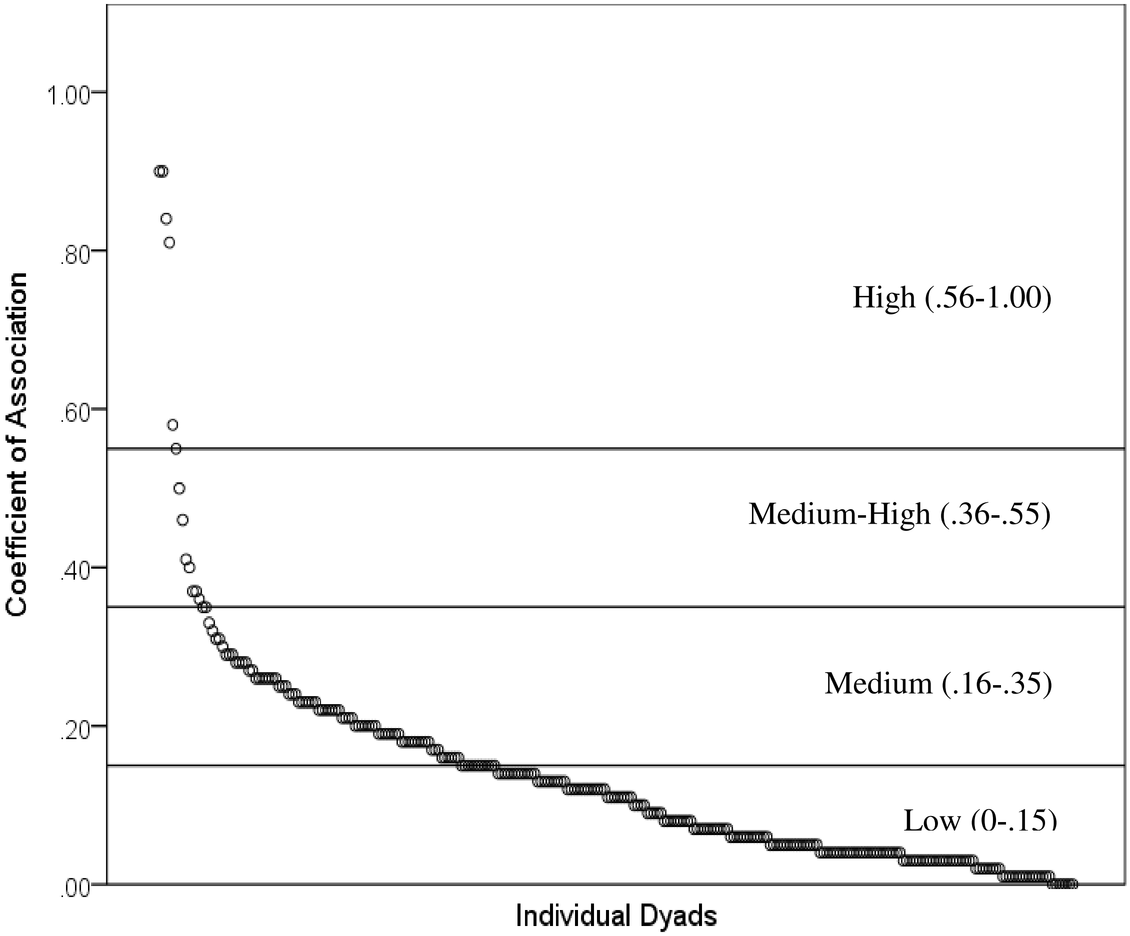

Figure 2. Mean Coefficient of Association by Individual Dyads.

A multivariate analysis of variance (MANOVA) was then performed to determine how each age, sex, and COA category of dyads spent their sampling periods in affiliative, agonistic, or socio-sexual behavior. Significant main effects were then further assessed with Tukey's HSD. To assess interaction effects, all calf-calf, juvenile female-calf female, and juvenile female-juvenile female dyads had to be removed from analysis because these categories were too small to statistically assess ($N < 5$) (Table 2). The remaining age-sex categories were assessed and all interaction effects were followed up with a simple effects test.

CHAPTER III

RESULTS

In 10.5 hours of assessed video data, there were 276 possible individual dyads and all but five of these pairs were observed, leaving 271 dyads to assess. Examination of these dyads based on sample periods yielded 890 behavioral contexts ($N = 752$, affiliative, $N = 98$, agonistic, $N = 40$, socio-sexual). The most common affiliative behavior was group swims (40%, $N = 299$), closely followed by pair swims (39%, $N = 293$). Open jaw display accounted for the majority of agonistic behaviors (67%, $N = 66$), and mounts were the predominant behavior observed (73%, $N = 29$) for socio-sexual behaviors.

The Chi square test using adult, sub-adult, juvenile, and calf as age categories was significant, X^2 (18, N =1553) = 128.41, $p < .05$. When the Chi square was reassessed collapsing the sub-adult age category into the adult category, it was also significant, X^2 (10, N =1553) = 66.85, $p < .05$. Therefore, these two categories were merged.

Associations

ANOVA and Interaction of Age and Sex

The ANOVA revealed a highly significant interaction effect of sex and age on COAs ($F_{(6,\,252)} = 7.21$, $p < .01$). This ANOVA result was followed with a simple effects analysis, which revealed that male-male dyads had significantly higher COAs on average than male-female dyads for adult-adult, adult-juvenile, and juvenile-juvenile dyads (Table 3). Female-female dyads also had statistically higher COAs on average than male-female dyads for the adult-adult, adult-juvenile, and adult-calf dyad categories

(Table 3). When it came to adult-calf dyads, however, male-male dyads had significantly lower COAs than both female-female and male-female dyads (Table 3).

Table 3

Simple Effects Test from ANOVA for the Interaction of Sex and Age on COA Values

Age Category	Sex Category	*P* Values
Adult-Adult	Male-Male vs. Female-Female	**.000**
	Male-Male vs. Male-Female	**.000**
	Female-Female vs. Male-Female	**.033**
Adult-Juvenile	Male-Male vs. Female-Female	**.047**
	Male-Male vs. Male-Female	**.000**
	Female-Female vs. Male-Female	**.038**
Adult-Calf	Male-Male vs. Female-Female	**.000**
	Male-Male vs. Male-Female	**.036**
	Female-Female vs. Male-Female	**.012**
Juvenile-Juvenile	Male-Male vs. Male-Female	**.002**
	Male-Male vs. Male-Female	.934

Note: Significant at $p < .05$. Significant values are bolded.

ANOVA and Main Effect of Sex

ANOVA revealed a highly significant main effect of sex on COAs ($F_{(2, 273)} = 17.47$, $p < .01$). Tukey's HSD revealed that male-female dyads had a significantly lower mean COA when compared to male-male (*p* = .000) and female-female (*p* = .000) dyads (Figure 3).

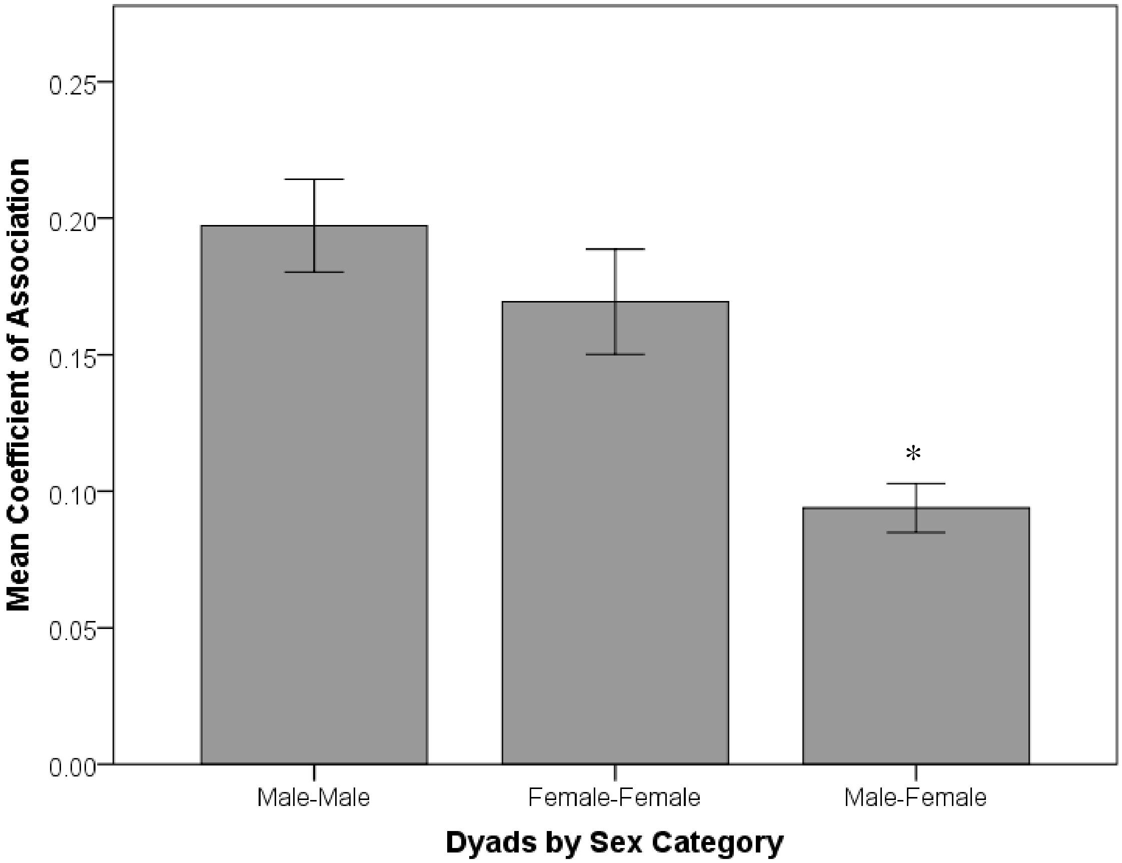

Figure 3. Mean Coefficients of Association by Sex Dyads. (* represents significant results at $p < .05$)

The overall mean association coefficient for all individuals was low ($\bar{x}_{\mathrm{HW\,I}}$= 0.13, *SD* = 0.04). Although the mother-calf dyads were not statistically analyzed, they did have the highest COAs on average ($\bar{x}_{\mathrm{HWI}}$ = 0.81, SD = 0.15) (Appendix B). Male-male dyads had the highest mean COAs when sex dyads were analyzed ($\bar{x}_{\mathrm{HWI}}$ = 0.20, *SD* = 0.14), followed by female-female dyads ($\bar{x}_{\mathrm{HWI}}$ = 0.17, *SD* = 0.16), and lastly male-female dyads ($\bar{x}_{\mathrm{HWI}}$ = .09, *SD* = 0.14). Individual dyad COAs are presented in Appendix B. Both males and females had their highest coefficient of association with a same sex individual, 67%. The highest same sex COA occurred between a male-male dyad (HWI = 0.81). The 33% that had their highest coefficient with a dolphin of the opposite sex were made up of two mother calf pairs, one mother and her juvenile son, and one adult-adult male-female pair.

ANOVA and Main Effect of Age

The main effect of age on COAs was non-significant ($F_{(5, 270)} = 1.69$, $p > .05$) (Figure 4).

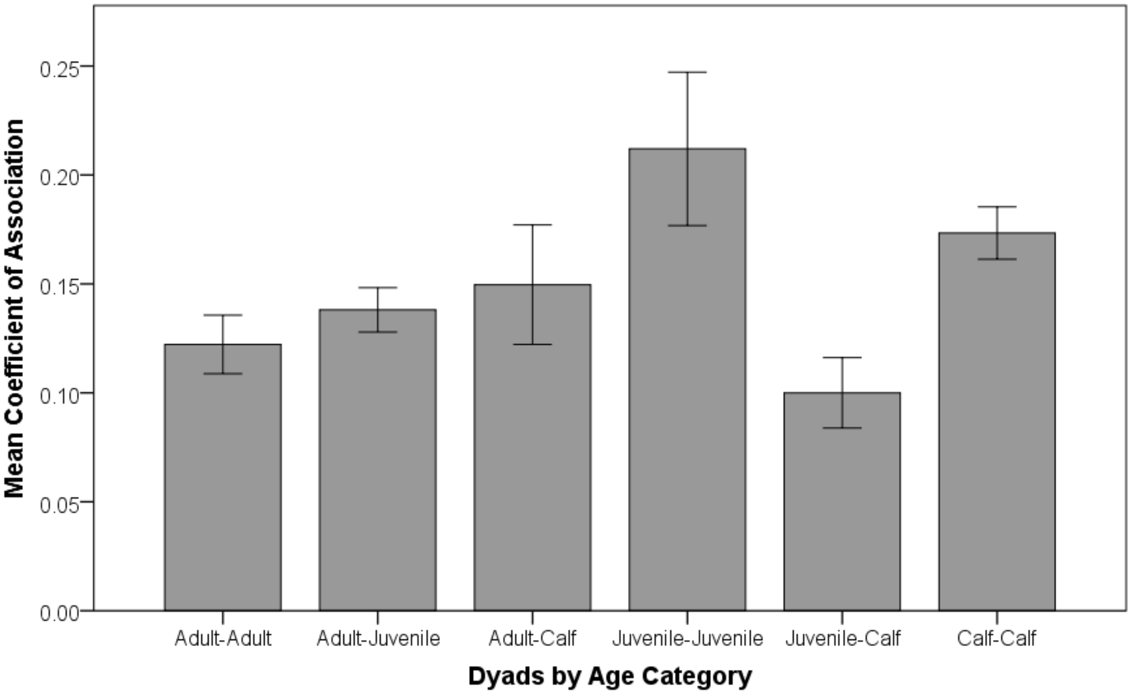

Figure 4. Mean Coefficients of Association by Age Dyad.

Individual dyads were grouped into the low, medium, medium-high or high COA categories (Figure 2). Male-female dyads were mostly in the low COA category (81%, $N = 116$). Female-female dyads were mostly in the low COA category ($N = 41$, 62%), and male-male dyads showed mostly medium COA category values (50%, $N = 33$).

Behavioral Contexts Overall

A MANOVA was run to determine the effects of these four COA categories, as well as how sex and age affected the sampling periods spent in either the affiliative, agonistic, or socio-sexual contexts. The overall MANOVA revealed a highly significant interaction of sex and age ($V = 0.27$, $F_{(18,756)} = 4.10$, $p < .01$) on behavioral contexts. A non-significant interaction of COA categories and sex ($V = 0.90$, $F_{(18,792)} = 1.37$, $p > .05$) and of COA categories and age on behavioral contexts was found ($V = 073$, $F_{(24, 777)} = 0.80$, $p > .05$). When it came to main effects, a highly significant effect of COA categories ($V = 0.22$, $F_{(9,816)} = 7.07$, $p < .01$), sex ($V = 0.32$, $F_{(6,544)} = 17.39$, $p < .01$) and age on the behavioral contexts were also found ($V = 0.15$, $F_{(15,810)} = 2.75$, $p < .01$). All significant interactions were followed with ANOVAs for each behavioral context and post hoc tests in the sections below.

Affiliative Behavior

ANOVA and Interaction of Sex and Age

The interaction of sex and age on behavior was highly significant for proportion of time spent in affiliative behavior ($F_{(6, 252)} = 3.75$ $p < .01$). The simple effects test revealed that male-male dyads had significantly higher mean proportions of sampling periods spent in the affiliative context than male-female dyads for adult-adult, adult-calf, and juvenile-juvenile dyads (Table 4). Female-female dyads had significantly higher proportions of sampling periods spent in the affiliative context than did male-female dyads for adult-adult, adult-juvenile, and adult-calf dyads (Table 4). Finally, for the adult-calf dyad category, female-female dyads spent a significantly greater proportion of sampling periods in affiliative context than male-male dyads.

Table 4

Simple Effects Test from ANOVA for the Interaction of Sex and Age on Behavioral Contexts

Behavioral Context	Age Category	Sex Category	*P* Values
Affiliative	Adult-Adult	Male-Male vs. Female-Female	.234
		Male-Male vs. Male-Female	**.005**
		Female-Female vs. Male-Female	**.000**
	Adult-Juvenile	Male-Male vs. Female-Female	.386
		Male-Male vs. Male-Female	.205
		Female-Female vs. Male-Female	**.040**
	Adult-Calf	Male-Male vs. Female-Female	**.000**
		Male-Male vs. Male-Female	**.031**
		Female-Female vs. Male-Female	**.002**
	Juvenile-Juvenile	Male-Male vs. Male-Female	**.037**
	Juvenile-Calf	Male-Male vs. Male-Female	.136
Agonistic	Adult-Adult	Male-Male vs. Female-Female	.459
		Male-Male vs. Male-Female	.618
		Female-Female vs. Male-Female	.107
	Adult-Juvenile	Male-Male vs. Female-Female	**.042**
		Male-Male vs. Male-Female	**.017**
		Female-Female vs. Male-Female	.861

Table 4 (continued).

Behavioral Context	Age Category	Sex Category	*P* Values
	Adult-Calf	Male-Male vs. Female-Female	**.000**
		Male-Male vs. Male-Female	**.000**
Agonistic	Adult-Calf	Female-Female vs. Male-Female	.793
	Juvenile-Juvenile	Male-Male vs. Male-Female	.119
	Juvenile-Calf	Male-Male vs. Male-Female	.220
Socio-sexual	Adult-Adult	Male-Male vs. Female-Female	**.000**
		Male-Male vs. Male-Female	**.000**
		Female-Female vs. Male-Female	.448
	Adult-Juvenile	Male-Male vs. Female-Female	**.000**
		Male-Male vs. Male-Female	**.000**
		Female-Female vs. Male-Female	.724
	Adult-Calf	Male-Male vs. Female-Female	.843
		Male-Male vs. Male-Female	.884
		Female-Female vs. Male-Female	.935
	Juvenile-Juvenile	Male-Male vs. Male-Female	**.017**
	Juvenile-Calf	Male-Male vs. Male-Female	.999

Note. Significant at $p < .05$. Significant values are bolded.

ANOVA and Interaction of COA category and Sex

The interaction of COA category and sex was non-significant ($F_{(6, 264)} = 1.43$ $p > .05$) for affiliative contexts.

ANOVA and Interaction of COA category and Age

The interaction of COA category and age on affiliative behavior was non-significant ($F_{(8, 259)} = 0.81$ $p > .05$).

ANOVA and Main Effect of COA

The follow up ANOVA revealed a significant effect of COA on affiliative behavior ($F_{(3,272)} = 13.78$, $p < .01$). Post-hoc analysis showed that dyads that exhibited a low COA value spent a significantly lower proportion of their time engaged in affiliative behavior than medium ($p = .000$), medium-high ($p = .002$), and high ($p = .000$) COA category dyads (Figure 5).

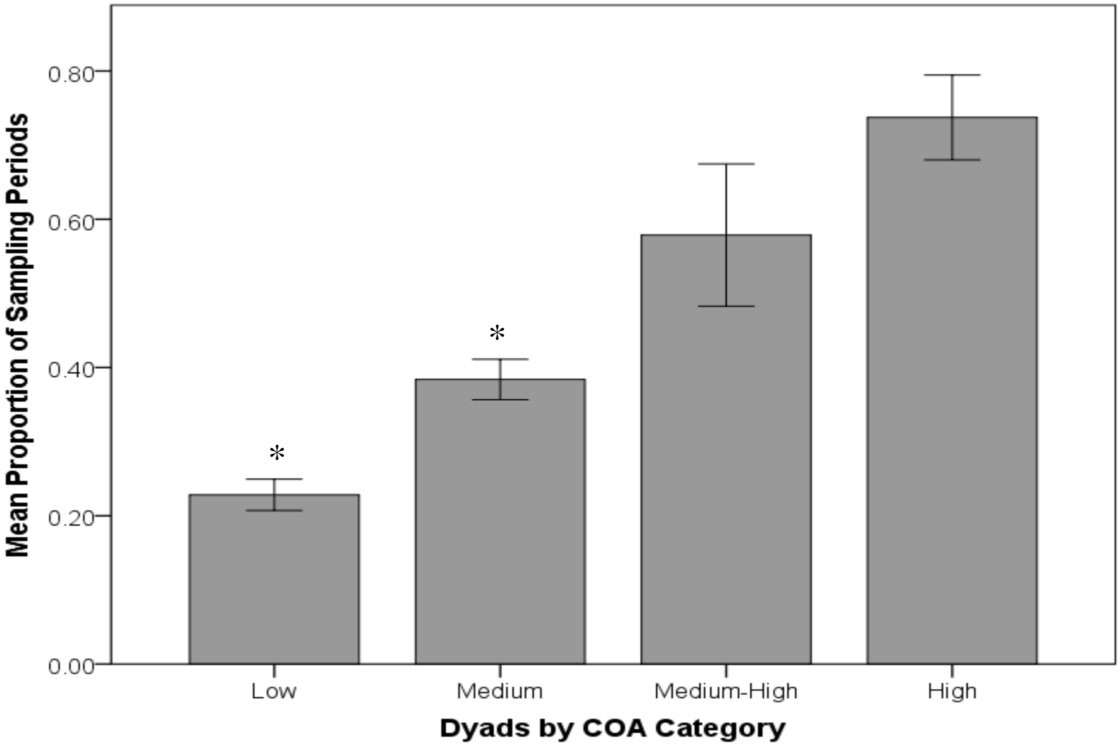

Figure 5. The Proportion of Sampling Periods Spent in Affiliative Behavior by COA Dyad Category. (* represents significant results at $p < .05$)

Additionally, the medium COA category was significantly lower than the high COA category ($p = .027$) (Figure 5). Although group swims accounted for the majority of behaviors observed for all four COA categories, the highest percentage of this behavior occurred for dyads that had medium (49%, *N* = 475), and low COA values (26%, *N* = 249). Dyads with a high (30%, *N* = 87) and medium-high (21%, *N* = 61) COA spent a greater percentage of their affiliative behaviors engaging in pair swims than group swims.

ANOVA and Main Effect of Sex

The follow up ANOVA revealed a significant effect of sex on affiliative behavior ($F_{(2,273)}$ =18.38, $p < .05$). Post-hoc analysis revealed that female-female dyads spent a significantly greater proportion of sampling periods in the affiliative context than did male-male ($p = .000$) or male-female dyads ($p = .000$) (Figure 6).

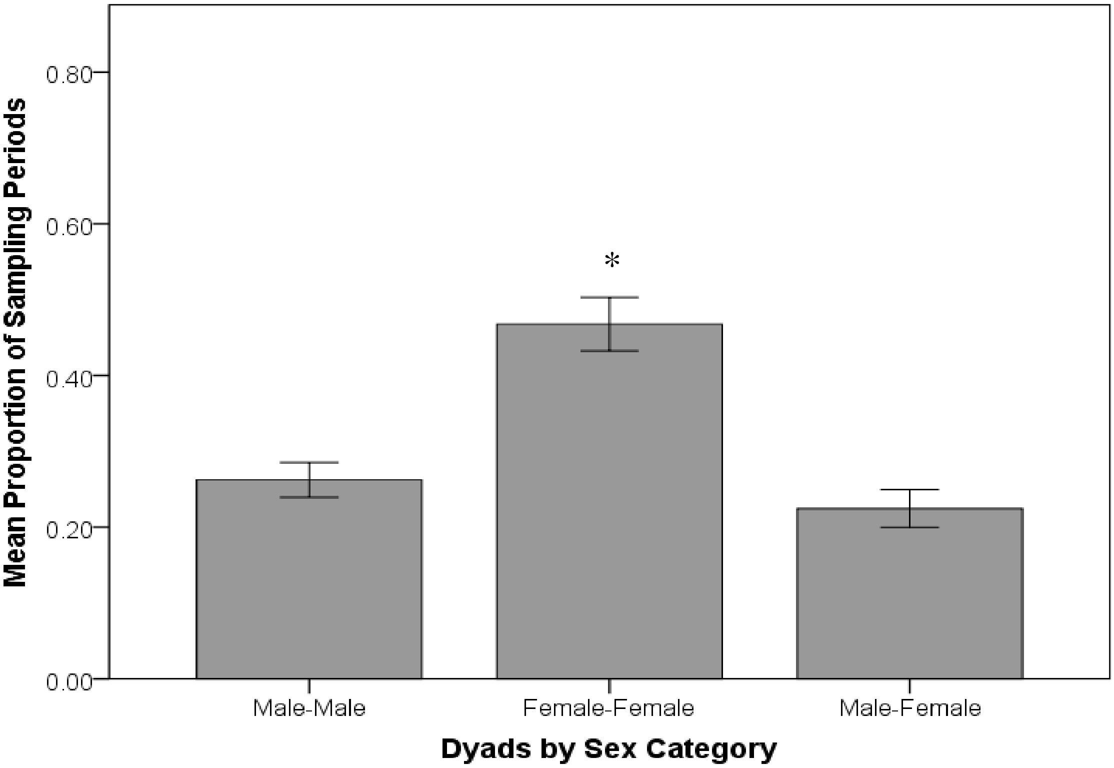

Figure 6. The Proportion of Sampling Periods Spent in Affiliative Behavior by Sex Dyad Category. (* represents significant results at $p < .05$)

Female-female dyads (78%, $N = 408$) had a higher percentage of group swims than male-male (64%, $N = 262$) and male-female dyads (63%, $N = 301$). Male-male (23%, $N = 94$) and male-female dyads (25%, $N = 119$) had a higher percentage of pair swim events than did female-female dyads (14%, $N = 94$). Other affiliative behaviors were not recorded often, however, of those that were males were more likely to initiate the behavior approach to both males (36%, $N = 31$) and females (29%, $N = 25$). Males followed other males (25%, $N = 10$) more often the females followed males (15%, $N = 6$). However, both sexes were observed engaging in follow behavior of females equally (30%, $N = 12$). Females but not males were the receivers of rubs from both males (50%, $N = 2$) and other females (50%, $N = 2$) in all four events. Pectoral fin rubs were initiated by females more often to both males (15%, $N = 3$) and females (55%, $N = 11$). While males only initiated pectoral fin rubs to males (25%, $N = 5$) and females (5%, $N = 1$) in six recorded events.

ANOVA and Main Effect of Age

Dyad ages were found to have a significant effect on affiliative interactions ($F_{(5,270)} = 5.16$, $p < .05$). Post-hoc analysis revealed that calf-calf dyads spent a significantly greater amount of their time engaged in affiliative behavior than did adult-juvenile ($p = .005$) and juvenile-juvenile dyads ($p = .022$) (Figure 7). Additionally, adult-calf dyads spent significantly more sampling periods in affiliative behavior when compared to adult-juvenile dyads ($p = .002$) (Figure 7).

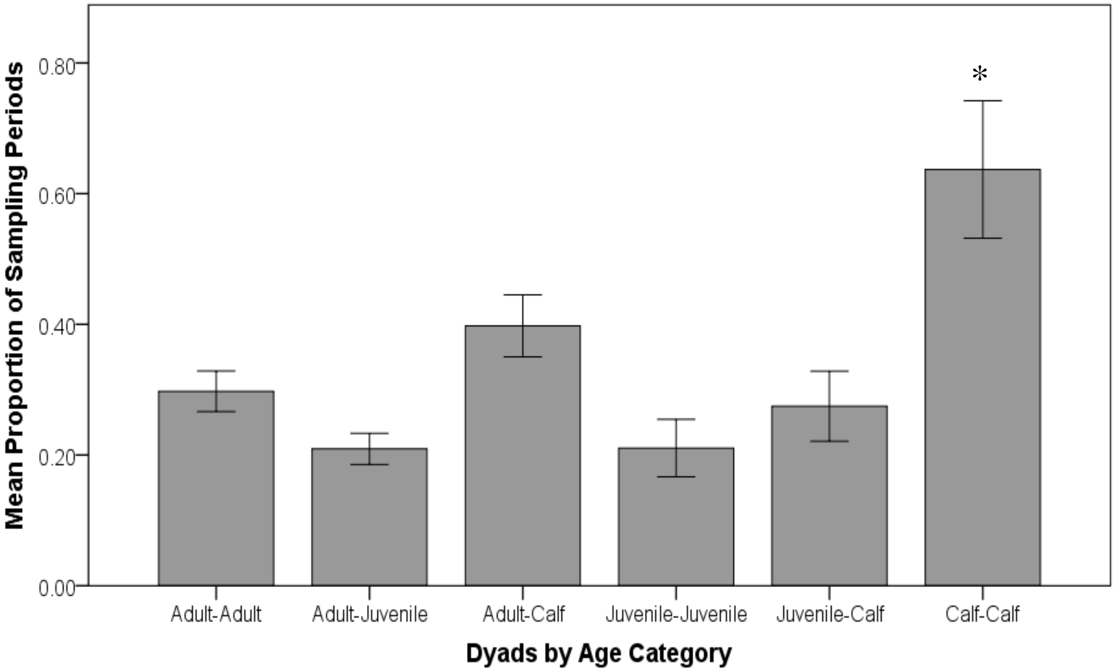

Figure 7. The Proportion of Sampling Periods Spent in Affiliative Behavior by Age Dyad Category. (* represents significant results at $p < .05$)

Calf-calf dyads spent 90% of their affiliative behavior on group swims with their mothers and mostly other females. Juvenile-juvenile (31%, $N = 45$) and adult-calf (24%, $N = 103$) dyads had the highest percentage of pair swims out of all possible dyads. Adults were most likely to approach other adults (28%, $N = 24$), while juveniles approached adults (20%, $N = 17$) almost as often as they approached other juveniles (16%, $N = 14$). Calves approached mostly adults (13%, $N = 11$). For follow behavior, adults followed other adults (35%, $N = 14$) most often and then calves (20%, $N = 8$). Juveniles also followed other adults (20%, $N = 8$) most often and then calves (13%, $N = 5$). Calves did not initiate the behavior follow. Pectoral fin rubs occurred most often between adult-adult dyads (30%, $N = 6$), followed by juvenile-juvenile dyads (25%, $N = 5$). Calves initiated pectoral fin rubs only once to an adult (5%, $N = 1$) and once to a juvenile (5%, $N = 1$) and were the receivers of pectoral fin rubs in two events that were initiated by adults (10%, $N = 2$).

Agonistic Behavior

ANOVA and Interaction of Age and Sex

The interaction between age and sex was highly significant for agonistic behavior ($F_{(6,252)} = 4.25$, $p < .01$). The simple effects revealed that male-male dyads had significantly greater mean proportions of sampling periods spent in the agonistic context than did female-female and male-female dyads for the adult-juvenile and adult-calf categories (Table 4). However, no agonistic contexts were recorded for female-female dyads in the adult-adult dyad category or for male-female dyads in the juvenile-juvenile age dyad category.

ANOVA and Interaction of COA category and Sex

The interaction between COA categories and sex dyads was non-significant for agonistic behavior ($F_{(6,264)} = 1.21$, $p > .05$).

ANOVA and Interaction of COA category and Age

The interaction between COA categories and age was also non-significant for agonistic behavior ($F_{(8,259)} = 0.65$, $p > .05$).

ANOVA and Main Effect of COA

MANOVA revealed a non-significant main effect of COA category (low, medium, medium-high or high) on agonistic behavior ($F_{(3,272)} = 2.03$, $p > .05$) (Figure 8).

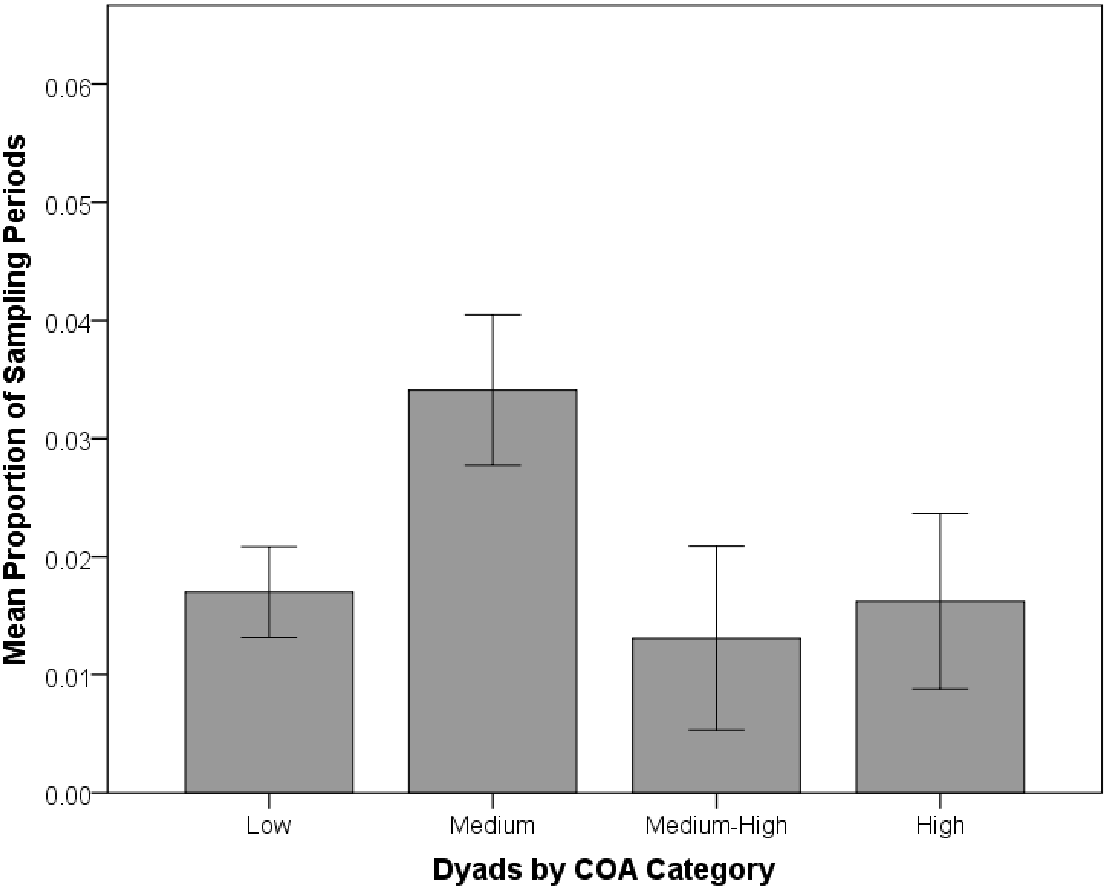

Figure 8. The Proportion of Sampling Periods Spent in Agonistic Behavior by COA Dyad Category.

ANOVA and Main Effect of Sex

With respect to agonistic behavior, MANOVA revealed a significant effect of sex on agonistic behavior ($F_{(2,273)} = 9.04$, $p < .05$). Post-hoc analysis revealed that male-male dyads spent a significantly greater proportion of sampling periods in the agonistic context than did both female-female ($p = .000$) and male-female dyads ($p = .002$) (Figure 9).

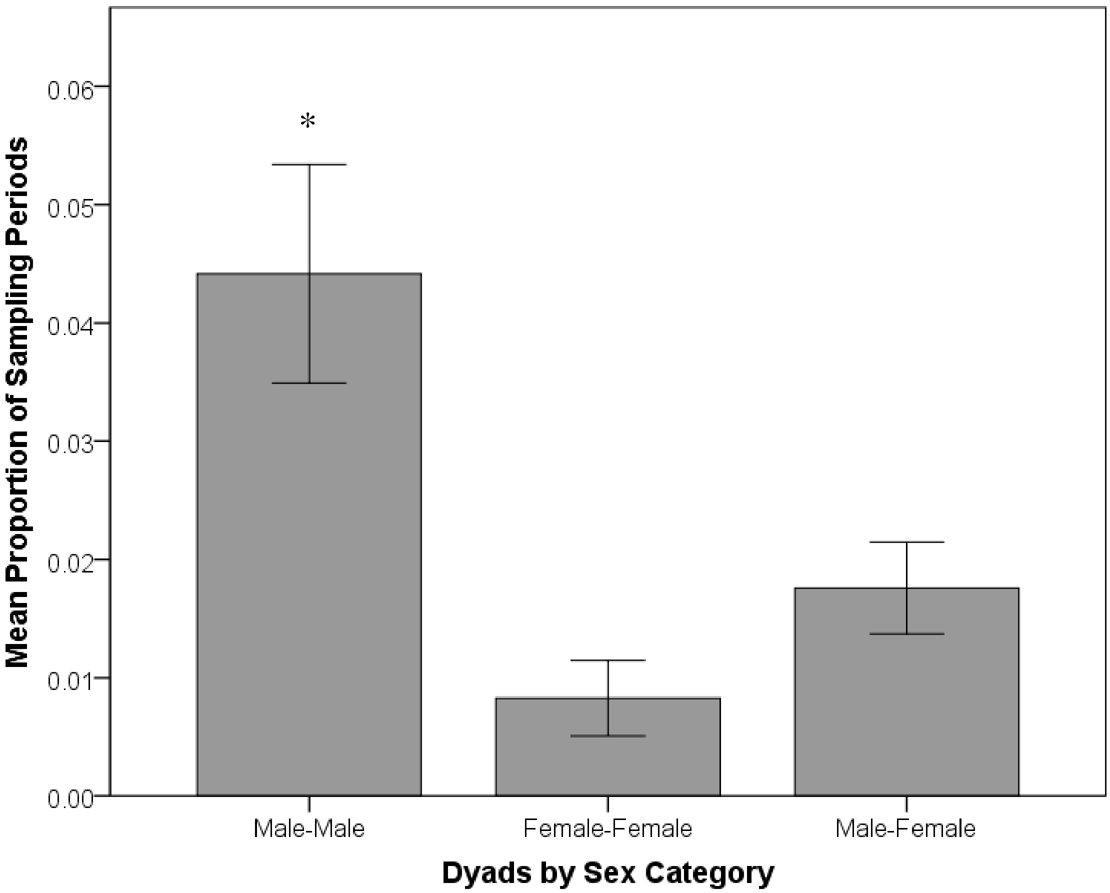

Figure 9. The Proportion of Sampling Periods Spent in Agonistic Behavior by Sex Dyad Category. (* represents significant results at $p < .05$)

Male-male dyads accounted for 47% ($N = 46$) of all agonistic behaviors observed while male-female dyads accounted for 42% ($N = 41$). Agonistic events occurring in female-female dyads were rarely observed (11%, $N = 11$). The events that were observed in female-female dyads were almost exclusively open jaw threats (90%, $N = 9$), with one bite occurring between a mother and her female calf (10%, $N = 1$). Male-male dyads engaged in a variety of agonistic behaviors but the most common included open jaw threat (61%, $N = 28$), interrupt (20%, $N = 9$), and chase (11%, $N = 5$) behaviors. Between male-female dyads, the behavior open jaw threat was initiated similarly to the opposite sex by both males (23%, $N = 15$) and females (21%, $N = 14$). Females did not initiate chase behavior to males, but males chased females in 4 observed events (44%, $N = 4$).

Females also did not initiate any bite behaviors to males, but males initiated bites to females (60%, $N = 3$).

ANOVA and Main Effect of Age

A non-significant effect of age was found for agonistic behavior ($F_{(5,270)} = 1.57$, $p > .05$). No agonistic events were observed in calf-calf dyads (Figure 10).

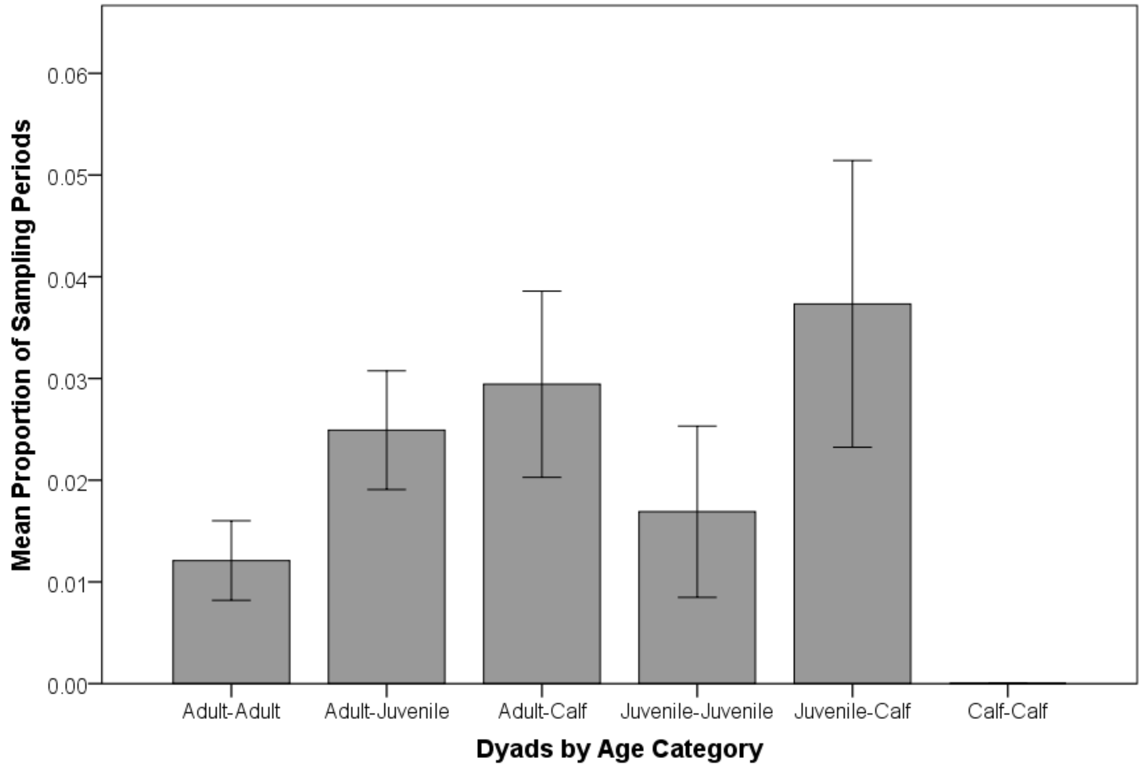

Figure 10. The Proportion of Sampling Periods Spent in Agonistic Behavior by Age Dyad Category.

Socio-sexual Behavior

ANOVA and Interaction of Age and Sex

The interaction between age and sex dyads was highly significant for socio-sexual behavior ($F_{(6,252)} = 5.26$, $p < .01$). Simple effect analysis revealed that male-male dyads spent a significantly greater proportion of sampling periods in the socio-sexual context than both female-female and male-female dyads for adult-adult, adult-juvenile, and juvenile-juvenile dyads (Table 4). The only age category that socio-sexual contexts were recorded and analyzed for calves was the adult-calf category. Additionally, none were recorded or analyzed for male-male dyads in the juvenile-juvenile age category.

ANOVA and Interaction of COA category and Sex

The interaction between COA categories and sex was non-significant for socio-sexual behavior ($F_{(6,264)} = 1.21$, $p > .05$).

ANOVA and Interaction of COA category and Age

The interaction of COA categories and age was also non-significant for socio-sexual behavior ($F_{(8,259)} = 1.13$, $p > .05$)

ANOVA and Main Effect of COA

A significant main effect of COA on socio-sexual behavior was found ($F_{(3,272)} = 5.38$, $p < .01$). Post-hoc analysis revealed that dyads with a medium-high COA spent more sampling periods in socio-sexual interactions than did dyads with both a low COA ($p = .002$) and medium COA ($p = .029$) (Figure 11).

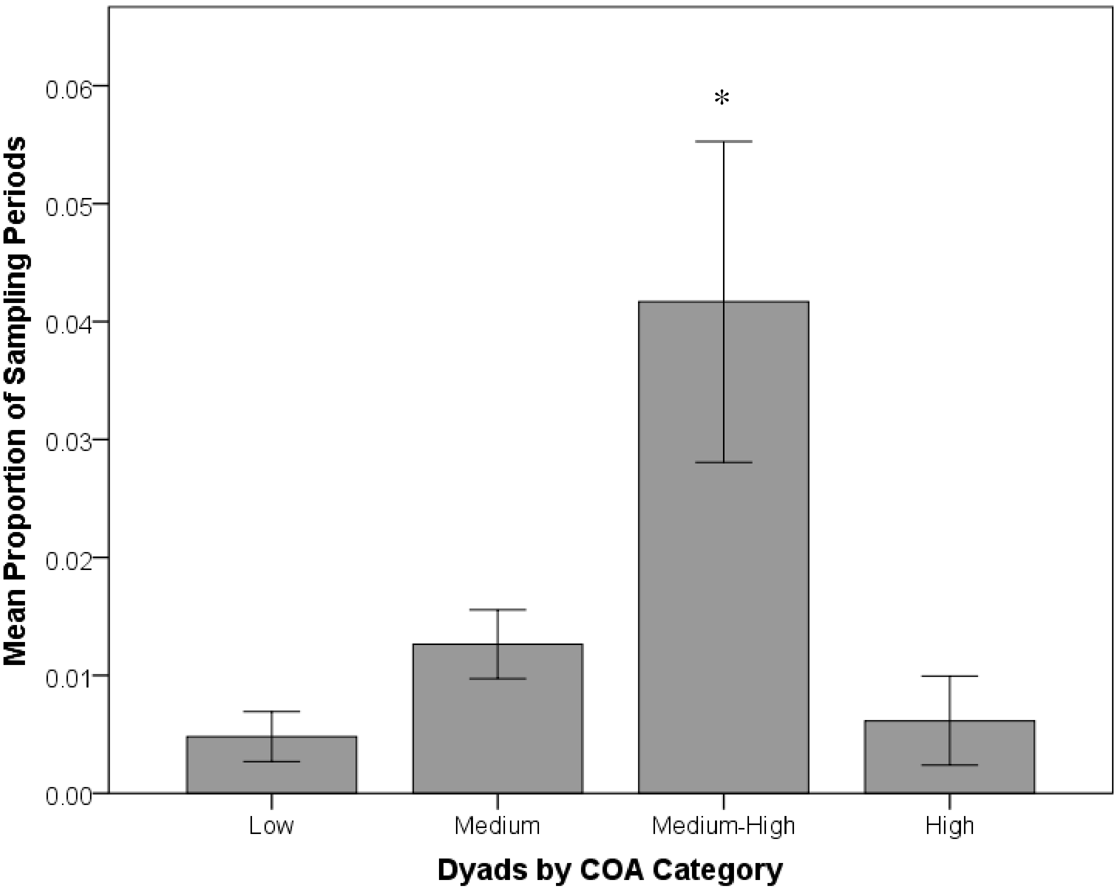

Figure 11. The Proportion of Sampling Periods Spent in Socio-sexual Behavior by COA Dyad Category. (* represents significant results at $p < .05$)

Goose behavior was observed in some dyads falling into all four COA categories. Mount behavior was observed to occur between some dyads in low, medium, and medium-high COA categories but not in the high COA category.

ANOVA and Main Effect of Sex

A dolphin's sex had a significant effect on socio-sexual interactions ($F_{(2,273)} = 24.07$, $p < .05$). Male-male dyads spent significantly more sampling periods engaged in socio-sexual behavior than did female-female dyads ($p = .000$) or male-female dyads ($p = .000$) (Figure 12).

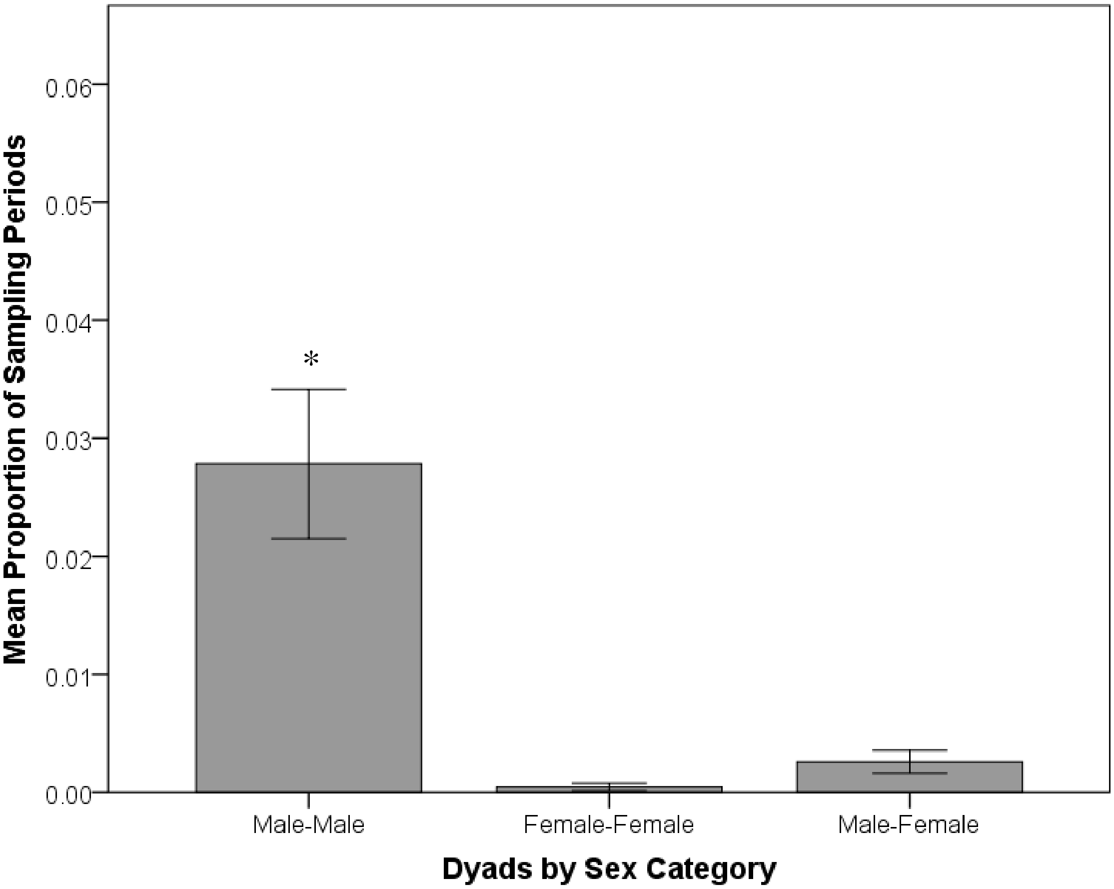

Figure 12. The Proportion of Sampling Periods Spent in Socio-sexual Behavior by Sex Dyad Category. (* represents significant results at $p < .05$)

Female-female dyads only engaged in goose behavior and these two events occurred in mother-calf pairs (22%, $N = 2$). The only male-female socio-sexual behavior to occur was mounts (3%, $N = 2$). Male-male dyads engaged in mostly mount behavior (81%, $N = 29$), with some goose behaviors (19%, $N = 7$) observed.

ANOVA and Main Effect of Age

A non-significant effect of age was found for socio-sexual behavior ($F_{(5,270)} = 1.68$, $p > .05$) (Figure 13).

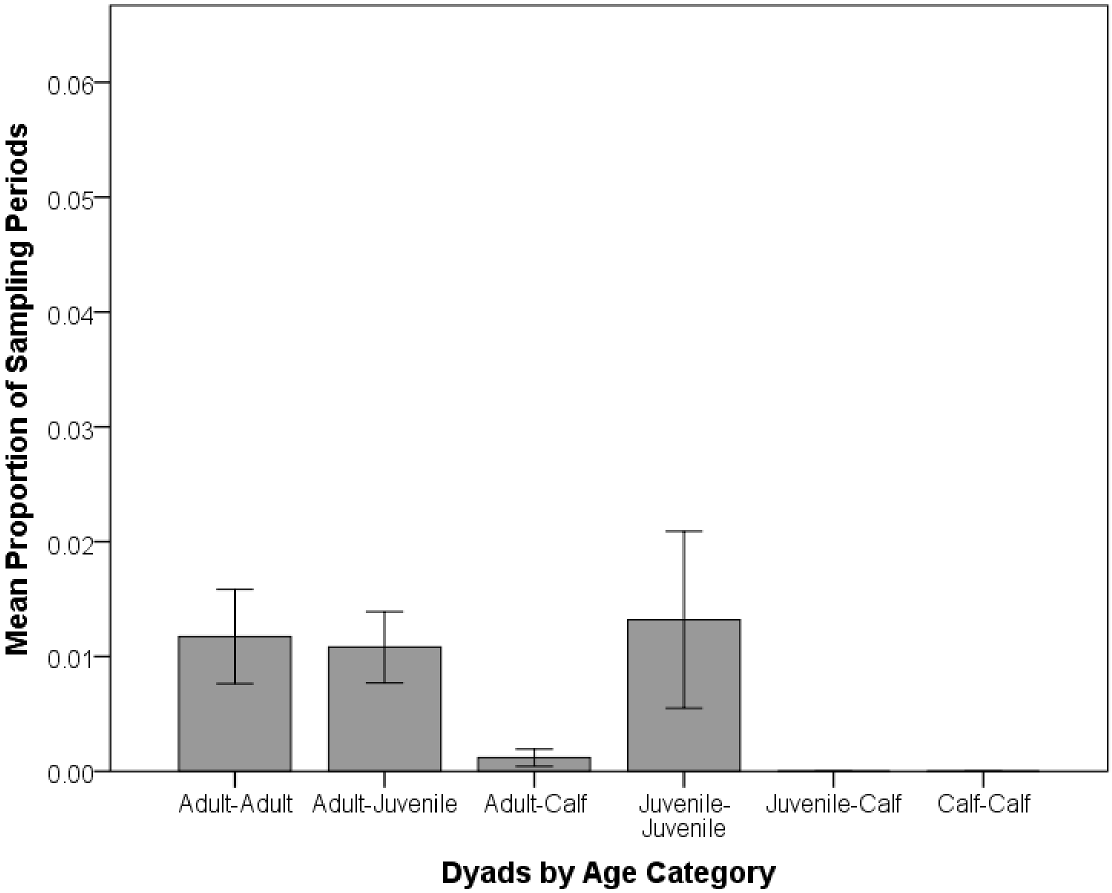

Figure 13. The Proportion of Sampling Periods Spent in Socio-sexual Behavior by Age Dyad Category.

CHAPTER IV

DISCUSSION

The results of this study suggest that aside from the mother-calf bond, individuals mainly associate with others of the same sex and age class. Association coefficients in the current study were found to be highest on average in mother-calf dyads, followed by male-male, female-female, and lastly male-female dyads. When individuals were spending time together, the context was most often categorized as affiliative followed by agonistic and then socio-sexual regardless of the age, sex, or COA category of the dyad. This suggests that sex and age specific life history strategies may be important factors when choosing with whom to associate for this population of bottlenose dolphins. Additionally, it appears that affiliative behavior is an important component of maintaining these associations for these dyads.

Associations

Similar to previous studies, the majority of dyads shared low coefficients of association (Quintana-Rizzo & Wells, 2001; Smolker et al., 1992; Wells et al., 1987). These COAs were highest on average between mother-calf dyads, followed by male-male, female-female, and then male-female dyads. These results are consistent with the general pattern reported by Pearson (2011), based on findings at Shark Bay, Sarasota, and Doubtful Sound (Lusseau et al., 2003; Smolker et al., 1992; Wells, 2003; Wells et al., 1987). Generally, associations are influenced by the differing reproductive strategies of the sexes (Connor et al., 2000; Smolker et al., 1992; Wells et al., 1987). Male reproductive strategies appear to be centered on gaining and maintaining access to cycling females, while female reproductive strategies tend to focus on calf protection from predators/conspecifics and access to food (Mann, Connor, Barre, & Heithaus, 2000).

Same sex dyads had significantly higher COAs as compared to male-female dyads; however, for this study, COAs were significantly influenced by the interaction between sex and age. This general pattern of COAs to be highest among male-male, female-female, and then male-female dyads only held true for adult-adult, adult-juvenile, and juvenile-juvenile dyads. Not surprisingly, dyads containing calves did not fit this pattern. Dyads involving calves had statistically lower COAs for male-male dyads compared to female-female and male-female dyads. This pattern reflects the low associations seen between adult and juvenile males with calves. The male-female dyads that did share the highest COAs were those involving either of the two male calves with their mothers or other females. Gibson and Mann (2008b) reported that mothers and calves appeared to avoid juvenile and adult males in Shark Bay, and suggested mothers did so to avoid aggression from males. The authors also suggested that males might find mother-calf groups less attractive unless a female is cycling. In this study, adult and juvenile males did in fact direct open jaw threats and engage in chases of calves in 12 events. Therefore, it is likely that females in this study might have engaged in avoidance behavior of males when escorting calves.

Interestingly, an adult male and adult female both had their highest level of association with each other. The female, Maury, also had higher association coefficients with all males in the population compared to those with females. Although a male sharing his highest coefficient of association with a female was reported once in the literature, excluding mother-offspring pairs, no information about relatedness or other suggestions as to the function of this association was provided (Quintana-Rizzo & Wells, 2001). However, in both Sarasota and Shark Bay, adult males have been reported to have higher levels of association with cycling females (Connor, Smolker, & Richards, 1992b; Moors, 1997; Owen et al, 2002; Smolker et al., 1992; Wells et al., 1987). Maury was in fact a nulliparous adult female who gave birth to her first calf later in the same year (K. Dudzinski, personal communication, January, 2015).

Behavioral Contexts

Affiliative Behavior

Affiliative behavior was the most commonly recorded behavioral context regardless of the COA category, sex, or age combination of the dyads. The development and maintenance of bonds is important to survival for a social species that may need to cooperate to obtain resources or defend against predators. Associating with others provides a benefit through mutual detection of predators and prey (Norris & Dohl, 1980; Würsig & Pearson, 2014). Dolphins often cooperate when searching for and capturing prey (Gazda, Connor, Edgar, & Cox, 2005; Leatherwood, 1975; Norris & Dohl, 1980; Rossbach, 1999; Vaughn, Würsig, & Packard, 2010), and it has been suggested that large group size reduces predation by sharks (Heithaus, 2001; Norris & Dohl, 1980; Wells et al., 1987). Sussman, Garber, and Cheverud (2005) suggested that in chimpanzees, cooperative interactions might serve a role in alliance formation, social relationships, social cohesion, and resource acquisition. Furthermore, chimpanzees and bonobos (*Pan Paniscus*) display a high level of cooperation and affiliation within their fission-fusion societies (Aureli et al., 2008; Sussman et al., 2005). In a recent study on female bonobos, Archie, Tung, Clark, Altmann, and Alberts (2014) found that as affiliative behavior with both sexes increased, so did the female's lifespan. Similarly, a recent study on survival of bottlenose dolphin male calves found that their infancy networks were predictive of their survival during the juvenile stage (Stanton & Mann, 2012). Furthermore, the number of associates was not a predicting factor, leading the authors to suggest that the quality of the social bonds between associates is more important in predicting survival than the number of associates (Stanton & Mann, 2012). These studies suggest that not only may affiliative behavior be important for maintaining and establishing bonds, but that these bonds may have important survival consequences for mammals as well.

When it came to sex dyads, female-female dyads spent a significantly higher proportion of sampling periods in the affiliative context than both male-male and male-female dyads. However, the interaction of sex and age showed that female-female dyads only had significantly higher proportions in the affiliative context for adult-juvenile and adult-adult dyads compared to male-female dyads and in the adult-calf category for both male-male and male-female dyads. Females spent the majority of their time in the affiliative context swimming in groups with other females (both adult and juvenile) and calves. Often these groups contained dyads with different COA categories. The occurrence of mixed COA category dyads seen in these female groups likely reflects the shared need for vigilance and protection from predators and male conspecifics (Möller & Harcourt, 2008). A recent study in Shark Bay, Australia, suggested that females with male calves need protection from juvenile males. Stanton and Mann (2012) found that male calves that died post weaning had stronger associations with juvenile males than those male calves that survived. They suggest that juvenile males directly harass male calves and in turn this stress decreases the calf's fitness (Stanton & Mann, 2012).

Therefore, it is likely that mothers with calves (especially male calves) may benefit from increasing their female associates and spending more time in larger groups for protection. Other studies have reported that females with young calves are found associating with larger groups of other females, often ones that also have young calves (Mann et al., 2000; Wells, 1991). An alternative explanation for female groups containing mixed COA category dyads is that other adult and juvenile females who normally do not associate with a particular mother, may be attracted to her calf. Studies have reported that it is common for juvenile females to show interest in calves (Gibson & Mann, 2008a; Mann & Smuts, 1998; Tavolga & Esspaian, 1957), and that adult females might even adopt lone calves (Howells et al., 2009; Simard & Gowans, 2004). The learning-to-parent hypothesis suggests that females gain parenting experience by associating with calves, which leads to increased survival of their own offspring in the future (Stanton, Gibson, & Mann, 2011).

Agonistic Behavior

Rates of agonistic behavior have been reported to be generally low among dolphins (Samuels & Gifford, 1997; Scott et al., 2005; Weaver, 2003). The current study also found that the proportion of time spent in agonistic behavior was low. When sex was assessed alone, male-male dyads spent significantly more sampling periods in the agonistic context than female-female and male-female dyads. Other studies also support these results; for example, Scott et al. (2005) found that males were largely responsible for rake marks assessed on both sexes, and Samuels and Gifford (1997) found that males were involved in the highest rates of agonism. Scott et al. (2005) suggested that higher rates of aggressive behavior are seen between male-male dyads due to competitive bouts and frequent sexual practice, both strategies used by males to obtain access to females. Females in the current study did receive higher rates of agonistic behavior from males, rather than the converse. Scott et al. (2005) also reported that females received more rake marks from males when they were cycling, suggesting that sexual coercion might be used as a mating strategy. This might be a plausible explanation in the current study, as the majority of agonistic interactions directed at females were to the two nulliparous sub-adult females (Fiona and Maury who were analyzed as adults) who were possibly receptive during this time (K. Dudzinski, personal communication, January 2015). It is also possible that agonism may increase between male-female dyads when the current calves are all weaned and the adult females are receptive.

Although, the interaction of age and sex showed this was only the case for adult-juvenile and adult-calf dyads, juvenile-juvenile male dyads had a similar mean proportion of sampling periods spent in agonistic behavior as the adult-juvenile male dyads. It is likely that we would have found the same pattern for this age class if a larger sample of juvenile females were available to assess. It is also possible that some of the observed agonistic behavior was play as previously discussed. Future studies should try to distinguish between the contexts of agonistic behavior.

Socio-sexual Behavior

Dyads with a medium-high COA spent significantly more time in the socio-sexual context than those with low and medium COAs. The dyads that engaged in socio-sexual behavior in the medium-high COA category were all male-male dyads. This pattern is similar to other studies that have found same-sex socio-sexual interactions to be prevalent in male-male dyads (Mann, 2006; McBride, 1940; McBride & Hebb, 1948; Östman, 1991; Tavolga & Essapian, 1957). The interaction of age and sex revealed that this was only true for adult-adult, adult-juvenile, and juvenile-juvenile dyads.

Several hypotheses have been proposed for why same sex socio-sexual interactions occur. Östman (1991) hypothesized that socio-sexual behavior was a function of dominance based on his observations of two captive males. He found that whichever dolphin initiated more aggression during a time period was also responsible for either all or most of the mountings. Although dominance was not assessed in the current study, within adult-adult dyad socio-sexual interactions the same three males were always the receivers. The majority of socio-sexual behaviors between adult dyads were initiated by one of the two males that shared a high association (HWI = 0.81). This COA suggests they share a bond similar to the males described in Shark Bay, Australia (Connor, Smolker, & Richards, 1992a). Together, these two males initiated socio-sexual behaviors with other adult males with whom they shared lower COAs. In a study looking at same-sex socio-sexual interactions in calves, Mann (2006) found that certain male calves were mounted more than others. Furthermore, these male calves were often chased by other males and often rolled belly up or displayed slap behaviors in an attempt to avoid mounts from these other males. Although she suggested that early dominance relationships might be a factor, she stated that more research was needed (Mann, 2006). The dominance hypothesis has generally not received much support for same-sex socio-sexual behavior.

A more common hypothesis for why same-sex socio-sexual interactions might occur is that these interactions function to establish and strengthen bonds between male-male dyads (Bailey & Zuk, 2009; Mann, 2006). Juvenile males in Shark Bay often switch roles when engaging in herding behavior and socio-sexual bouts, lending support to the hypothesis that these behaviors help mediate the development of bonds in male-male dyads (Furuichi, Connor, & Hashimoto, 2014). Similarly, in this study, juveniles most frequently engaged in these behaviors with other juveniles and the roles of the initiator and receivers were often switched between juvenile-juvenile dyads but not for adult-adult dyads. For juveniles, it seems that socio-sexual behavior may function to mediate the development of male-male bonds, as suggested by Mann (2006).

A third hypothesis suggests the function may be related to practice for future mating opportunities with females. Mann (2006) observed that several males were typically involved in socio-sexual interactions. She suggested this pattern reflected the consortships described in Shark Bay (Connor et al., 1992a), and therefore that socio-sexual behavior might also function as practice for future sexual encounters. The same pattern was observed in this study, with males in triads commonly involved in socio-sexual bouts. For example, Hector and Han acted together and took turns mounting and goosing other adult and juvenile males. Furthermore, these two males were never observed engaging in socio-sexual behavior with each other. This could suggest these two males were practicing as a team for future mating opportunities. In primates, social learning has been suggested to play a key role in sexual behavior (Furuichi et al., 2014). According to Furuichi et al. (2014), primates raised in isolation have had difficulties successfully breeding or performing copulatory behaviors, supporting the idea that practice is key for sexual reproduction.

Socio-sexual behavior in calves was rare and only recorded in four instances. All four instances occurred in adult-calf dyads. Both the female calves were goosed by their mothers, which were the only two female-female socio-sexual events recorded. The other two events involved one male calf (Mickey) that attempted to mount both nulliparous adult females. Although Mann (2006) reported high rates of socio-sexual behavior in calves, she considered calves to be 6 years of age and under. In this study, all calves were only 6 months of age. It is likely that the socio-sexual behaviors in these calves will greatly increase as they age.

Study Implications

Overall, the study indicates that association patterns follow sex and age specific strategies. These results suggest that age and sex are more predictive of behavioral contexts than COAs. When it came to behavioral contexts, affiliative behavior in particular appears to be an important component of the relationships between bottlenose dolphins. Affiliative behavior may allow an individual to acquire resources, maintain or advance their social position, or increase reproductive opportunities (reviewed in Sussman et al., 2005).

Studies using quantitative measures of individual behavior to evaluate social relationships have found multifaceted patterns of social behavior in several other species including giraffes (Bashaw et al., 2007), ravens (Fraser & Bugnyar, 2010, 2011), chimpanzees (Fraser, Schino, & Aureli, 2008; Fraser, Stahl, & Aureli, 2010), elephants (*Loxodonta africana*) (Wittemyer, Douglas-Hamilton, & Getz, 2005), Bechstein's bats (*Myotis bechsteinii*) (Kerth & Konig, 1999), and meerkats (Madden, Drewe, Pearce, & Clutton-Brock, 2009). Similar to those reports, this study found that relationships vary within and between ages and sex in their strength and type. For example, most male dyads exhibited high association patterns with other males, while one adult-adult dyad shared a strong association indicative of a long-term bond (Connor et al., 1992b); yet another adult male had his highest association with an adult female. Although the population sample was small and the study was short in duration, a large amount of data was collected suggesting that relationships of varying quality existed between the individuals in this study. Variation in social relationships within and between groups has been suggested to account for the pattern, distribution, and functions of many behaviors (Kutsukake, 2006). The patterns observed in the current study appear to be reflective of reproductive strategies and social skills needed in a long-lived species. Other species with similar life histories share some of these patterns, for example male chimpanzees also form male coalitions to guard receptive females (Watts, 1998), and increase aggression towards cycling females (Muller, Kahlenberg, Thompson, & Wrangham, 2007), both strategies that increase their reproductive success.

This study aimed to describe the social relationships in bottlenose dolphins by looking at all the interaction types and the associations individuals engage in. This study could be expanded upon in the future by adding analysis of acoustic signals, which might elucidate the context of some of these observed interactions. This study is an important step in understanding how age, sex, and COAs influence the different behavioral interactions occurring within a group of captive bottlenose dolphins. Such research furthers our understanding of how bottlenose dolphins express their social relationships, giving us insight into the functional significance of their social behavior. Future research should focus on assessing the effects of maturation and kinship with respect to how relationships evolve.

APPENDIX A

BEHAVIORAL DEFINITIONS

Code	Name	Description
Affiliative		
APP	Approach	One animal approaches another at an oblique angle
EXC	Exchange	One dolphin gives something to another, e.g. fish, seaweed
FLW	Follow	One animal follows another animal
NDG	Nudge	One dolphin pushes rostrum on another dolphin’s body part
RZZ	Reciprocal nuzzle	Dolphins rubbing rostrums against each other's bodies
PRB	Pectoral fin rub	One dolphin actively rubs another's body part with its pectoral fin
PET	Petting	Pectoral fin to pectoral fin rubbing where active movement between pectoral fins of two dolphins is observed
RUB	Rubbing	A rubbing event where a body part besides the pectoral fin is used against another dolphin
PSW	Pair swim	Two dolphins swimming together in same direction within a body length
Agonistic		
HHA	Head to head approach	One dolphin swiftly approaching another head on
APR	90 ° right	Swift perpendicular approach from the right
APL	90 ° left	Swift perpendicular approach from the left
BTE	Bite	Dolphin bites or rakes teeth on another dolphin
BSL	Body Slam	One dolphin slams its body into another
CHS	Chase	One or more dolphins swiftly following other dolphin(s)
CHG	Charge	Fast speed, direct approach to another dolphin

FLE	Flee	One dolphin flees from another who has given chase
FLI	Flinch	A 'cowering" response by one dolphin to another's aggressive behavior
FHT	Fluke hit	One dolphin hits another using its flukes
FST	Fluke swat	Attempted fluke hit with no contact
ITR	Interrupt	An interaction between at least 2 dolphins that is disturbed by another dolphin(s)
JCP	Jaw clap	Dolphin open and closes jaws rapidly
OPJ	Open jaw	Open jaw display by one animal to another
PUU	Push up	One dolphin pushes another up
PDD	Push down	One dolphin pushes another down
RAM	Ram	One dolphin hits another's body with its body at fast speed
RHT	Rostrum hit	One dolphin hits another dolphin with rostrum
Socio-sexual		
MNT	Mounting	Activity involving dorso-ventral, lateral-ventral or ventral-ventral mounts, where one individual attempts to make intromission with another individual in the genital area.
GOO	Goosing	One dolphin brings its beak into contact with the genital area of another dolphin.
PUU	Push-up	One dolphin pushes up the genital area of another dolphin, usually with its head or rostrum
SSP	Socio-sexual petting	One dolphin strokes or inserts its pectoral fin into the genital slit of another.

Note: Definitions and codes adapted from (Dudzinski, 1996; Holobinko & Waring, 2010; Mann, 2006; Samuels & Gifford, 1997)

APPENDIX B

COAS BY INDIVIDUAL DYADS

Dyads	*Sex*	*Age*	*COA*
Alita Anthony	Male-Female	Adult-Juvenile	.01
Alita Bailey	Female-Female	Adult-Juvenile	.13
Alita Bill	Male-Female	Adult-Adult	.03
Alita Carmella	Female-Female	Adult-Adult	.02
Alita Cedena	Female-Female	Adult-Adult	.18
Alita Dixon	Male-Female	Adult-Juvenile	.01
Alita Fiona	Female-Female	Adult-Adult	.08
Alita French	Male-Female	Adult-Juvenile	.05
Alita Gracie	Female-Female	Adult-Adult	.50
Alita Han	Male-Female	Adult-Adult	.03
Alita Hector	Male-Female	Adult-Adult	.04
Alita Ken	Male-Female	Adult-Juvenile	.01
Alita Luna	Female-Female	Adult-Calf	.46
Alita Margarita	Female-Female	Adult-Juvenile	.14
Alita Maury	Female-Female	Adult-Adult	.04
Alita Mickey	Male-Female	Adult-Calf	.00
Alita Mika	Female-Female	Adult-Adult	.15
Alita Mrs Beasley	Female-Female	Adult-Adult	.18
Alita Paya	Male-Female	Adult-Adult	.03
Alita Pigeon	Female-Female	Adult-Calf	.16
Alita Ritchie	Male-Female	Adult-Adult	.01
Alita Ronnie	Male-Female	Adult-Adult	.00
Alita Vin	Male-Female	Adult-Calf	.15
Anthony Bailey	Male-Female	Juvenile-Juvenile	.13
Anthony Dixon	Male-Male	Juvenile-Juvenile	.20
Anthony Fiona	Male-Female	Adult-Juvenile	.13
Anthony French	Male-Male	Juvenile-Juvenile	.29
Anthony Ken	Male-Male	Juvenile-Juvenile	.55
Anthony Luna	Male-Female	Juvenile-Calf	.05
Anthony Margarita	Male-Female	Juvenile-Juvenile	.11
Anthony Mickey	Male-Male	Juvenile-Calf	.12
Anthony Pigeon	Male-Female	Juvenile-Calf	.04
Anthony Vin	Male-Male	Juvenile-Calf	.04
Bailey Dixon	Male-Female	Juvenile-Juvenile	.10
Bailey Fiona	Female-Female	Adult-Juvenile	.31

Bailey French	Male-Female	Juvenile-Juvenile	.22
Bailey Ken	Male-Female	Juvenile-Juvenile	.14
Bailey Luna	Female-Female	Juvenile-Calf	.12
Bailey Margarita	Female-Female	Juvenile-Juvenile	.35
Bailey Mickey	Male-Female	Juvenile-Calf	.00
Bailey Pigeon	Female-Female	Juvenile-Calf	.24
Bailey Vin	Male-Female	Juvenile-Calf	.15
Bill Anthony	Male-Male	Adult-Juvenile	.32
Bill Bailey	Male-Female	Adult-Juvenile	.07
Bill Carmella	Male-Female	Adult-Adult	.05
Bill Cedena	Male-Female	Adult-Adult	.07
Bill Dixon	Male-Male	Adult-Juvenile	.20
Bill Fiona	Male-Female	Adult-Adult	.14
Bill French	Male-Male	Adult-Juvenile	.20
Bill Gracie	Male-Female	Adult-Adult	.01
Bill Ken	Male-Male	Adult-Juvenile	.31
Bill Luna	Male-Female	Adult-Calf	.01
Bill Margarita	Male-Female	Adult-Juvenile	.04
Bill Maury	Male-Female	Adult-Adult	.23
Bill Mickey	Male-Male	Adult-Calf	.09
Bill Mika	Male-Female	Adult-Adult	.05
Bill Mrs Beasley	Male-Female	Adult-Adult	.04
Bill Pigeon	Male-Female	Adult-Calf	.07
Bill Ronnie	Male-Male	Adult-Adult	.20
Bill Vin	Male-Male	Adult-Calf	.02
Carmella Anthony	Male-Female	Adult-Juvenile	.04
Carmella Bailey	Female-Female	Adult-Juvenile	.01
Carmella Cedena	Female-Female	Adult-Adult	.00
Carmella Dixon	Male-Female	Adult-Juvenile	.30
Carmella Fiona	Female-Female	Adult-Adult	.04
Carmella French	Male-Female	Adult-Juvenile	.01
Carmella Gracie	Female-Female	Adult-Adult	.07
Carmella Han	Male-Female	Adult-Adult	.05
Carmella Hector	Male-Female	Adult-Adult	.06
Carmella Ken	Male-Female	Adult-Juvenile	.03
Carmella Luna	Female-Female	Adult-Calf	.08
Carmella Margarita	Female-Female	Adult-Juvenile	.07
Carmella Maury	Female-Female	Adult-Adult	.03
Carmella Mickey	Male-Female	Adult-Calf	.03
Carmella Mika	Female-Female	Adult-Adult	.04

Carmella Mrs Beasley	Female-Female	Adult-Adult	.16
Carmella Paya	Male-Female	Adult-Adult	.00
Carmella Pigeon	Female-Female	Adult-Calf	.00
Carmella Ritchie	Male-Female	Adult-Adult	.05
Carmella Ronnie	Male-Female	Adult-Adult	.03
Carmella Vin	Male-Female	Adult-Calf	.16
Cedena Anthony	Male-Female	Adult-Juvenile	.02
Cedena Bailey	Female-Female	Adult-Juvenile	.15
Cedena Dixon	Male-Female	Adult-Juvenile	.06
Cedena Fiona	Female-Female	Adult-Adult	.15
Cedena French	Male-Female	Adult-Juvenile	.05
Cedena Gracie	Female-Female	Adult-Adult	.11
Cedena Han	Male-Female	Adult-Adult	.03
Cedena Hector	Male-Female	Adult-Adult	.03
Cedena Ken	Male-Female	Adult-Juvenile	.02
Cedena Luna	Female-Female	Adult-Calf	.14
Cedena Margarita	Female-Female	Adult-Juvenile	.16
Cedena Maury	Female-Female	Adult-Adult	.05
Cedena Mickey	Male-Female	Adult-Calf	.15
Cedena Mika	Female-Female	Adult-Adult	.23
Cedena Mrs Beasley	Female-Female	Adult-Adult	.20
Cedena Paya	Male-Female	Adult-Adult	.02
Cedena Pigeon	**Female-Female**	**Adult-Calf**	**.84**
Cedena Ritchie	Male-Female	Adult-Adult	.00
Cedena Ronnie	Male-Female	Adult-Adult	.04
Cedena Vin	Male-Female	Adult-Calf	.18
Dixon Fiona	Male-Female	Adult-Juvenile	.09
Dixon French	Male-Male	Juvenile-Juvenile	.23
Dixon Ken	Male-Male	Juvenile-Juvenile	.28
Dixon Luna	Male-Female	Juvenile-Calf	.02
Dixon Margarita	Male-Female	Juvenile-Juvenile	.06
Dixon Mickey	Male-Male	Juvenile-Calf	.06
Dixon Pigeon	Male-Female	Juvenile-Calf	.07
Dixon Vin	Male-Male	Juvenile-Calf	.12
Fiona French	Male-Female	Adult-Juvenile	.19
Fiona Ken	Male-Female	Adult-Juvenile	.15
Fiona Luna	Female-Female	Adult-Calf	.08
Fiona Margarita	Female-Female	Adult-Juvenile	.21
Fiona Mickey	Male-Female	Adult-Calf	.22

Fiona Pigeon	Female-Female	Adult-Calf	.14
Fiona Vin	Male-Female	Adult-Calf	.17
French Ken	Male-Male	Juvenile-Juvenile	.36
French Luna	Male-Female	Juvenile-Calf	.04
French Margarita	Male-Female	Juvenile-Juvenile	.06
French Mickey	Male-Male	Juvenile-Calf	.12
French Pigeon	Male-Female	Juvenile-Calf	.04
French Vin	Male-Male	Juvenile-Calf	.05
Gracie Anthony	Male-Female	Adult-Juvenile	.03
Gracie Bailey	Female-Female	Adult-Juvenile	.12
Gracie Dixon	Male-Female	Adult-Juvenile	.04
Gracie Fiona	Female-Female	Adult-Adult	.21
Gracie French	Male-Female	Adult-Juvenile	.04
Gracie Han	Male-Female	Adult-Adult	.04
Gracie Hector	Male-Female	Adult-Adult	.04
Gracie Ken	Male-Female	Adult-Juvenile	.03
Gracie Luna	**Female-Female**	**Adult-Calf**	**.90**
Gracie Margarita	Female-Female	Adult-Juvenile	.15
Gracie Maury	Female-Female	Adult-Adult	.11
Gracie Mickey	Male-Female	Adult-Calf	.12
Gracie Mika	Female-Female	Adult-Adult	.13
Gracie Mrs Beasley	Female-Female	Adult-Adult	.22
Gracie Paya	Male-Female	Adult-Adult	.03
Gracie Pigeon	Female-Female	Adult-Calf	.14
Gracie Ritchie	Male-Female	Adult-Adult	.04
Gracie Ronnie	Male-Female	Adult-Adult	.01
Gracie Vin	Male-Female	Adult-Calf	.22
Han Anthony	Male-Male	Adult-Juvenile	.25
Han Bailey	Male-Female	Adult-Juvenile	.13
Han Bill	Male-Male	Adult-Adult	.37
Han Dixon	Male-Male	Adult-Juvenile	.19
Han Fiona	Male-Female	Adult-Adult	.19
Han French	Male-Male	Adult-Juvenile	.29
Han Hector	Male-Male	Adult-Adult	.81*
Han Ken	Male-Male	Adult-Juvenile	.26
Han Luna	Male-Female	Adult-Calf	.03
Han Margarita	Male-Female	Adult-Juvenile	.05
Han Maury	Male-Female	Adult-Adult	.12
Han Mickey	Male-Male	Adult-Calf	.07
Han Mika	Male-Female	Adult-Adult	.06

Han Mrs Beasley	Male-Female	Adult-Adult	.05
Han Paya	Male-Male	Adult-Adult	.08
Han Pigeon	Male-Female	Adult-Calf	.03
Han Ritchie	Male-Male	Adult-Adult	.41
Han Ronnie	Male-Male	Adult-Adult	.27
Han Vin	Male-Male	Adult-Calf	.05
Hector Anthony	Male-Male	Adult-Juvenile	.29
Hector Bailey	Male-Female	Adult-Juvenile	.17
Hector Bill	Male-Male	Adult-Adult	.28
Hector Dixon	Male-Male	Adult-Juvenile	.26
Hector Fiona	Male-Female	Adult-Adult	.23
Hector French	Male-Male	Adult-Juvenile	.26
Hector Ken	Male-Male	Adult-Juvenile	.26
Hector Luna	Male-Female	Adult-Calf	.03
Hector Margarita	Male-Female	Adult-Juvenile	.06
Hector Maury	Male-Female	Adult-Adult	.11
Hector Mickey	Male-Male	Adult-Calf	.07
Hector Mika	Male-Female	Adult-Adult	.07
Hector Mrs Beasley	Male-Female	Adult-Adult	.03
Hector Paya	Male-Male	Adult-Adult	.08
Hector Pigeon	Male-Female	Adult-Calf	.04
Hector Ritchie	Male-Male	Adult-Adult	.40
Hector Ronnie	Male-Male	Adult-Adult	.22
Hector Vin	Male-Male	Adult-Calf	.03
Ken Luna	Male-Female	Juvenile-Calf	.02
Ken Margarita	Male-Female	Juvenile-Juvenile	.10
Ken Mickey	Male-Male	Juvenile-Calf	.14
Ken Pigeon	Male-Female	Juvenile-Calf	.04
Ken Vin	Male-Male	Juvenile-Calf	.04
Luna Mickey	Male-Female	Calf-Calf	.14
Luna Pigeon	Female-Female	Calf-Calf	.15
Luna Vin	Male-Female	Calf-Calf	.19
Margarita Luna	Female-Female	Juvenile-Calf	.14
Margarita Mickey	Male-Female	Juvenile-Calf	.24
Margarita Pigeon	Female-Female	Juvenile-Calf	.23
Margarita Vin	Male-Female	Juvenile-Calf	.27
Maury Anthony	Male-Female	Adult-Juvenile	.15
Maury Bailey	Female-Female	Adult-Juvenile	.11
Maury Dixon	Male-Female	Adult-Juvenile	.12
Maury Fiona	Female-Female	Adult-Adult	.11

Maury French	Male-Female	Adult-Juvenile	.19
Maury Ken	Male-Female	Adult-Juvenile	.21
Maury Luna	Female-Female	Adult-Calf	.07
Maury Margarita	Female-Female	Adult-Juvenile	.06
Maury Mickey	Male-Female	Adult-Calf	.28
Maury Paya	Male-Female	Adult-Adult	.37*
Maury Pigeon	Female-Female	Adult-Calf	.04
Maury Ritchie	Male-Female	Adult-Adult	.14
Maury Ronnie	Male-Female	Adult-Adult	.21
Maury Vin	Male-Female	Adult-Calf	.14
Mickey Vin	Male-Male	Calf-Calf	.16
Mika Anthony	Male-Female	Adult-Juvenile	.08
Mika Bailey	Female-Female	Adult-Juvenile	.28
Mika Dixon	Male-Female	Adult-Juvenile	.05
Mika Fiona	Female-Female	Adult-Adult	.18
Mika French	Male-Female	Adult-Juvenile	.10
Mika Ken	Male-Female	Adult-Juvenile	.09
Mika Luna	Female-Female	Adult-Calf	.14
Mika Margarita	Female-Female	Adult-Juvenile	.20
Mika Maury	Female-Female	Adult-Adult	.12
Mika Mickey	**Male-Female**	**Adult-Calf**	**.58**
Mika Paya	Male-Female	Adult-Adult	.03
Mika Pigeon	Female-Female	Adult-Calf	.22
Mika Ritchie	Male-Female	Adult-Adult	.06
Mika Ronnie	Male-Female	Adult-Adult	.08
Mika Vin	Male-Female	Adult-Calf	.18
Mrs Beasley Anthony	Male-Female	Adult-Juvenile	.05
Mrs Beasley Bailey	Female-Female	Adult-Juvenile	.11
Mrs Beasley Dixon	Male-Female	Adult-Juvenile	.12
Mrs Beasley Fiona	Female-Female	Adult-Adult	.12
Mrs Beasley French	Male-Female	Adult-Juvenile	.06
Mrs Beasley Ken	Male-Female	Adult-Juvenile	.04
Mrs Beasley Luna	Female-Female	Adult-Calf	.18
Mrs Beasley Margarita	Female-Female	Adult-Juvenile	.26
Mrs Beasley Maury	Female-Female	Adult-Adult	.15
Mrs Beasley Mickey	Male-Female	Adult-Calf	.13
Mrs Beasley Mika	Female-Female	Adult-Adult	.11
Mrs Beasley Paya	Male-Female	Adult-Adult	.06
Mrs Beasley Pigeon	Female-Female	Adult-Calf	.20

Mrs Beasley Ritchie	Male-Female	Adult-Adult	.01
Mrs Beasley Ronnie	Male-Female	Adult-Adult	.03
Mrs Beasley Vin	**Male-Female**	**Adult-Calf**	**.90**
Paya Anthony	Male-Male	Adult-Juvenile	.13
Paya Bailey	Male-Female	Adult-Juvenile	.09
Paya Bill	Male-Male	Adult-Adult	.18
Paya Dixon	Male-Male	Adult-Juvenile	.08
Paya Fiona	Male-Female	Adult-Adult	.03
Paya French	Male-Male	Adult-Juvenile	.19
Paya Ken	Male-Male	Adult-Juvenile	.13
Paya Luna	Male-Female	Adult-Calf	.03
Paya Margarita	Male-Female	Adult-Juvenile	.04
Paya Mickey	Male-Male	Adult-Calf	.02
Paya Pigeon	Male-Female	Adult-Calf	.01
Paya Ritchie	Male-Male	Adult-Adult	.08
Paya Ronnie	Male-Male	Adult-Adult	.09
Paya Vin	Male-Male	Adult-Calf	.04
Pigeon Mickey	Male-Female	Calf-Calf	.18
Pigeon Vin	Male-Female	Calf-Calf	.22
Ritchie Anthony	Male-Male	Adult-Juvenile	.33
Ritchie Bailey	Male-Female	Adult-Juvenile	.10
Ritchie Bill	Male-Male	Adult-Adult	.35
Ritchie Dixon	Male-Male	Adult-Juvenile	.24
Ritchie Fiona	Male-Female	Adult-Adult	.12
Ritchie French	Male-Male	Adult-Juvenile	.26
Ritchie Ken	Male-Male	Adult-Juvenile	.26
Ritchie Luna	Male-Female	Adult-Calf	.01
Ritchie Margarita	Male-Female	Adult-Juvenile	.03
Ritchie Mickey	Male-Male	Adult-Calf	.07
Ritchie Pigeon	Male-Female	Adult-Calf	.01
Ritchie Ronnie	Male-Male	Adult-Adult	.23
Ritchie Vin	Male-Male	Adult-Calf	.01
Ronnie Anthony	Male-Male	Adult-Juvenile	.25
Ronnie Bailey	Male-Female	Adult-Juvenile	.16
Ronnie Dixon	Male-Male	Adult-Juvenile	.17
Ronnie Fiona	Male-Female	Adult-Adult	.18
Ronnie French	Male-Male	Adult-Juvenile	.19
Ronnie Ken	Male-Male	Adult-Juvenile	.25
Ronnie Luna	Male-Female	Adult-Calf	.01
Ronnie Margarita	Male-Female	Adult-Juvenile	.05

Ronnie Mickey	Male-Male	Adult-Calf	.13
Ronnie Pigeon	Male-Female	Adult-Calf	.06
Ronnie Vin	Male-Male	Adult-Calf	.04

Note: Mother-calf pairs are represented in bold. Other COAs of note are starred.

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